THE DYNAMICS OF PASTURE USE BY WILDEBEESTE (AND CATTLE) IN THE AMBOSELI BASIN.

By

DAVID K. ANDERE

A thesis submitted in partial fulfilment for the Degree of Master of Science in the University of Nairobi.

1975

I, David K. Andere, hereby declare that this thesis is my original work and has not been presented for a degree at any other University.

David K. Andere

We, Dr, H. Croze and Professor F.A. Mutere, hereby declare that this thesis has been submitted for examination with our approval as University Supervisors.

Dr. H, Croze

Professor F.A. Mutere

Nairobi, 27 February, 1975

TABLE OF CONTENTS

LIST OF TABLES, FIGURES AND PLATES.

PLATES

SUMMARY

The study has two main components; population ecology and pasture use. These are fused together for probable implications of density-dependent regulation on wildebeeste and cattle populations in the study area.

As a basis to this study, the vegetation and ecology of pastures in the study area are discussed. Rainfall is considered as the main underlying factor in determining the available food resources and animal movements in both the dry and wet season ecosystems. Under such circumstances rainfall records over a 5 year period are compared and these records suggest that possibly 1973 was a drier year. The implications of these climatic variations are discussed in relation to pasture use and animal density in the basin.

The numbers of wildebeeste and cattle populations in the basin and methods used for estimation of numbers are discussed. Emphasis is however, mainly on wildebeeste and data on age determination, mortality, reproduction and life table are discussed.

Grazing sequence in the basin is discussed under the changing conditions of the environment and limited food resources. Competition of resources at the peak of dry season between cattle and wildebeeste is implied. Data on primary productivity; quality and leaf: stem and sheath ratio are discussed in relation to pasture use in the basin. Water provided by the swamps was considered as the main attraction leading to the concentration of both cattle and wildebeeste in the basin during the dry season.

Conclusions are discussed in the light of population regulation, rainfall and food supply. As a management strategy, more detailed work on habitat research is suggested.

ACKNOWLEDGEMENTS

This project would not have been possible without the financial support from the Ford Foundation and the Ministry of Tourism and Wildlife. Their support is hereby gratefully acknowledged.

I would also wish to express my thanks to the Chief Game Warden, Mr. J.K. Mutinda for having relieved me from normal Game Department research duties to undertake this study. My thanks are also due to Professor M. Hyder, Professor J.B. Sale and Professor F.A. Mutere for their encouragement. I am grateful to all of them.

Helpful discussions and criticisms given by Drs. R.M. Watson, P.J. Jarman, J.J.R. Grimsdell, D. Western, and Messrs. T.R.E. Ryan and P. Duncan were very much appreciated and I am grateful to all of them.

The assistance given by Dr. I.A. Chawdry, Messrs. J. Mwangi, H.M. Nyali, Waziri Ali (Pilot Game Department), Otieno P.G. of the National Agriculture Laboratories Kabete, who kindly analysed the grass samples, and many other people whom I have not mentioned, but helped in one way or another, many thanks to all of them.

My thanks to Professor R.J. Olembo for having allowed me to use a Botany Department Annex for writing up my thesis.

And lastly I would like to express my thanks to Dr. H. Croze for having supervised my work throughout the study period and finally to Mrs. M. Fernandes for having typed the thesis well.

CHAPTER I

INTRODUCTION

1.1 Ecological Research Model: A study on the dynamics and pasture use by wildebeeste, *Connochaetes taurinus* (Burchell) and cattle *Bos indicus* (Gray) in the Amboseli basin, was becoming increasingly vital in the light of ecological changes in the habitat, and the changes in land tenure within the entire Amboseli Game Reserve. The relationship between the basin, now a National Park, and the Game Reserve is illustrated by a map (Fig. 2).

The basin is a dry season concentration area for the water-dependent animal communities within the entire Amboseli ecosystem. In this thesis, the basin is defined as the dry season ecosystem and the dispersal areas outside the basin as the wet season ecosystem (Western 1973). Both ecosystems make up the entire Amboseli ecosystem. As shown in this thesis (Fig. 4) the year of study 1973, was comparatively dry, and hence a large proportion of the water-dependent animal communities spent most of that year in the basin. This study therefore reflects, on the dynamics of pasture use by wildebeeste and cattle only during the dry season.

An ecological research model (Fig. I) containing both endogenous and exogenous variables was therefore devised as a basis for this study. In this model, rainfall was considered as the most important single variable determining vegetation production and the availability of surface water and hence influencing seasonal pasture use, behaviour and the dynamics of grazing herbivores in the basin.

1.2 The Problem: Western and Van Praet (1973), have stated that the basin is in a state of vegetation change from hydrophytic dense woodland to halophytic plant

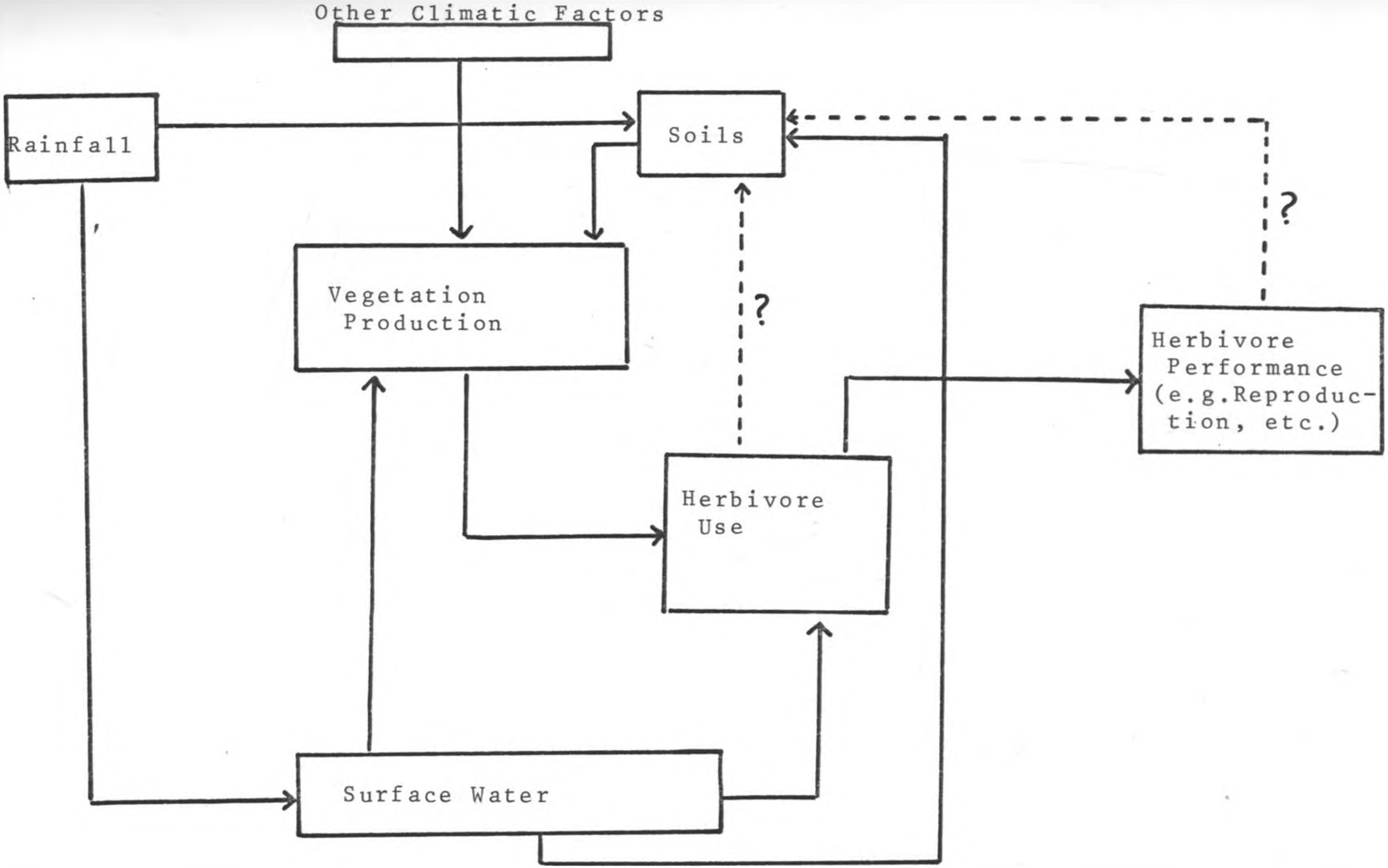


FIG.1 Ecological Research Model.

community. They measured the mortality of Acacia xathophloea as indicator of these changes. Over 90% of A. xathophloea have been measured to have died off in the last two decades, and are being replaced by Sueda monoica a bush resistant to salinity. Salinization of the habitat and changes in the water table have been given as factors inducing changes in the vegetation. These changes have therefore resulted in restricted grazing area available for herbivores. It was therefore important for the conservation of the habitat to look into pasture use by wildebeeste and cattle under the changing conditions of the available grazing area.

It is clear that East African grasslands have been recognised to have high biomass density : Bourliere (1962); Lamprey (1962); Talbot and Talbot (1963a); Swank and Petrides (1965); and Stewart (1966). Calculations of biomass density for the basin during the dry season show that it supports 15,000 kg/km^2 of biomass (Western, 1973), 64% of the biomass density was considered to be cattle and the rest wildlife. The situation is further precipitated by the high density of tourist vehicles restricted to within easy reach of wildlife resulting in the degredation of the habitat. Therefore the two main problems facing the basin were:

(i) The changing conditions of the habitat, resulting in restricted grazing area. A situation was therefore created whereby tourist circuit was also limited and thus the high density of tourist vehicles also greatly affected the habitat.

(ii) High biomass density/km^2 of both livestock (cattle, goats, Capra hircus, and sheep, Ovis aries)and wildlife grazing in this limited area. Human settlement around and within the basin formed an integral part of the ecosystem.

The fact that a National Park was proposed to be created in the basin for the conservation of the habitat with restricted grazing for wildlife only, the study was therefore set up with the following objectives:-

(i) To look into the habitat utilization under the changing conditions of the available food resources.

(ii) to predict the status of wildebeeste population when cattle, considered a dominant grazing herbivore in the dry season, are finally barred from utilizing the basin for grazing. This was subject to implementation of previous management recommendation that water be provided for livestock outside the basin (Western, 1973).

1.3 Literature review: Previous studies carried on wildebeeste include that of: Talbot and Talbot (1963) on the general ecology in Western Masailand; Estes (1966) on Behaviour and Reproduction in Ngorongoro Crater; Watson (1967) on Population ecology in the Serengeti National Park. Much of this work was on dynamics with less emphasis on habitat utilization.

However, similar studies related to this study, particularly on vegetation utilization by other wild animals was carried out by: Vesey-FitzGerald (1960, 1965, 1966, 1969 and 1974) on grazing succession among East African game animals, and habitat utilization by buffalo *Syncerus caffer* (Sparrman) in Rukwa Valley, Lake Manyara and Arusha National Parks; Lamprey (1963b) on the ecological separation of large mammal species in Tarangire Game Reserve; Gwynne and Bell (1968) and Bell (1969) on selection of grazing components by grazing ungulates in the Serengeti National Park. All these studies were carried out in Tanzania.

Studies have also been done especially on dynamics not only on wildebeeste, but also of some other species which have some relevance to this study. These include: Rogerson (1966 and 1968); Grimsdell (1969); Norton-Griffiths (1973); Sinclair (1973); Spinage (1973) and Western (1973).

STUDY AREA

2.1 Topography: The study area is the Amboseli basin covering about 400 km^2, and is demarcated by the boundaries of the proposed National Park (Ref. Fig. 2). These boundaries have however since changed due to conflicting interests in land use. The study area was part of the entire Maasai Amboseli Game Reserve which covers an area of about 3000 km^2.

The basin which was Pleistocene lake dried in the recent epoh was colonised by vegetation (Williams 1967). Today a small portion of the basin floods seasonally and is referred to as Lake Amboseli. Major features of the study area are: perennial springs along the edges of the dry lake bed; depressions mainly in the open woodlands to the west and south east of the study area; two main swamps, Enkongo Narok from which a canal was dug and drains into Lake Conch; and Longiye Swamp.

Significant features in the study area include laval rocks to the south across to south west and passing through extinct volcanic hills: Ilmeireshari, Endoinyo Ositet, Enameshera, (Observation Hill) and Kiturua.

Soils of the basin vary from north lateritic red soil contrasting sharply with grey-white, saline and alkaline soils in the centre of the basin. South, and

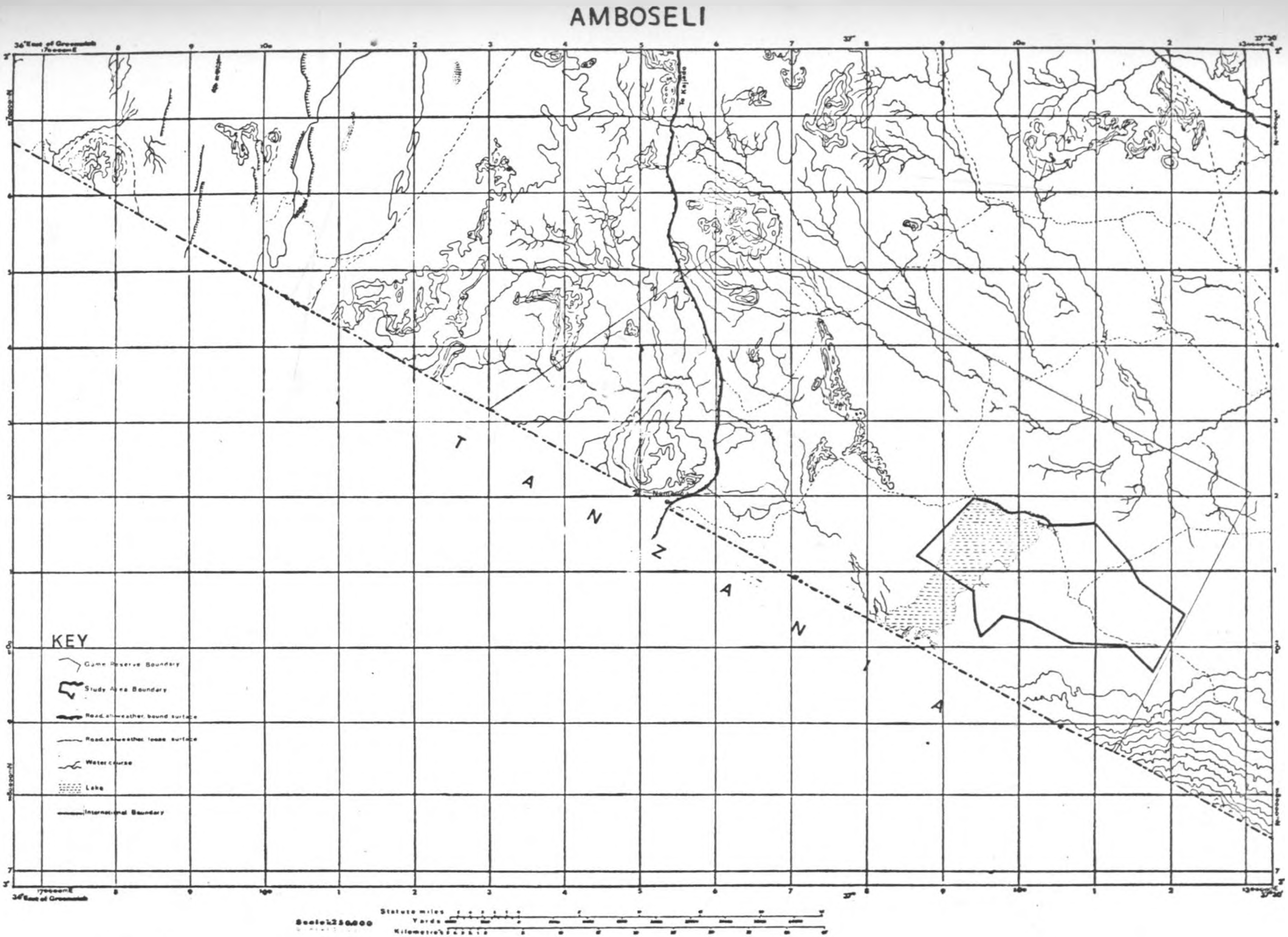


FIG.2 A Map of the study area including the entire Amboseli Game Reserve.

north east, black clays and olivine basalts bordering the basin. In the west the shores of Lake Amboseli are banked by aeolin deposits. Mt. Kilimanjaro to the south of the study area is the main water catchment of the basin.

2.2 Vegetation Types: Fig. 3 shows the distribution of vegetation types of the study area (this is based on 1967 photographs, Western, 1973). The area was sub-divided into seven vegetation types:

1. Acacia xathophloea woodlands.
2. Acacia tortilis woodland.
3. A. tortilis/A. mellifera and Balanites glabra woodlands.
4. Commiphora sp./A. mellifera woodland.
5. Bushlands.
6. Swamps.
7. Grasslands.

1. The A. xathophloea occupy a major portion of the basin and are associated with high water table. Basically this woodland is sub-divided into three categories:

(a) Thick A. xathophloea woodland. This is the only thick woodland present in the study area following the vegetation changes in the basin. The role of A. xathophloea as an indicator of vegetation changes has been discussed (Western and Van Praet, 1973) and is further demonstrated in this thesis, (Ref. Chapter III). Within this woodland is Phonix reclinata with Cynodon dactylon grassland as the main grass cover. A characteristic feature in this woodland is the distribution of smaller swamps and water-holes an addition dry season grazing amenity.

V E G E T A T I O N   T Y P E S

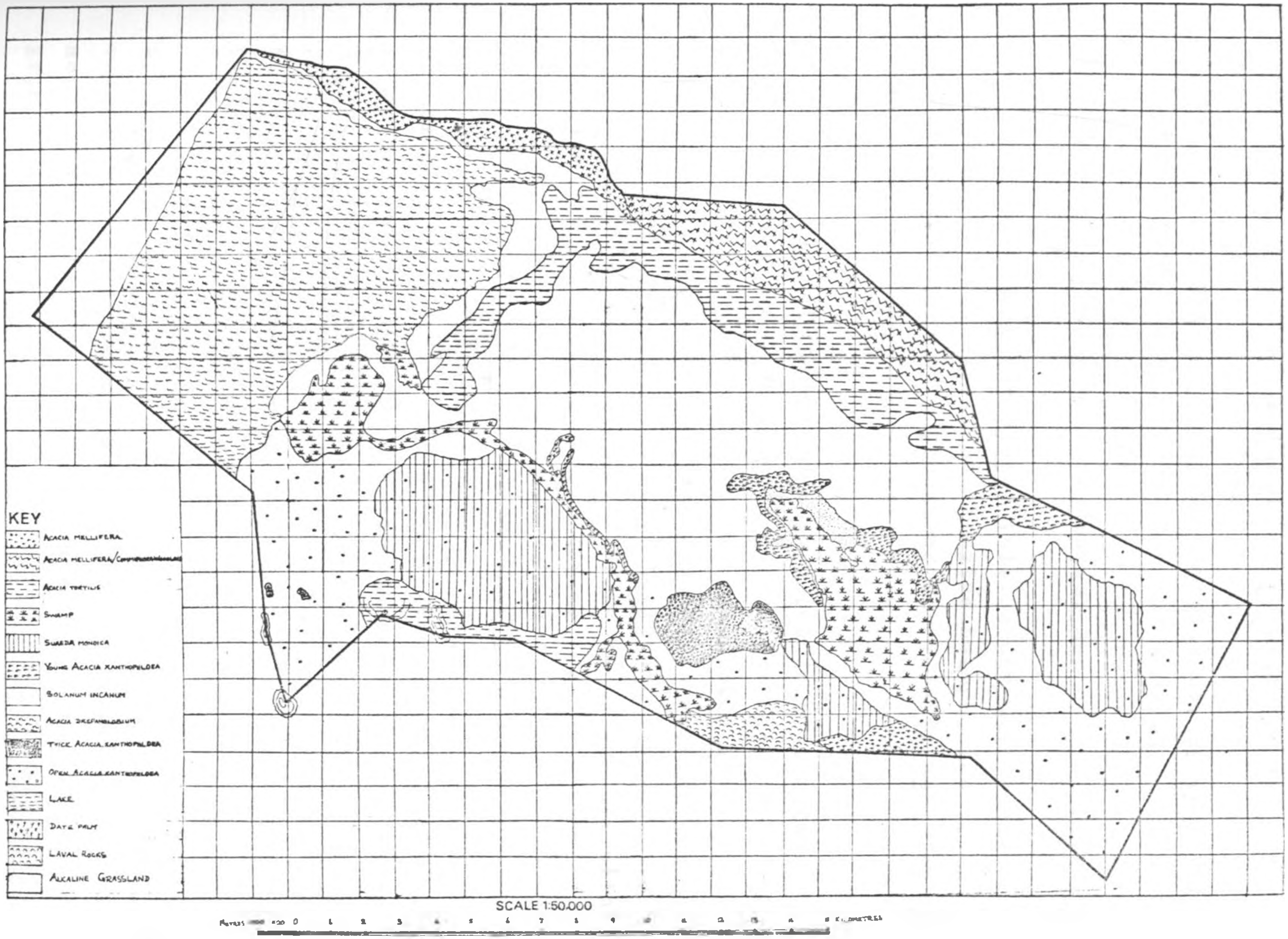


FIG.3 A Map of vegetation types of the study area.

(b) Open A. xathophloea: This has been formed mainly as a result of the declining density of the woodlands. The main grasslands in this woodland are: Sporobolus consmilis, Sporobolus marzinatus, Sporobolus spicatus, and C. dactylon. Within the woodland is a series of swamps and water holes. The main bushes are: Salvodora persica, Azima tetracantha, and Sueda monoica.

(c) Young A. xathophloea: This occupy mainly the fringes of Enkongo Narok, and Langiye Swamps, and around Ol Tukai area. The main grassland cover is C. dactylon with Solonum incanum as the main bush.

2. The A. tortilis woodland occupy the drier portion of the study area and virtually surrounds the basin in a semi-circle flow. The woodland is associated with Sanseviera sp., a succulent bush, a characteristic feature of arid areas. S. persica and A. tetracantha bushes are scattered within the woodland. The woodland was dry with no grassland undercover, except during the rainy season when S. marginatus springs up.

3. The A. tortilis/A. mellifera/Balanite sp. woodlands occupy more arid areas of the study area with very little grassland cover except to the north eastern side which had S. marginatus, Aristidia keniensis, Chloris gayana. Scattered to the eastern side of this vegetation belt was S. monoica and on the fringes of the bush, higher up on the black clays A. drepanolobium trees.

4. The Commophora Sp./A. mellifera woodlands - this vegetation belt surround the edges of the basin to the north and north eastern side of the study area. The ground cover was dominated by S. marginatus, A. keniensis, C. gayana. The dominant bushes were Sericocompsis spp. and Barleria sp.

(b) Open A. xathophloea: This has been formed mainly as a result of the declining density of the woodlands. The main grasslands in this woodland are: Sporobolus consmilis, Sporobolus marzinatus, Sporobolus spicatus, and C. dactylon. Within the woodland is a series of swamps and water holes. The main bushes are: Salvodora persica, Azima tetracantha, and Sueda monoica.

(c) Young A. xathophloea: This occupy mainly the fringes of Enkongo Narok, and Langiye Swamps, and around Ol Tukai area. The main grassland cover is C. dactylon with Solonum incanum as the main bush.

2. The A. tortilis woodland occupy the drier portion of the study area and virtually surrounds the basin in a semi-circle flow. The woodland is associated with Sanseviera sp., a succulent bush, a characteristic feature of arid areas. S. persica and A. tetracantha bushes are scattered within the woodland. The woodland was dry with no grassland undercover, except during the rainy season when S. marginatus springs up.

3. The A. tortilis/A. mellifera/Balanite sp. woodlands occupy more arid areas of the study area with very little grassland cover except to the north eastern side which had S. marginatus, Aristidia keniensis, Chloris gayana. Scattered to the eastern side of this vegetation belt was S. monoica and on the fringes of the bush, higher up on the black clays A. drepanolobium trees.

4. The Commophora Sp./A. mellifera woodlands - this vegetation belt surround the edges of the basin to the north and north eastern side of the study area. The ground cover was dominated by S. marginatus, A. keniensis, C. gayana. The dominant bushes were Sericocompsis spp. and Barleria sp.

(b) Open A. xathophloea: This has been formed mainly as a result of the declining density of the woodlands. The main grasslands in this woodland are: Sporobolus consmilis, Sporobolus marzinatus, Sporobolus spicatus, and C. dactylon. Within the woodland is a series of swamps and water holes. The main bushes are: Salvodora persica, Azima tetracantha, and Sueda monoica.

(c) Young A. xathophloea: This occupy mainly the fringes of Enkongo Narok, and Langiye Swamps, and around Ol Tukai area. The main grassland cover is C. dactylon with Solonum incanum as the main bush.

2. The A. tortilis woodland occupy the drier portion of the study area and virtually surrounds the basin in a semi-circle flow. The woodland is associated with Sanseviera sp., a succulent bush, a characteristic feature of arid areas. S. persica and A. tetracantha bushes are scattered within the woodland. The woodland was dry with no grassland undercover, except during the rainy season when S. marginatus springs up.

3. The A. tortilis/A. mellifera/Balanite sp. woodlands occupy more arid areas of the study area with very little grassland cover except to the north eastern side which had S. marginatus, Aristidia keniensis, Chloris gayana. Scattered to the eastern side of this vegetation belt was S. monoica and on the fringes of the bush, higher up on the black clays A. drepanolobium trees.

4. The Commophora Sp./A. mellifera woodlands - this vegetation belt surround the edges of the basin to the north and north eastern side of the study area. The ground cover was dominated by S. marginatus, A. keniensis, C. gayana. The dominant bushes were Sericocompsis spp. and Barleria sp.

This vegetation belt connects A. tortilis, A. mellifera and A. drepanolobium to the eastern side of the study.

5. Swamp Vegetation - the main swamps in the study area are the Enkongo Narok and Longiye, and within the A. xathophloea woodlands are a number of smaller swamps, about thirty in all. The main vegetation cover in the swamps were the sedges. an indication of standing water. The main sedges were: Cyperus immenses, C. papyrus and C. laerigatus. On the edges of these swamps, C. dactylon was the main grassland. The main bushes on the fringes of the swamps were S. incanum, Triplocephalum holstii, Sesbania goetzei, Abutilon sp., Lyeium europaem, Withania somnifera and Anchyrantha aspera.

6. The Bushlands - these have been discussed above, but one bush that deserves mention is S. monoica. This bush is particularly important in terms of the vegetation changes taking place in the basin. It is a bush resistent to salinity and associated with saline areas of the basin, (Ref. to Plate 2b) and has been observed to be growing in areas where there is high mortality of A. xathophloea. It does not, however, provide good forage for herbivores utilizing the basin, and usually no grass grows in between the bushes, except during the rains when animals have dispersed from the basin. It is discussed further under vegetation changes in the basin (Chapter III).

Amboseli basin has three main types of pastures: The alkaline, swamps and secondarily induced pastures.

2.3.1 The alkaline pastures:- These are mainly open grasslands: S. spicatus, S. homblei, S. marginatus, S. consmilis and O. jaegeri. These are associated with grey-white saline and alkaline soils, growing in association with C. obtusiflorus and C. laevigatus.

S. spicatus: This is a perennial stoloniferous grass that grows on alkaline flats where the water-table is high. It is a narrow, wiry shaped sward and vegetates and flows during the dry season. It is considered a grass of low palatability (Bogdan, 1958).

S. homblei: This is a tufted, perennial grass with flat hard leaves having sharp and spiny ends. It occurs on alkaline flats and dries up quickly although it responds quickly to rainfall depending on the available water for its growth.

S. marginatus: This is a caesipitose perennial grass which grows on the edges of alluvial fans and between woodlands. In the basin it is mainly found on alkaline flats. It has the characteristic feature of having its cushions spaced apart to facilitate the growth of other grasses like S. spicatus, S. homblei and sedges. The sward responds to light rainfall and hence produces fresh growth from perennial cushions. It is a palatable grass of high growing value (Bogdan, 1958).

S. consmilis: This is a beach grass and grows in zones which marks high water limits of the lake. Other than growing on the dry lake bed, the grass is patchily distributed in the basin. The patchy areas where this grass grows possibly indicate the previous boundaries of the lake. It is a coarse grass with long leaves and a thick stem. S. consmilis provides good forage only in the dry season.

O. jaegeri: This grows in shallow, warm and alkaline water around the fringes of the dry lake bed. It is also found in alkaline flats in association with S. spicatus.

O. jaegeri forms a short spiny sward and remains green and in flower all the year round.

C. laevigatus: This is a perennial rhizomatus sedge that grows on alkaline bogs where the soil is wet throughout the year. In the basin this particular pasture was found mainly on the edges of the dry lake bed. It is a dense sward with a continuous mat, evergreen and flowering throughout the year. An important ecological feature on the edges of the lake are number of water springs, and surrounding the springs is this sedge.

C. obtusiflorus: This grows in association with *S. spicatus*, *S. homblei* and *S. marginatus* on the alkaline flats. This sward responds quickly to rainfall but dries up quickly.

2.3.2 The Swamps: The swamp pasture acts as a reservoir pasture at the peak of the dry season. The pasture is ecologically important because it clearly demonstrates grazing succession among the large herbivores that utilize the basin during the dry season.

2.3.3 Secondarily Induced Pastures: These are pastures formed as a result of effect of fire and redistribution of soils or changes in lake levels, rivers and drainage areas. In the basin an example of this type of pastures is provided by *C. dactylon*, *C. plectostachyus*, *C. gayana* and *Cenchrus ciliariasis*.

C. dactylon in particular forms a very important pasture for grazing herbivores during the dry season. It grows on badly drained black soils with high water table. In the study it is associated with *A. xathophloea* woodland. It is a sward that remains green throughout the year and regenerates as a result of grazing pressure.

The leaf/culm and crude protein/fibre values and primary productivity are discussed later in this thesis (Ref. Chapter III).

2.4 <u>Environmental conditions</u>: As mentioned in this thesis (Ref. Section 1.1 and 1.2), this study was carried out in a dry season ecosystem, and is therefore important to define the climatic pattern of the study area. This is easily demonstrated by comparing the rainfall data available for the last six years (Ref. to Fig. 4) and temperatures for 1972 and 1973 (Ref. Table 1). It is therefore clear that 1973 and early part of 1974 were comparatively dry periods under which this study was conducted.

Environmental conditions, and especially rainfall had a lot of bearing on the dynamics and pasture use of wildebeeste and cattle in basin discussed in the proceeding chapters.

TABLE I - BASIN TEMPERATURES

	1972		1973	
MONTHS	°C. MAX.	°C. MIN.	°C. MAX.	°C. MIN.
1	28.2	13.7	30.4	17.3
2	28.3	15.1	33.0	17.4
3	29.8	14.8	26.0	18.3
4	30.1	14.2	23.6	11.1
5	28.5	15.6	28.8	10.2
6	27.7	12.6	19.8	11.2
7	26.4	11.4	19.8	11.2
8	27.2	12.0	27.9	12.5
9	-	-	23.3	11.3
10	-	-	30.0	13.1
11	-	-	27.0	12.7
12	-	-	31.0	19.0

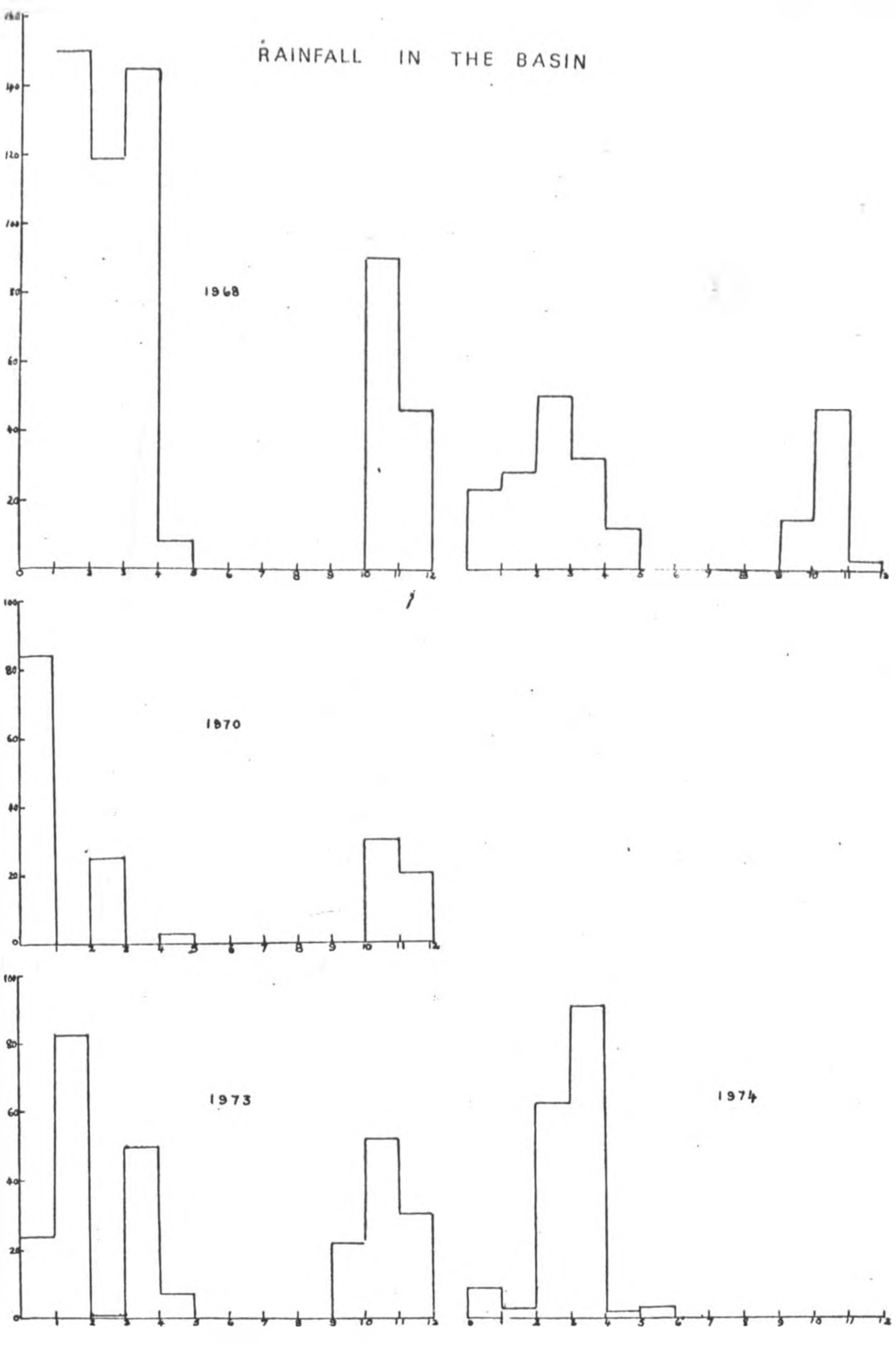
The mean monthly for 1973 MAX = 26.21 °C
MIN = 13.85

- = Data was not available

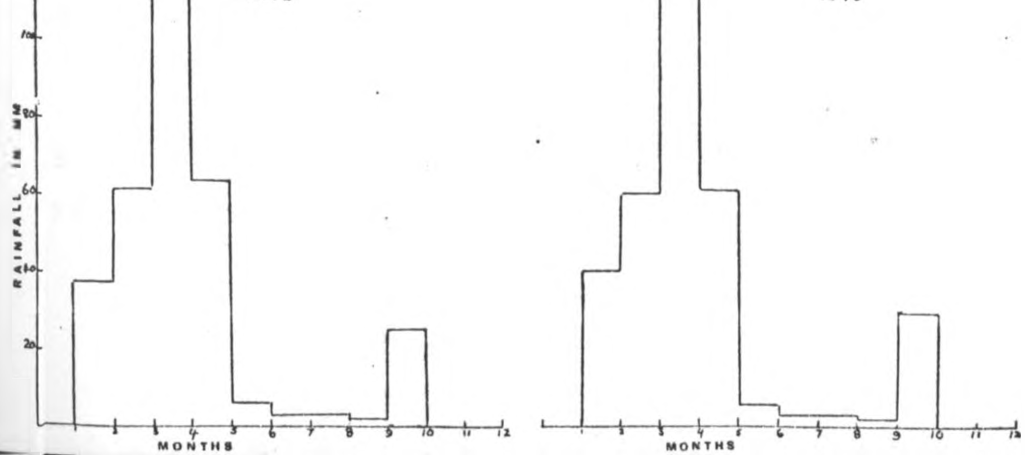
FIG.4 Rainfall records in the basin and at Mashuru - outside the basin.

(Data was not available for 1971 and 1972 in the basin and at Mashuru all other years).

RAINFALL IN THE BASIN



RAINFALL AT MASHURU



CHAPTER II

INTRODUCTION

Depending on time, space and the available food resources, wildebeeste and cattle were the most numerous herbivores in the basin (Pennycuick and Western, 1972). There were therefore important, among other herbivores, in the grazing sequence and management of the basin. But despite this significance, little is known of their population ecology.

Today, wildlife biology is arousing great interest among ecologists and conservationists, not only because of its aesthetic values, but also a possible threat to its survival as a result of conflicts of interest in the land use. The problem is therefore, how do we manage our wildlife to ensure its survival? Already there are some areas in East Africa occupied by wildlife under pressure for cattle ranching and human settlement. And although I do not belong to the school of thought of human isolation from wildlife, I think more information is required into the behaviour population and utilization of wildlife for the economic benefit of man. It is therefore, with these reasons in mind, I decided to concentrate on some aspects of the population ecology of Amboseli wildebeeste. This is reflected in this chapter.

METHODS AND MATERIALS

3.1 Census: Total and sample counts were the methods used in determining numbers in the basin and areas outside the basin only during the wet season.

Since the study area was relatively small, it was divided into convinient blocks with characteristic vegetation types and distinctive features like swamps, dry lake bed and extinct volcanic hills. The map of the study area was marked with 1 x 1 kilometre grids. It was also possible with constant observations to know where animals would be at particular times of the day. These factors made it easy to determine total counts with manimum difficulty.

3.1.1 <u>Total counts</u>: These were determined by systematic driving in the blocks using a L.W.B. Toyota Land Cruiser. From the top of the vehicle, and using a field binoculars 7 x 50, numbers of animals observed were counted and recorded in a field note book. The grid in which animals were observed was at the same time recorded. Counting was on monthly basis and at fixed times of the month.

3.1.2 <u>Sample counts</u>: Aerial sampling was done on 1/5/73 using a Cessna 180 with Waziri Ali, Pilot of the Game Department, P.J. Jarman and myself as main observers.

Flight lines were from north to south of the study area (this time of the year animals had dispersed within the dry and wet season ecosystems). Counting strips were fixed by means of streamers on the struts of the plane using a similar procedure used by Pennycuick and Western (1972).

Jolly's (1969) method (2) was used in estimating wildebeeste and cattle populations where the population estimate (Y) is given by:

$$\hat{Y} = \frac{\sum N\bar{y}}{Z} Z \quad \ldots\ldots\ldots\ldots (1)$$

where N = total number of units in the area.

$\bar{y}$ = average numbers of animals per unit over the units sampled.

$\hat{Z}$ = total area surveyed.

Z = total area under survey.

$\sum$ = summation over all strata.

and the standard error for the estimate SE(Y) given by

$$\sqrt{Var\ \hat{Y}_1} \quad \text{where } \hat{Y} = \frac{\sum N(M-n)}{N} Sy^2$$

$$\text{and } Sy^2 = \frac{1}{n-1} \left(\sum y^2 - \frac{(\sum y)^2}{n}\right) - 2\bar{d} \left(\frac{1}{n-1}\right)$$

$$\left(\sum zy - \frac{(\sum z)(\sum y)}{n}\right) + \bar{d}\left(\frac{1}{n-1}\right) \left(\sum z^2 - \frac{\sum z^2}{n}\right)$$

and where

z = area of each sampled unit

n = number of units sampled

y = number of animals in individual unit

N = total number of units in study area

$\bar{d} = \frac{N\bar{y}}{Z}$ as the density per unit area

Samples were assumed to have been selected at random, each unit having the same chance of selection irrespective of size.

3.1.3 Photographic count: Census in which aerial photography has been used in conjunction with direct total counts are numerous e.g. Watson (1969) Sinclair (1973) and Bell et. al., (1973). This method was used as a supplementary to the above methods, in estimating numbers of wildebeeste in the basin.

The method was used on 4/7/73. Using a Cessna 180 with Waziri Ali as a Pilot and I.A. Chawdry of the Game Department and myself as observers, wildebeeste counted and recorded in a tape recorder. Herds which were large and could not be easily counted, overlapping aerial photographs were taken. A Minolta SRT 101 with 58 mm lens was used with 35 mm Trix Kodac film at a speed of 1/500th per second. A total of twenty exposures were taken. These were developed and printed to convenient visibility size.

Counting was done by using a 3 x 10 microscope and with the aid of a needle each wildebeeste counted was pricked to avoid counting twice.

Assuming that this photographic count was a sample one, the ratio (R) of the recount to the initial count of the sample was found by (Jolly, 1969b):

$$R = \frac{\Sigma y}{\Sigma x} = \frac{\bar{y}}{x_1} = \frac{\text{mean count per print from initial count}}{\text{mean count per print from count}}$$

where y is the initial count and x_1 the recount from the same print. The counting bias (β) expressed as a percentage is $100 = \Sigma y - \Sigma x_1$.

3.2 Mortality Data: This was based on skulls collected in the study area and attention laid on freshly killed skulls. Collection was done by driving and searching in the study area. Sometimes information from rangers on fresh kills was helpful in locating skulls. Information recorded in the filed note book about collected skulls included: sex, date of collection, area of collection marked on a gridded sheet of paper which representated the study area. Usually the skulls were serially numbered, and in cases where a lower jaw was found accompanied, a complimentary number was given. Unaccompanied lower jaws were also collected, but given separate numbers. This was done throughout the study period.

3.3 <u>Age determination</u>: The determination of the age of Amboseli wildebeeste was largely based on the recovered skulls and lower jaws from the basin. Four main methods used were:

(i) Tooth eruption sequence.
(ii) Measurement of enamel height of maxillary M_1 tooth extracted from the upper jaw.
(iii) Counts of cementum lines in the cementum pad of M_1 sectioned as shown in Fig. 9.
(iv) Tooth wear pattern (Fig. 11).

3.3.1 <u>Eruption Sequence</u>: Tooth eruption sequence was bsed on the criteria developed by Watson (1967) and modified by Sinclair (unpublished). Samples of lower jaws were grouped and aged according to the progress of their tooth eruption. The relative eruption stages are described (Rep. to pg. 23).

3.3.2 <u>Enamel height</u>: The measurement of enamel height was done by measuring the heights of four cusps on the buccal side using a vernier calipers. The mean of the four recordings was then calculated and used in the determination of age by referring to a graph, Sinclair (unpublished) (Refer to Appendix Fig. 1a). A total of 123 male teeth and 69 female teeth were used in the determination of age.

3.3.3 <u>Cementum lines</u>: A number of these teeth (assumed to be a random number n=39) were taken from each age group. These were sectioned using a geological saw. These sections were cut from each tooth. They were then polished and examined under a dissecting microscope using a reflected light. Incremental cementum lines were counted where this was possible on each of the sections. In cases where determining and counting of

cementum lines was difficult, sections were stained with methylene blue and casbol fuchsin. The stained teeth were then cleaned with a light brush dipped in 70% alcohol. The mean number of incremental cementum lines from the counted sections was then determined and recorded.

3.3.4 Tooth wear: In determining age from tooth wear a reference collection of lower jaws recovered from the study area was used. The criteria of determining age was largely based on knowledge of the above methods. The criteria of determining the wear is described (Refer to page

3.3.5 Live population: Efforts were also made to determine the age of the living population. In this case Watson's (1967) method using the horn shape was used. Sketches of horns of a particular age group were drawn, and with the help of a binocular (7 x 50) ages of living population was determined. This was actually done of herds distributed randomly in the study area. I must admit it was difficult to differentiate particular ages in older animals, especially those beyond 5 years.

3.3.6 Reproduction: Although this project was not specifically aimed at studying reproduction of Amboseli wildebeeste, observations were made on some of the aspects of reproductive behaviour.

cementum lines was difficult, sections were stained with methylene blue and casbol fuchsin. The stained teeth were then cleaned with a light brush dipped in 70% alcohol. The mean number of incremental cementum lines from the counted sections was then determined and recorded.

3.3.4 Tooth wear: In determining age from tooth wear a reference collection of lower jaws recovered from the study area was used. The criteria of determining age was largely based on knowledge of the above methods. The criteria of determining the wear is described (Refer to page

3.3.5 Live population: Efforts were also made to determine the age of the living population. In this case Watson's (1967) method using the horn shape was used. Sketches of horns of a particular age group were drawn, and with the help of a binocular (7 x 50) ages of living population was determined. This was actually done of herds distributed randomly in the study area. I must admit it was difficult to differentiate particular ages in older animals, especially those beyond 5 years.

3.3.6 Reproduction: Although this project was not specifically aimed at studying reproduction of Amboseli wildebeeste, observations were made on some of the aspects of reproductive behaviour.

cementum lines was difficult, sections were stained with methylene blue and casbol fuchsin. The stained teeth were then cleaned with a light brush dipped in 70% alcohol. The mean number of incremental cementum lines from the counted sections was then determined and recorded.

3.3.4 Tooth wear: In determining age from tooth wear a reference collection of lower jaws recovered from the study area was used. The criteria of determining age was largely based on knowledge of the above methods. The criteria of determining the wear is described (Refer to page

3.3.5 Live population: Efforts were also made to determine the age of the living population. In this case Watson's (1967) method using the horn shape was used. Sketches of horns of a particular age group were drawn, and with the help of a binocular (7 x 50) ages of living population was determined. This was actually done of herds distributed randomly in the study area. I must admit it was difficult to differentiate particular ages in older animals, especially those beyond 5 years.

3.3.6 Reproduction: Although this project was not specifically aimed at studying reproduction of Amboseli wildebeeste, observations were made on some of the aspects of reproductive behaviour.

RESULTS

4.1 Total counts: The seasonal fluctuations in numbers of wildebeeste and cattle is shown in Table 2. The graph (Fig. 5) illustrates the fluctuation of wildebeeste numbers only. I wish to mention here that results obtained in cattle counts were only estimates recorded to the nearest hundred. Those of wildebeeste were complete total counts.

4.2 Photographic count: It was found that visual estimates of herd size were nearly always underestimates of the photographic count (Ref. Fig. 6). Eye estimates of herds (ranging from 7 - 146) were underestimated by a mean factor of 22.1% (based on 18 herds within the basin area). A total of 1770 wildebeeste were counted from photographs.

During the course of the photographic counts, data of numbers recorded in tape recorder analysed gave a total number of 1338 wildebeeste counted. Thus for the month of July using both photographic and total count methods, the estimate of wildebeeste population in the basin was 3108 (combined figure).

Assuming that this figure was the accurate wildebeeste population from aerial total counts for the month of July, 1973, the bias in counting on the ground for July (Table 2) was by 24.4%.

4.3 Sample count: A sample count for wildebeeste and cattle carried out in May 1973 covered an area of about 1800 km^2. The area covered most of the dry and wet season ecosystems because at this time of the year animals had dispersed from the basin. Results of the sample count are shown in Table 3.

TABLE 2 - NUMBERS

1973	Wildebeeste	Cattle
January	283	-
February	2313	5000
March	3333	6000
April	3620	7000
May	600	3000
June	1498	9500
July	2350	10700
August	3717	12800
September	3831	15300
October	4146	20200
November	1822	9000
December	1751	5000
1974		
January	3601	16000
February	3675	20000
March	1803	8000

TABLE 2 - NUMBERS

1973	Wildebeeste	Cattle
January	283	-
February	2313	5000
March	3333	6000
April	3620	7000
May	600	3000
June	1498	9500
July	2350	10700
August	3717	12800
September	3831	15300
October	4146	20200
November	1822	9000
December	1751	5000
1974		
January	3601	16000
February	3675	20000
March	1803	8000

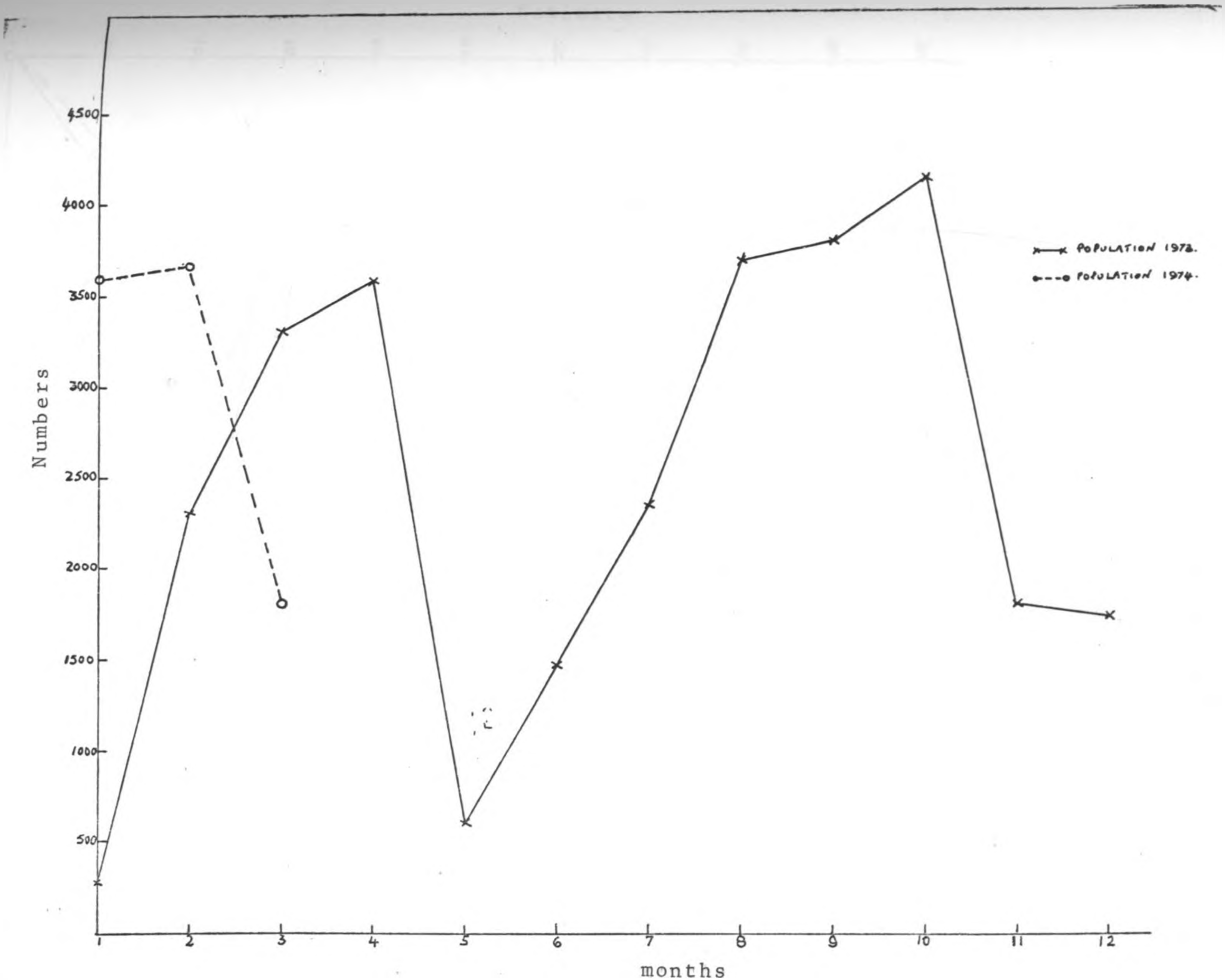


FIG.5 Seasonal changes in numbers of wildebeeste in the basin.

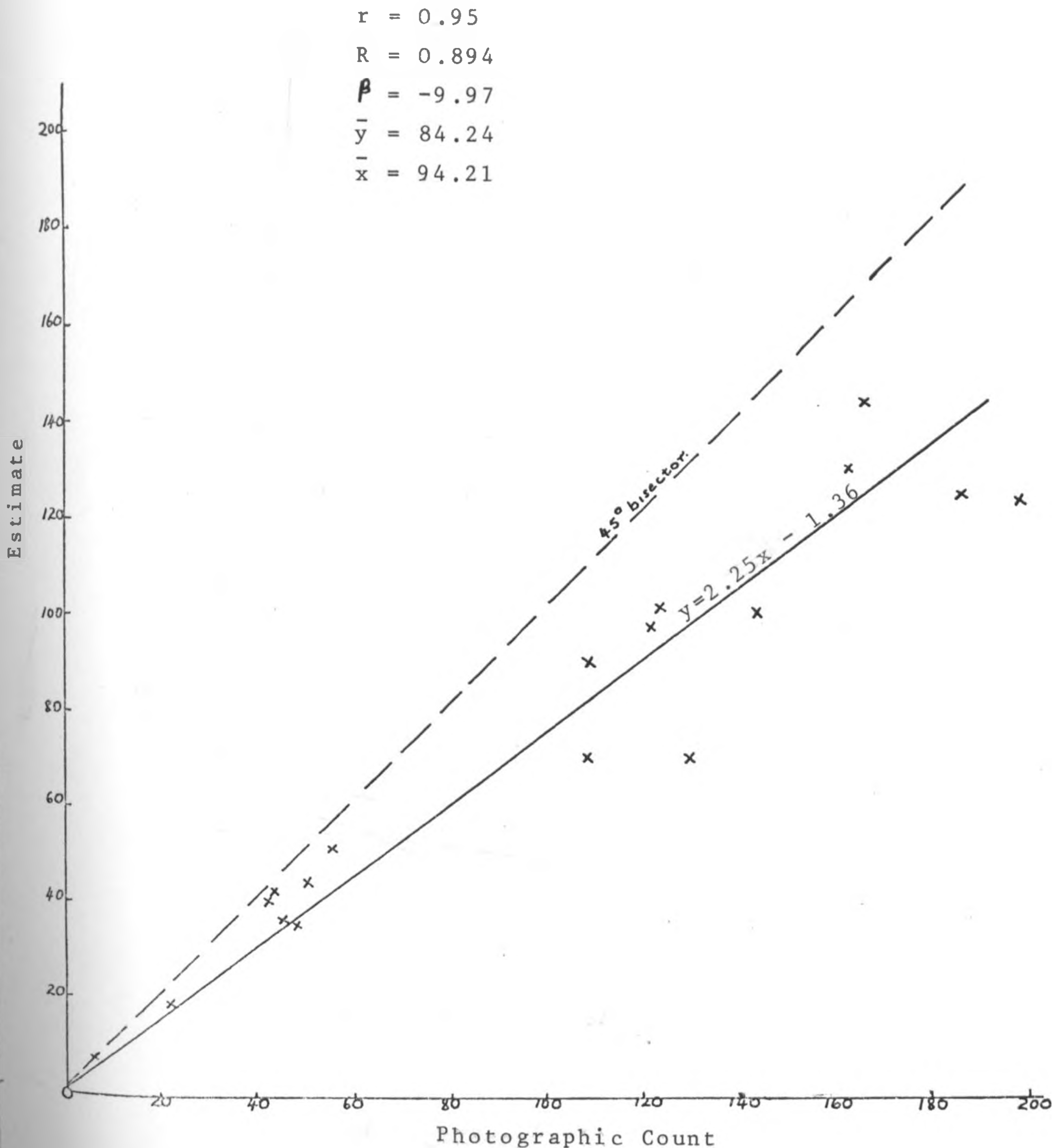


FIG.6 Photographic count of wildebeeste in the basin.

TABLE 3 – <u>Sample count of May 1973</u>

	Wildebeeste	Cattle
Population total Y	6493	47999
Population Variance Var (Y)	1142997	40333074
Standard error SE (Y)	1069.1106	6350.8325
95% Confidence limits of (Y)	± 2095	± 12447
95% Confidence limits as % of Y	± 32%	± 26%

Sampling fraction = 7%

Height of sampling above the ground = 300 ft.

4.4 Mortality data: A total of 192 Wildebeeste skulls, freshly dead were collected within the basin (Ref. to Map in Appendix). Of these 2.6% were considered to have died of starvation. The criteria used in identifying a dead wildebeeste considered died of starvation were: the skull was still attached to the main body at the time of recovery; there was no clear cut scratch indicating that the wildebeeste might have been killed by either predation or spearing. Usually a wildebeeste killed by a lion had a twisted neck when dead. The other factor considered along with these features was the state of body. May be 2.6% could as well have died of disease. These were mostly females. 1.6% had died of spearing. These were mostly yearlings. A spear mark or something sharp used to kill the animal was easily identified. And 95.8% were considered to have died either of disease but mostly predation. (Reports from rangers and personal observation).

Further analysis indicated that of the skulls collected, 64.6% were males, 30.7% were females and 5.7% yearlings.

There were, however, cases where unaccompanied lower jaws were collected which were chiefly used in assessing the wear pattern. A total of 75 unaccompanied jaws were collected.

Some degree of bias was noticed in the kill recovery. 75% of these were recovered during the dry season months, while 25% in the wet season months. A large number of kills in the dry season was obviously related to the increase of wildebeeste numbers, with a proportionate increase of predators, Kruuk and Turner (1967), (an influx of tourist vehicles concentrated particularly on lion Pathera leo massaica (Neumann) and sighting reports from game rangers was used as a criteria in the judgement of lion population in the basin. At least an average of 60 lions were reported during the dry season alone).

4.5 Age determination: Results of the various methods used (Sect. 2.3 this Chapter) are shown below.

4.5.1 Eruption sequence: The dental formula for wildebeeste has been recorded by Talbot and Talbot (1963) and Watson (1967):

Deciduous dentition $2(I\frac{0}{3}\ C\frac{0}{1}\ Pm\frac{3}{3}) = 20$

Permanent dentition $2(I\frac{0}{3}\ C\frac{0}{1}\ Pm\frac{3}{3}) = 30$

The relative eruption sequence is given (Table 4). It was assumed that since calving season was a fixed time, the eruption sequence and wear would be relatively similar. This criteria was used in assessing the age of wildebeeste using the lower jaws in conjunction with previous work by Watson (1967).

4.5.2 Age distribution: The frequency of age distribution of dead skulls is shown (Fig. 7 and 7a) representing female and male skulls. In making the histograms for age distribution, it was assumed that all age classes were dying at the same rate (Deevey, 1947; Slobodkin, 1961). This assumption is reflected in the construction of a life table.

4.5.3 Age distribution of live population: As mentioned earlier (Refer to methods and materials - Sect. 2.3.5) it was only possible to age wildebeeste population up to the age 5 years. This is reflected in histograms (Fig. 8 and 8a).

TABLE 4 ERUPTION SEQUENCE

AGE	I 1	I 2	I 3	I 4	Pm 1	Pm 2	Pm 3	M 1	M 2	M 3	SAMPLE SIZE
6 months	D	D	D	D	D	D	D	(P)	-	-	2
12 months	D	D	D	D	D	D	D	P	(P)	-	6
18 months	P	(P)	D	D	D	D	D	P	P	-	4
24 months	P	P	D	D	D(P)	D(P)	P	P	P	(P)	5
30 months	P	P	(P)	D̸(P)	D/(P)	D/(P)	P	P	P	(P)	4
36 months	P	P	P	D/(P)	P	P	D/(P)	P	P	P	7
42 months	P	P	P	(P)	P	P	D/(P)	P	P	P	10
48 months	P	P	P	P	P	P	P	P	P	P	11

Notation

D = Deciduous tooth
P = Permanent tooth
( ) = Tooth in the process of eruption (both crisps of molars visible above the jaws)
D̸ = Tooth just emerging
/ = Either tooth present

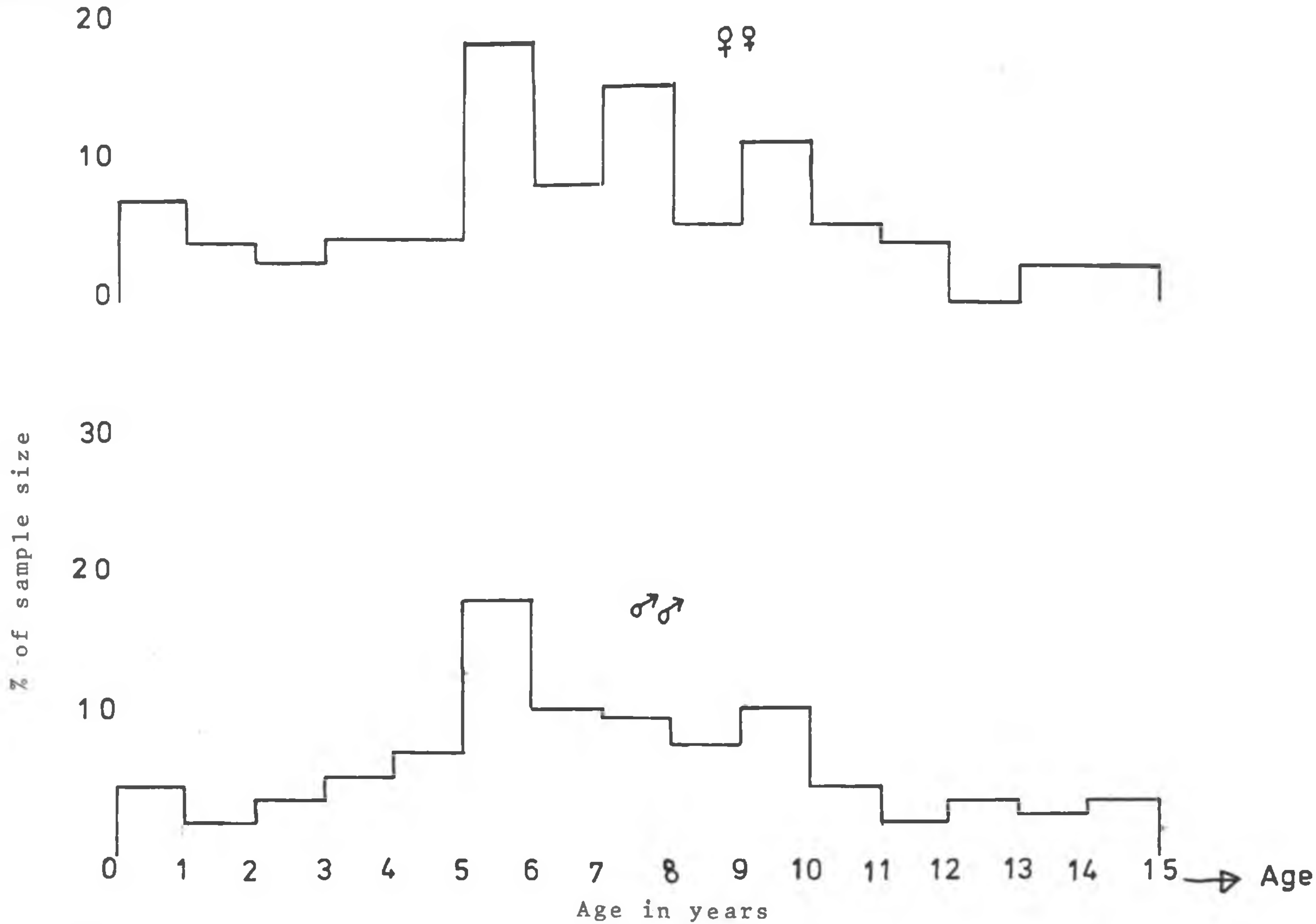


FIG.7 Frequency of age distribution from dead skulls for both male and female

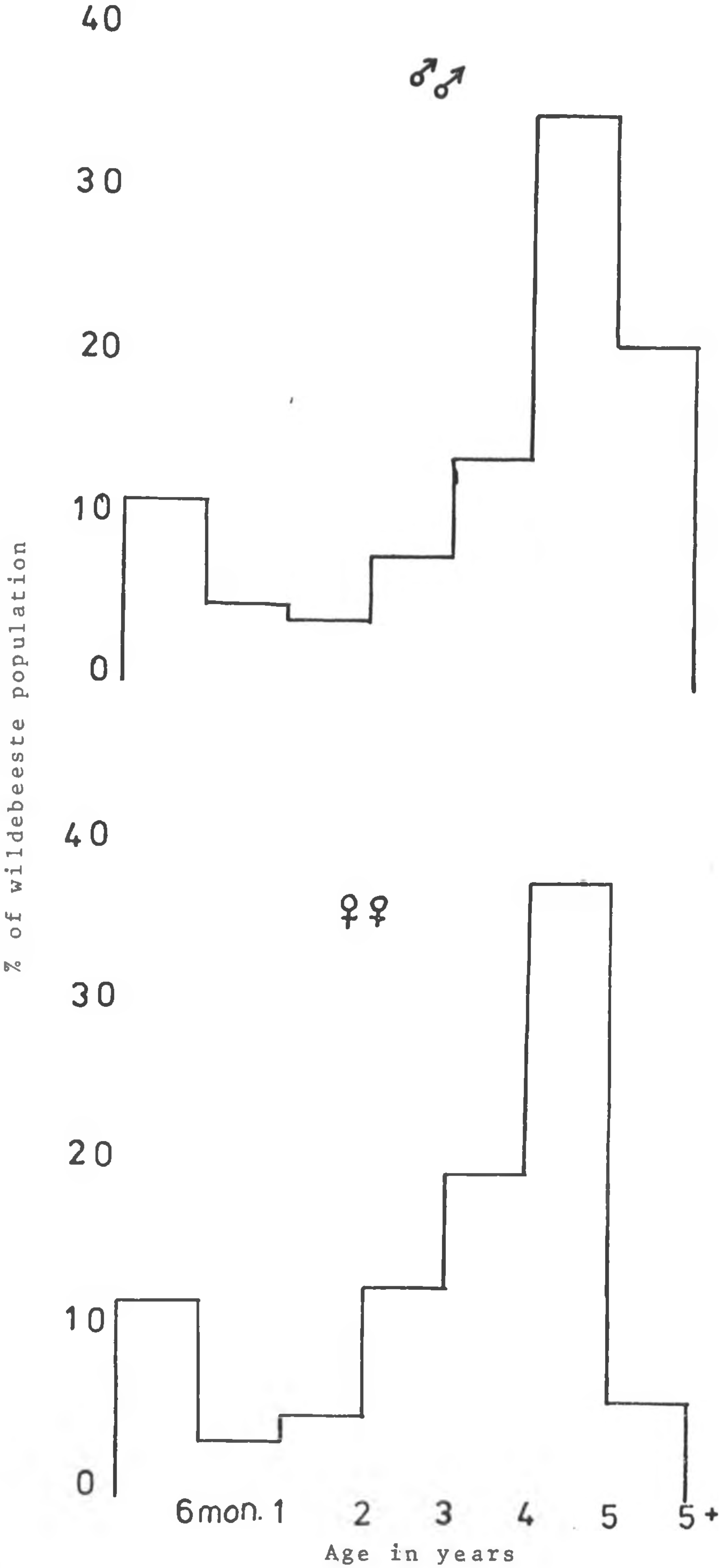


FIG.8 Age distribution of live population using Watson's method.

4.5.4 Cementum lines: The value of use of cementum lines for age determination was realised with respect to marine mammals (Laws, 1952) and to moose *Alces alces* using incisor teeth (Sergeant and Pimlott, (1959). Since then a number of other workers, e.g. Watson (1967), Spinage (1967), Grimsdell (1969) and Sinclair (1970)) have adapted this method for age determination on East African herbivores.

In using this method, I decided to make sections of M_1 as shown (Fig. 9) rather a less sophisticated method than making slides because it was quick and cheap. In fact with care, although strenous and laborious results may just be as good as those from slides (Grimsdell, 1969). The presence of annual layers in the cementum pad of M_1 has also been reasonably accurate method of determining age (Mitchell, 1963 and 1967 on red deer *Cervus elaphus*).

When the mean crown height was plotted with age, it was clear that crown height decreased with age (Fig. 10), this would be expected, but the rate of wear was not linear. In correlating cementum lines, treated as independent variable, with enamel height, as the dependent variable, a negative exponential curve of the form $Y = Ae^{-ac}$ was derived (Fig. 11) (n = 39) where

A = a constant (my own notation)
c = cementum lines

The values of A, e and c are shown in (Fig. 11). The correlation coefficient (r) = -0.95 ($P < .001$).

4.5.5 Tooth wear: In establishing age from tooth wear, a reference collection of lower jaws was made for the Amboseli wildebeeste. A total of 120 lower jaws were collected, and ten wear classes were established (Fig. 12).

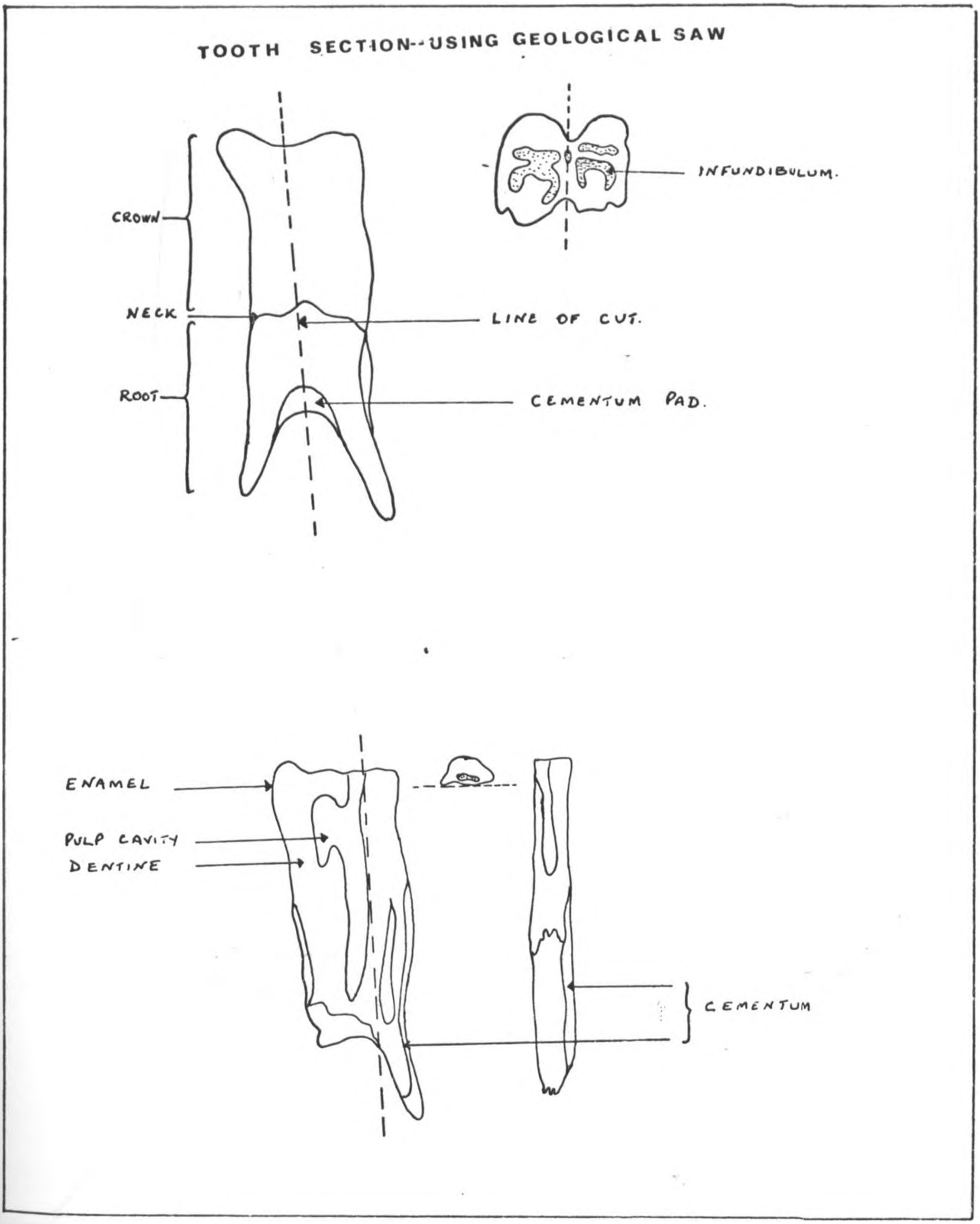


FIG.9 Tooth section of M_1 - used to determine cementum lines in the cementum pad.

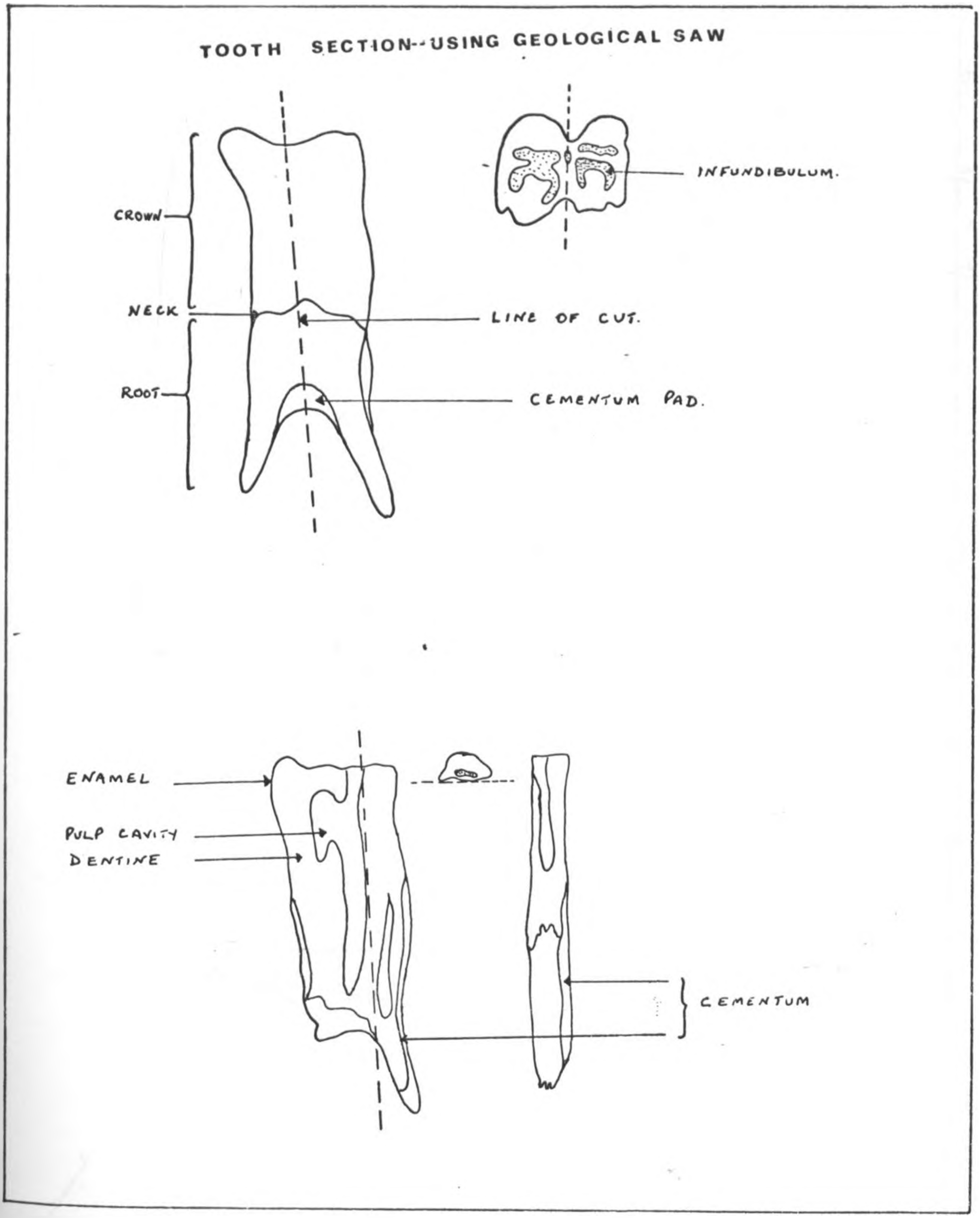


FIG.9 Tooth section of M_1 - used to determine cementum lines in the cementum pad.

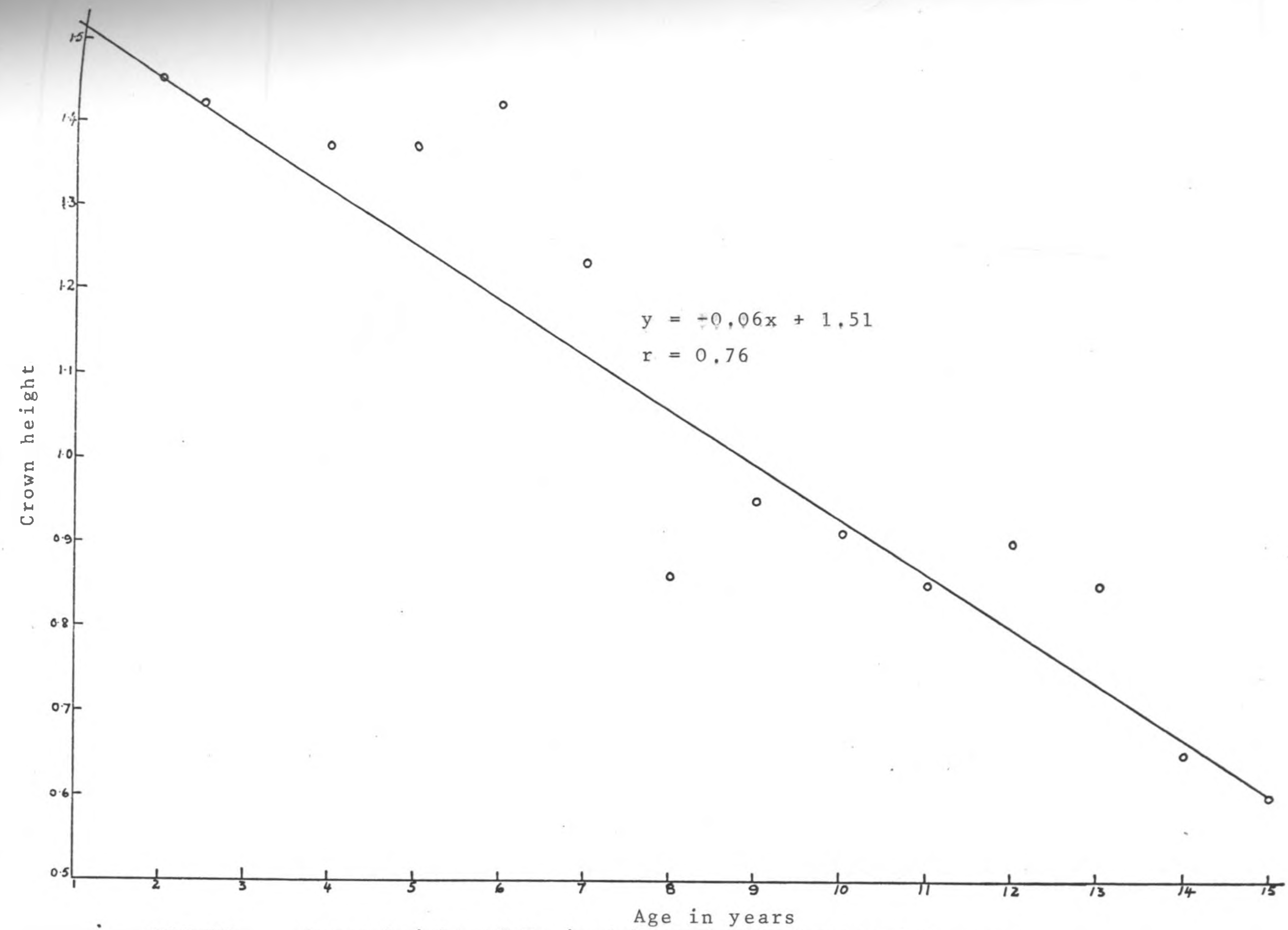


FIG.10 Crown height of M_1 in Amboseli wildebeeste V.S. age.

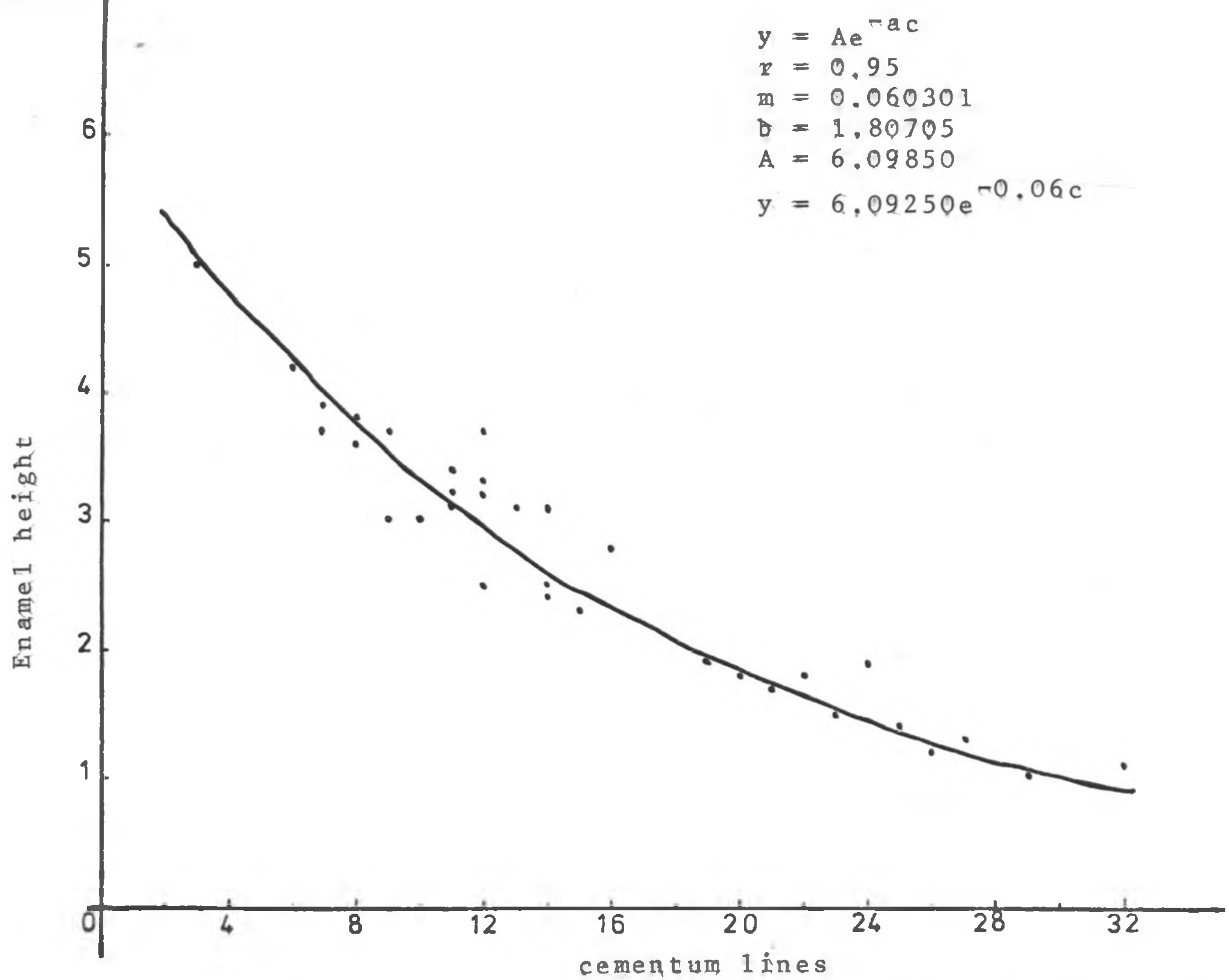


FIG.11 Exponential curve for age determination of Amboseli wildebeeste

The criteria used to establish each class and approximate age are described below with reference to the figure:

CLASS A

Deciduous pre-molar still present. M_3 emerging from the jaw and infundibular still very prominent. Approximate age group 1-2 years old. 2.5% of jaws collected were in this class.

CLASS B

Permanent pre-molars cutting and M_3 cutting on all lobes. Approximate age group 2-3 years old. 3.3% of the jaws collected were in this class.

CLASS C

M_3 cutting and anterior infundibulum complete. Approximate age group 3-4 years old. 3.3% of the jaws collected were in this class.

CLASS D

M_3 completely cut. Both infundibula complete and no infundibula shows signs of wear. This class contributed 63.3% of the total jaws collected. The approximate age group was 5-8 years old.

CLASS E

Pm_3 starts to disintegrate and there is a relative wear of infundibula on all teeth. Approximate age group 8-10 years old. 10.0% of the jaws collected contributed to this class.

CLASS F

Anterior infundibulum on M_1 gone and a relative wear of infundibula on M_2 and M_3 is distinctly shown.

WEAR CLASSES

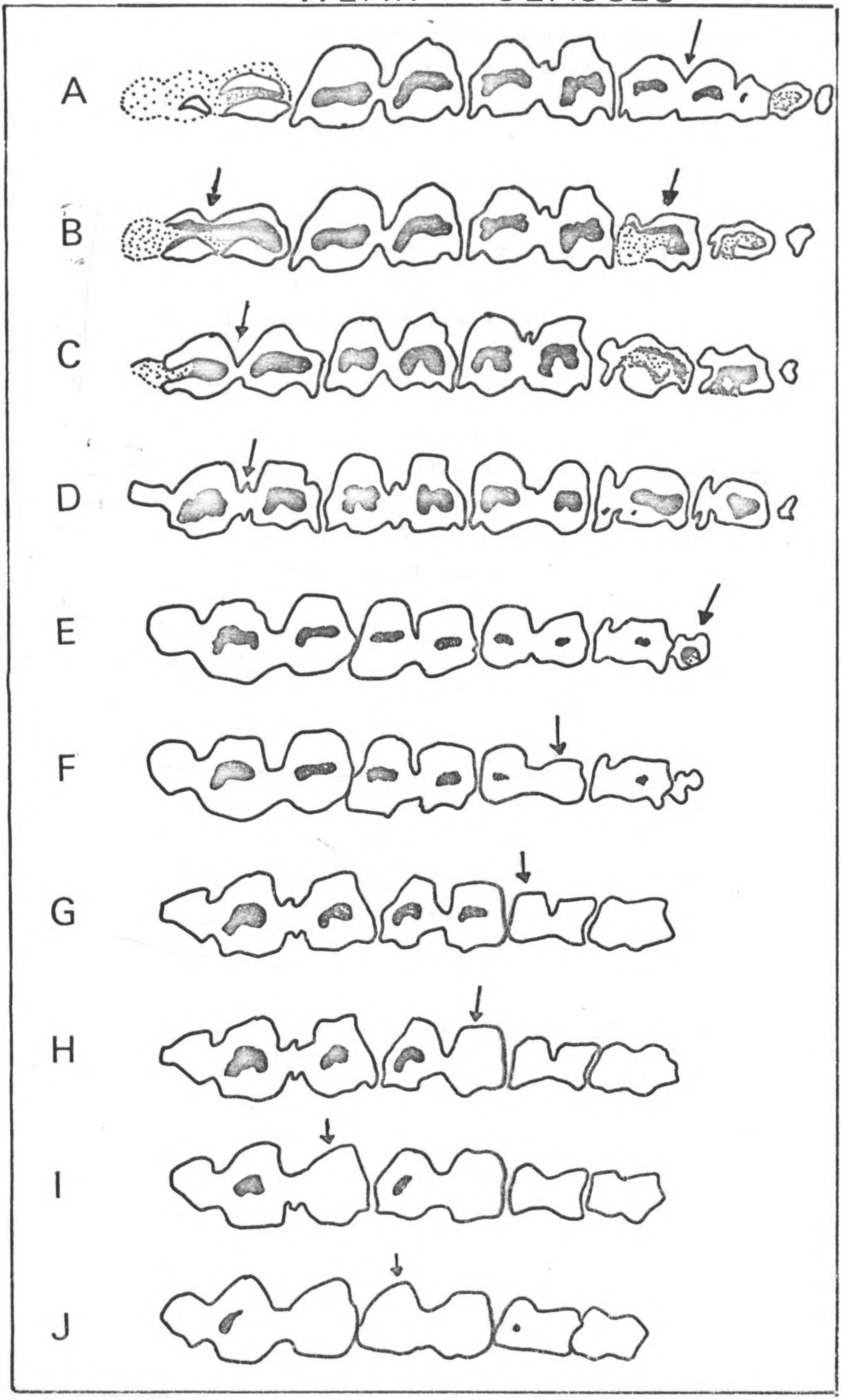


FIG.12 Wear classes for Amboseli wildebeeste

9.1% of the jaws collected contributed to this class. Approximate age group was 10-12 years old.

CLASS G

Both infundibula on M_1 gone. There is a differential wear pattern on M_1, M_2 and M_3 teeth. M_1 wear earlier than M_2 and M_3. 2.5% of the lower jaws collected contributed to this class. The approximate age group 12-14 years old.

CLASS H, I and J

These classes show very similar characteristics. There is a progressive disappearance of infundibula on M_2 until only posterior infundibulum on M_3 is left. Class H contributed 3.3%; Class I 1.6%; and Class J 0.8%. The approximate age group of these Classes was 14-16 years old.

The advantage of the tooth wear method for age determination is that it can be used for visual age estimation without resorting to sectioning of teeth. However this only can be used for Amboseli wildebeeste. The method of visual age estimation has been used by other workers, e.g. Severinghans (1949) on white tailed deer Odocoileus virginianus and Lowe (1967) on red deer, although they tested their findings with known age specimens.

LIFE TABLE

Most studies in population ecology include an attempt to determine age specific mortality, usually necessary for calculating reproductive values for each age class; the ages susceptible to natural selection, the population rate of increase, mean life expectancy at birth, mean generation length, and the percentage of the population that dies each year. The importance of this statistics in wildlife management need not be over-emphasized. This data is contained in a life table, Deevey (1947) and Caughley (1966).

In constructing a life table for the Amboseli wildebeeste, a number of postulates have been considered (Caughley, 1966) and one such postulate used in this case is the recording of ages at death (dx) by determining the age of carcasses, in this case skulls, from a population that is assumed stationary in age distribution. It is also assumed that small fluctuations in density will not greatly affect the results. The age distribution used in constructing the life table is shown (Ref. Fig. 7 and 7a) except that a life table of combined sexes is constructed because of the small samples of aged skulls. In this case the results are recorded for future reference since it is not intended to go into details of the 'age specific fecundity' (Mx) and the net reproduction rate (Ro) of the Amboseli female wildebeeste. This is a subject for future research relevant for management purposes. However, in estimating the number of calves surviving in the first year, (Refer to Table 5) the number of calves surviving for every 100 females was counted and recorded throughout the study period.

TABLE 5 - Life Table of Amboseli Wildebeeste 1973.

Age (x)	d^1x	dx	lx	qx	ex
Birth	-	0	1000	-	5.4
1	-	343	657	520	6.6
2	6	22	635	30	6.3
3	7	25	610	40	5.2
4	10	36	574	60	4.4
5	25	43	531	80	4.0
6	30	128	403	320	4.0
7	19	69	334	210	3.3
8	23	84	250	340	3.1
9	14	38	212	180	2.7
10	21	77	135	570	2.6
11	10	36	99	360	2.3
12	6	22	77	290	1.9
13	5	18	59	310	1.5
14	6	23	36	630	1.0
15	7	12	24	500	0.5
16	3	12	12	1000	0

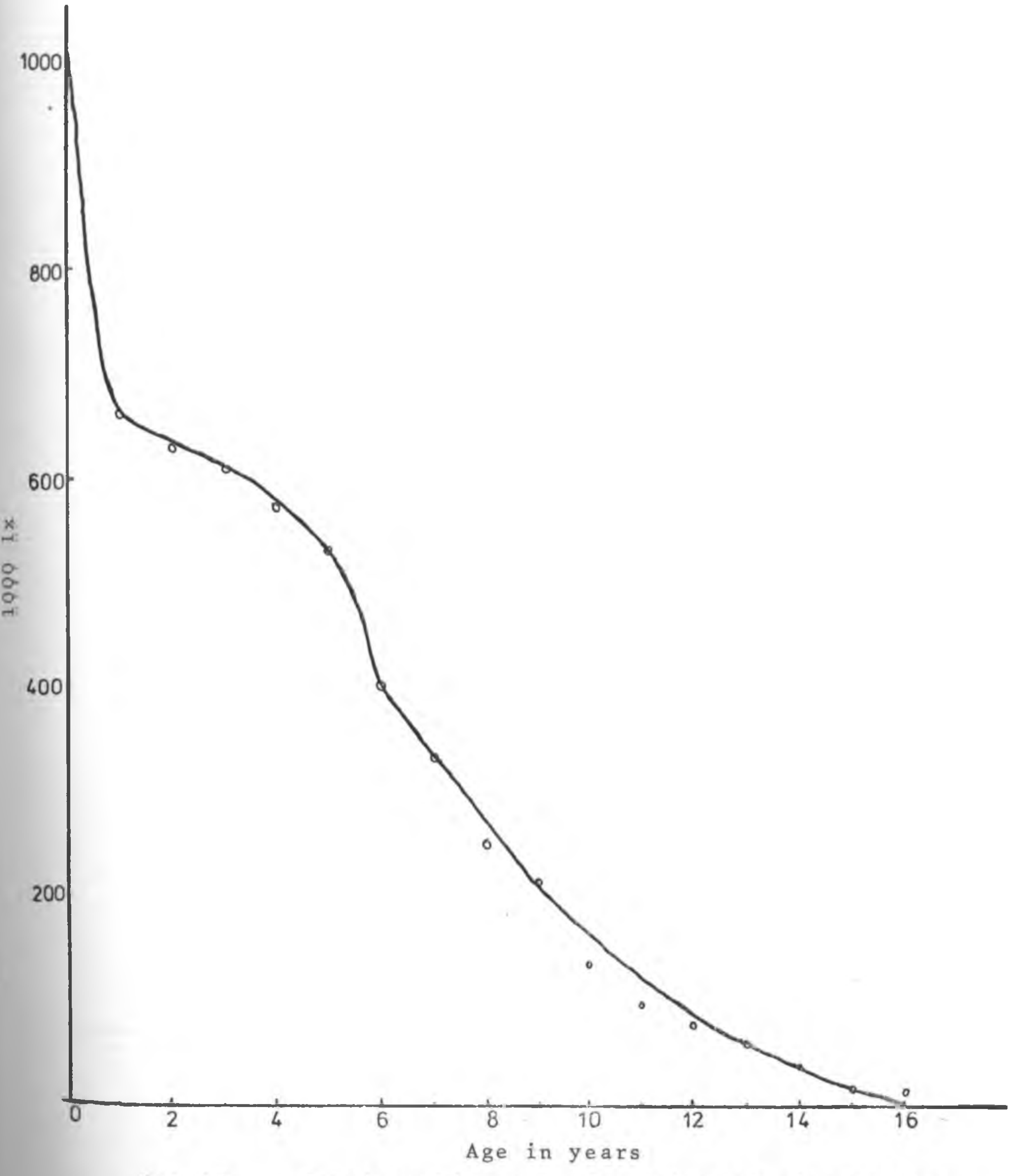


FIG 13 Survivorship curve for Amboseli wildebeeste

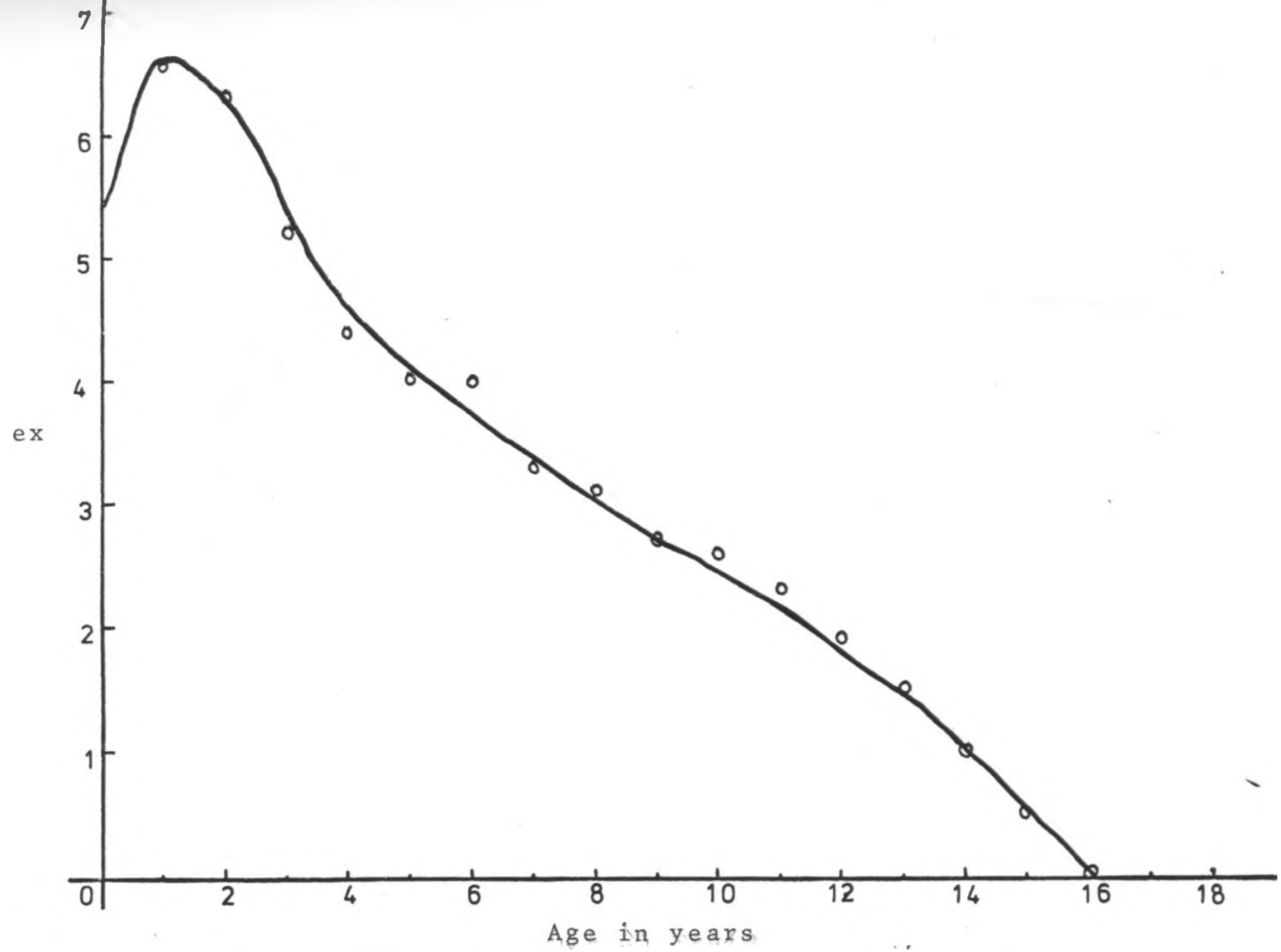


FIG. 14 Life expectation curve for Amboseli wildebeeste

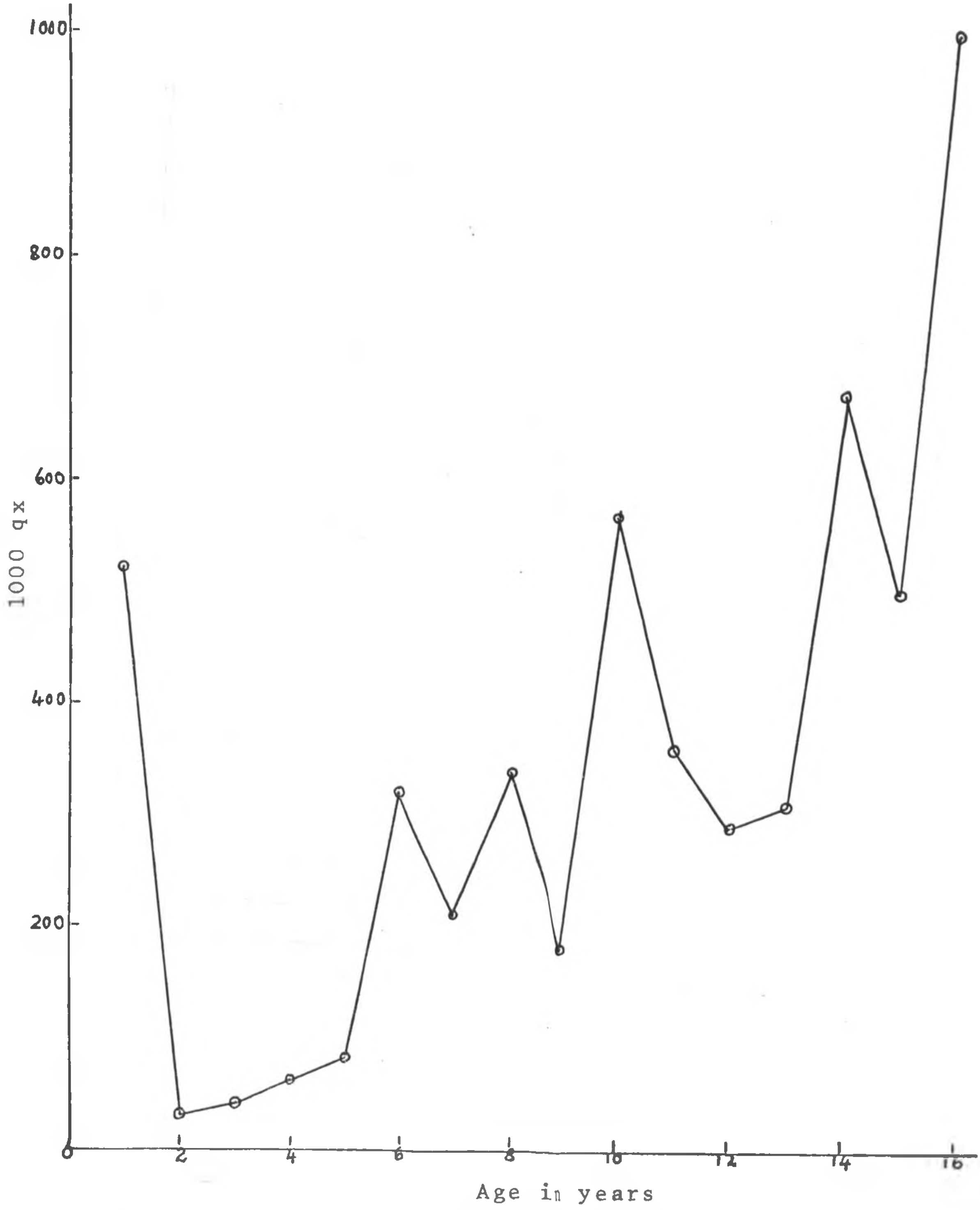


FIG. 15 Age specific mortality curve for Amboseli wildebeeste

Fig. 13 illustrates the survivorship curve (1x), Fig. 14, life expectation curve (ex) and Fig. 15 illustrates the mortality rate (1000 qx). The curves as might be predicted represent a wild population facing a variety of hazards throughout life. This therefore brings in the validity of the assumption of stable populations existing among the wild game. This is discussed (refer to the discussions and conclusions of this chapter).

5.1 Population structure: The use of life tables in studies involving population ecology of animals has been well established, e.g. Deevey (1947), Birch (1948), Laws (1966), Watson (1967) and Sinclair (1970). The life table of Amboseli wildebeeste (Table 5) summarizes some aspects of the population structure although of combined sexes, and reasons for not treating sexes separately have been discussed above (page 27).

However, field analysis of herds in the study area, show that the adult sex ratio in the population was 33% males and 67% females. A ratio of 1:2. At the peak of calving time, March 1973, population sampling showed that 20% were males, 37.5% females, 12.5% yearlings and 30% calves. In March 1974 similar field sampling of the population showed that 25% were males. 40% females, 15% yearlings and 20% calves. (Population sampling in this context defined simply counting male, female, yearlings and calves separately to determine the ratio of each in the population at fixed times of the year).

In all cases, the ratio of adult male to female in the population is approximately 1:2. This compares favourably with the Tarangire wildebeeste population. Lamprey (1963b), whereas Watson (1967) found the adult ratio to be 1:1 for the Serengeti wildebeeste.

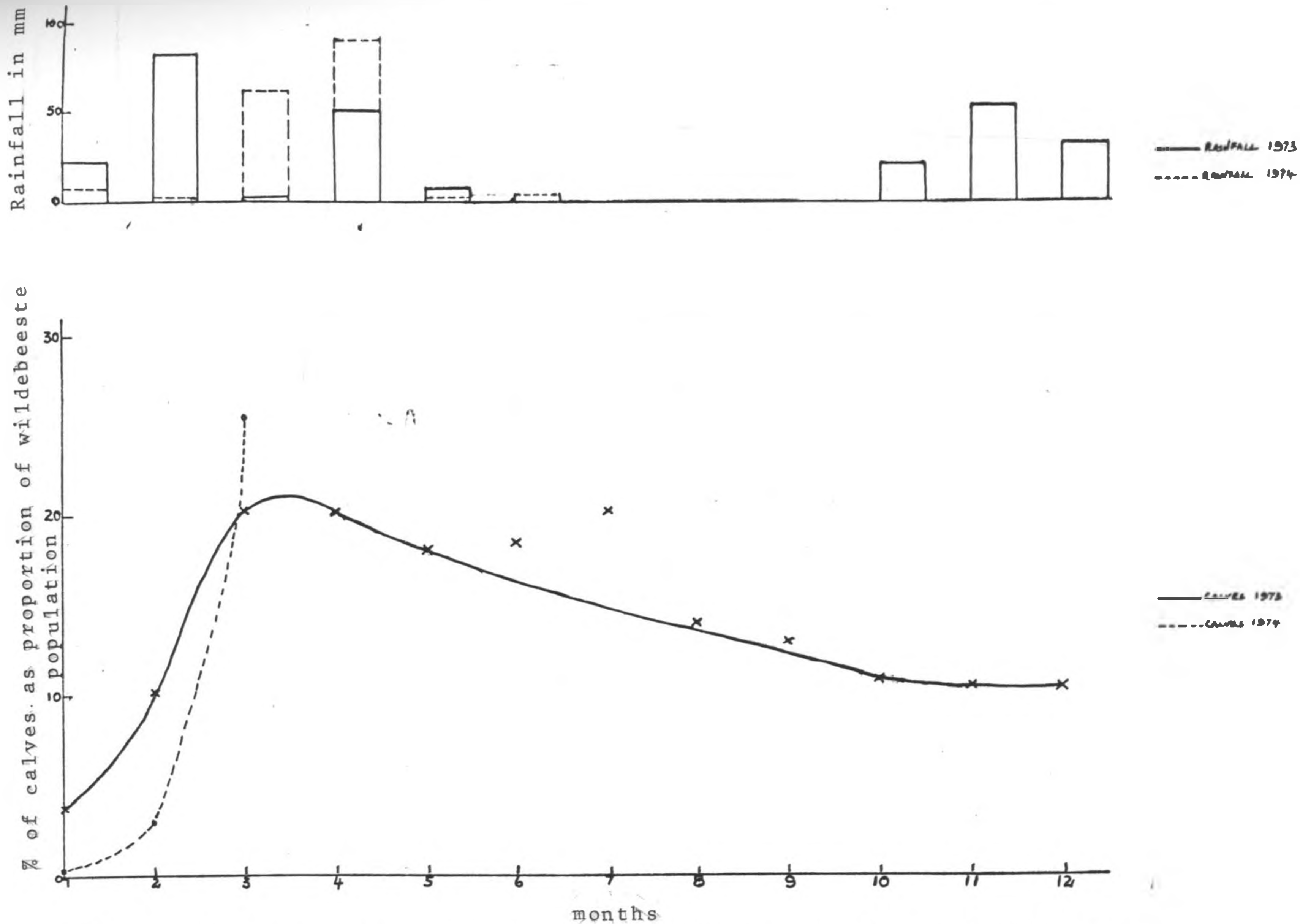


FIG.16 % of calves as proportion of wildebeeset population in the basin.

In assessing the number of pregnant females, again using field sampling method, I found that at least 78% of Amboseli female wildebeeste population were pregnant after the rutting period.

6.1 Reproduction: There was seasonal synchrony in the rutting and calving activity of Amboseli wildebeeste (Pers. Obs.). These activities took place after or during the start of the long rain season. Amboseli has a bimodal distribution of rainfall (Ref. Fig. 4, Chapter I). The long rain season of March-May and the short rain season of November-December.

6.1.1 Rutting: This took place after the long rain season of March-May and was indicated by clamped groups of female wildebeeste with yearlings and a dominant male. The number in a herd under a dominant male varied between 25-35 in the basin.

The behaviour of the territorial male in the herd, e.g. ritualised and flehmen displays, mounting and mating conformed with similar observations made on the reproductive behaviour of Ngorongoro wildebeeste (Estes, 1966).

6.1.2 Gestation period: Estimation of the gestation period for the Amboseli wildebeeste was based on the records of the rut and calving peak periods. It was estimated to around 7-8½ months. This is similar to other wildebeeste populations (Estes, 1966, and Watson, 1967).

6.1.3 Calving: Calving was synochronised with rainfall (Ref. Fig. 16), and is between the months of February and March. Fig. 16 reflects that wildebeeste in the study area, for the year 1973 and 1974, tended to calve at periods when there was rainfall to effect vegetation growth. This ensured the survival of both the mother and calf. This period is referred to as the optimum period when environmental conditions are conducive for survival (Sadleir, 1969).

Records from total ground counts indicated that 80% of the calves were born between February and March. I must admit that no observations were made on parturition and related behaviour because details of reproduction behaviour of Amboseli wildebeeste was not part of the initial plan of the project. However, I assume that parturition and related behaviour should be similar to other wildebeeste populations (e.g. Estes, 1966, and Watson, 1967 and 1969).

DISCUSSION

It is evident from the results on numbers, with due allowance on biases and errors, that population changes in the basin were seasonal. There was a marked correlation between rainfall and the fluctuation of wildebeeste and cattle numbers. This suggests that this phenomena may be related to the availability of food supply and water, a subject of discussion in the following chapters in this thesis.

The techniques of estimating numbers have been applied and obviously they have some limitations. For example, in estimating numbers from ground counts, mobility of animals from one area to another, may have resulted in counting some animals twice. Migrations of animals into basin after the counts, terrain of the habitat and personal judgements may have been some of the limitations in accurate counting from the ground.

However, to eliminate this limitations, an attempt to estimate the numbers by a total count from the air supplemented by photographic method bearing in mind of time of day and month was used. This was considered to be relatively accurate. The bias in counting from the ground and from the air was found to be 24.4%. This I considered to be not too bad in view of the constancy in fluctuation of numbers in the basin; and at least over 75% of wildebeeste population were counted. Photographic method could have well been used on cattle, but this would have been expensive in costs and time. It was however, a valid method where total counts were involved and in the elimination of the proposed errors. The errors in photographic counts were eliminated by methods suggested by Jolly (1969b).

The bias and errors in aerial sampling have been considered by many authors e.g. Jolly (1969a), Pennycuick and Western (1972 and Norton Griffiths (1972) and need no elaboration. However, accuracy of my sampling method are revealed by the confidence limits which in the case of wildebeeste was 32% and cattle 26%, with a sampling fraction of 7%.

As far as age determination is concerned, with reference to the frequency of age distribution of the living and the dead population (Ref. Figs. 7, 7a, 8 and 8a) a chi-squared was applied to test if there was any relation because it appeared to me that the frequence of distributions in both case followed a similar pattern. The null hypothesis was that age determination by Watson's method of the living population and Sinclair's method of the dead population, was in fact from the same statistical population, and the assumption that both living and the dead population should show similar age frequency up to age of 5 years (χ = 0.3445 p = 0.5 d.f,4) (Bailey, 1959). The chi-squared was not statistically significant and therefore the null hypothesis was true. There are evidence of similarity of periodicity in age distribution up to 5 years (Ref. Fig. 7, 7a, 8 and 8a).

Age determination by use of cementum lines on East African herbivores has been discussed very largely by Grimsdell (1969 and 1973) and Spinage (1973). I do agree with Spinage (1973) that there is a great need to determine the ages of larger African mammals concomitant with increasing management. A number of authors have in this case used either incissor teeth Spinage (1973); Maxillary M_1 Grimsdell (1969) and Sinclair (1970), Mandibular M_3 Watson (1967) in establishing cementum lines to determine the ages. I decided to use M_1 on the basis of the same reasons used by Grimsdell (1973) that M_1 was more centrally situated on the jaw, and therefore it was more likely to be worn consistently than either M_3 or other jaw teeth. M_1 is a first permanent tooth to erupt and is therefore more representative of the age of the animal under investigation. The reasons for using a geological saw to make sections unlike other methods of decalcifying and consequently using a microtome have been discussed (Refer to Methods Sect. 3.5.4). It was also intended to develop a method for age determination for Amboseli wildebeeste, although I realise that I should have had known age animals to develop a system for determining the age of living population.

The results (Fig. 11) show that the wear pattern of Amboseli wildebeeste follows a negative exponential curve of the form $Y = Ae^{-ac}$. The values calculated based on my data were $Y = 6.0925e^{-0.06c}$, ($r = 0.95$ $P < 0.001$). Spinage (1973) in describing age determination by teeth of mammals, with special reference to Africa has quoted Kerwin and Mitchell (1971) of having found a similar relationship in wear pattern of pronghorn antelope Antilocarpa americana. I therefore conclude that the pattern of attrition in the tooth of M_1 for Amboseli wildebeeste follows a negative exponential, and the graph (Fig. 11) should be able to be used in determining the ages of Amboseli wildebeeste by measuring the crown height. In my case I used enamel height as the dependent variable (y) and age as the independent variable (x) whereas Grimsdell (1973) used age as the dependent variable. It is infact the deposition of cementum that is a function of age and consequently age should be the independent variable.

Predation by lion (Pers. Obs. and reports from rangers) was considered to be the main cause of mortality for the adult Amboseli wildebeeste. Kruuk and Turner (1967), Watson (1967) report that lion is also the main predator for the Serengeti wildebeeste. In the case of calves Watson (1967) suggests abandonment was a major cause of calf mortality or may be by malnutrition on suggested by Hirst (1969). Possibly this may also be the causes of calf mortality in the basin, although cases of cheetah Acinonyx jubatus raineye preying upon wildebeeste calves in the basin has been reported (Personal communication D.M. Warobi).

Results of age-specific mortality (Fig. 15) are interesting, although a small sample size was analysed, they show what was expected. The greatest mortality was in the younger and older animals. However, the assumptions of constant mortality, stationary age distributions and stationary populations as advocated by Deevey (1947), Slobodkin (1961) and Caughley (1966) are very unlikely on wild game, particularly in view of the unstability in environmental conditions. It is therefore possible that the survivorship curve (Fig. 13) may not be representative of Amboseli wildebeeste. And far from the validity of these assumptions, sampling errors in one age group may have been carried into the calculation of the other age group, and therefore this survivorship curve is only approximate. To eliminate this bias, Caughley (1966) suggests that the use of age-specific mortality curve. This is because this curve (qx) is independent of frequencies in younger age classes, and as it is, skulls of dead immature animals were not easily located. This was possibly because they decayed faster than the old mature skulls which were easily recovered from the basin.

Despite the validity of the assumptions of constructing life tables, I think it is helpful to construct life tables because, although being approximations, they quickly tell us information about the age structures, mortality rates, mean life expectancy, and reproductive values of animal populations.

METHODS AND MATERIALS

7.1 Distributions: Daily and monthly distribution of mainly wildebeeste and cattle was mapped over the background of the preferred vegetation types. 'Preferred' vegetation types in this case is defined as the vegetation types where wildebeeste and cattle were grazing whether as discrete herds or in association with other grazing herbivores. A vegetation map of the study area (Fig. 3 was used for thispurpose. Numbers observed were recorded as discussed (Chapter I, Sec. 3.1.1).

However, instead of using the actual vegetation map in the field, an open map was drawn on the same scale, but marked with 1 x 1 kilometre grids and main features of the study area like Volcanic hills, roads and swamps. The marking of the main features was for the purpose of easy determining of grids where the animals grazed. It was also possible using either Enameshara hill (Observation Hill) or Kiturua hill as observation points to determine using a binoculars, the distribution and mapping of wildebeeste and cattle. This was only possible for the open alkaline grasslands. Efforts were however made to drive into the actual areas where the animals were grazing.

The open map was then superimposed on the actual vegetation map and the vegetation types where animals were distributed was recorded in a field note book. This was done throughout the study period.

Observations were also made on movements on different pastures in the basin recording time of day

7.2 Leaf table: This is defined as the mean height of foliage on the grass. This was assessed seasonally

METHODS AND MATERIALS

7.1 Distributions: Daily and monthly distribution of mainly wildebeeste and cattle was mapped over the background of the preferred vegetation types. 'Preferred' vegetation types in this case is defined as the vegetation types where wildebeeste and cattle were grazing whether as discrete herds or in association with other grazing herbivores. A vegetation map of the study area (Fig. 3 was used for thispurpose. Numbers observed were recorded as discussed (Chapter I, Sec. 3.1.1).

However, instead of using the actual vegetation map in the field, an open map was drawn on the same scale, but marked with 1 x 1 kilometre grids and main features of the study area like Volcanic hills, roads and swamps. The marking of the main features was for the purpose of easy determining of grids where the animals grazed. It was also possible using either Enameshara hill (Observation Hill) or Kiturua hill as observation points to determine using a binoculars, the distribution and mapping of wildebeeste and cattle. This was only possible for the open alkaline grasslands. Efforts were however made to drive into the actual areas where the animals were grazing.

The open map was then superimposed on the actual vegetation map and the vegetation types where animals were distributed was recorded in a field note book. This was done throughout the study period.

Observations were also made on movements on different pastures in the basin recording time of day

7.2 Leaf table: This is defined as the mean height of foliage on the grass. This was assessed seasonally in the vegetation types where wildebeeste and cattle were grazing. The purpose of the leaf table was to categorise and determine the feeding level of wildebeeste and cattle.

Measurements were done by using a metre rule on numbered and marked transects in the preferred vegetation types. Measurements taken along a transect were recorded at an interval of one metre from one point to another. In determining the grass heights a number of measurements of grasses at any one point was determined from which a mean was calculated. Pressence or absence of culms was determined by measuring both the leaf and culm heights. Measurements were determined at fixed times of the mon and the mean of accumulated reading was determined as the leaf and culm height of a particular month.

In the course of making this recordings state of growth and condition of grass was recording using an arbitary scale:

Vegetation condition	Scale
Dry	1
Medium green	2
Green	3
Lush	4

Growth stages	
New growth	1
Mature growth, ungrazed	2
Mature growth grazed	3
Mature growth, dry, in clumps	4

7.3 <u>A. xathophloea tree evaluation:</u> In effort to determine the successive vegetation changes in the basin, *A. xathophloea* and *S. monoica* bush were used as indicators. Transects were set up West of Enameshera Hill (Observation Hill) which is at centre of the basin. A total of five belt transetcs each 1.5 km long and 30 metres wide were set up. Data collected in these transects was on: numbers of alive, fallen and dead trees, and clumps of S. monoica bushes. The only other tree recorded was A. tortilis. Transects were running from north to south.

Running through the transects, usually done by ground sampling, was done periodically. It was possible from previous recordings, to determine the most recent fallen tree. The frequency distribution of alive fallen and dead trees was compared in each of the five transects from the centre of the basin to the fringes of the basin. The aim was to determine areas with high mortality rate of A. xathophloea as related to salinity in the basin. Much of the detailed work was done by Van Praet and Western (1973).

7.4 Net primary productivity: Since this study was concerned with grazing, I considered it necessary to monitor primary productivity on the basis of standing crop only.

The main objectives of monitoring productivity were:

(i) to assess the productivity of each of the main open grasslands and relate the results to habitat use.

(ii) to determine herbage intake on the assumption that the differences between clipped grass in and outside exclosures was equal to off take.

(iii) to determine quality of the clipped grass and relate the quality to seasonal pasture use.

(iv) to determine from the clipped grass the % proportion of leaf, sheath and stem and relate it to seasonal pasture use.

Exclosures were set up in each of the main vegetation types. Each exclosure had the dimension of 5' x 3' x 1½' made of wooden frames and wire netting surrounding the whole exclosure. The exclosure was constructed in such a way that it excluded all the herbivores grazing in the basin, and also easy to clip inside with minimum trampling on the grass.

These exclosures were set up after determining the preferred habitats of wildebeeste in the basin as soon as they moved into the basin. Human interference with exclosures was considered in the choice of sites for the exclosures.

Sampling of the vegetation was on monthly basis usually at fixed times of the month. Grass clipping was done by harvesting method using garden shears.

A quadrat 50 cm x 50 cm was used and clipped grass was put in a paper-bag. Grass clipping was done both inside and outside exclosures. The area clipped outside the exclosure was randomly chosen by throwing a metre rule and where it dropped was the area clipped. The area clipped was marked with pegs so that it was not clipped again during the following month. If by chance the metre rule fell at the same place as the previous month, another area was chosen. Each of the paper-bag was marked with number of the exclosure, species of grass, and date.

Grass samples clipped were then sun-dried, leaf, stem and sheath separated and then dry weight determined and recorded. The samples were then put back in the respective paper bag and submitted to National Agricultural Laboratories for crude protein and crude fibre analysis.

Data collection on primary productivity was done for 14 months.

Calculations for primary productivity, herbage intake, % leaf, stem and sheath in the sampled grass are shown in the results.

7.5 Assessment of condition: A number of ecologists have used various methods for estimating condition of ungulates as an aspect of population regulation, e.g. Klein and Olson (1960); Riney (1955, 1960 and 1970); Smith (1970); Sinclair (1970); Sinclair and Duncan (1972) and Jarman (Personal communication). The use of kidney fat index has been widely used and recommended as one of the best method for assessing condition in animals. Riney (1955) has however, discussed various other methods applicable to animal populations where it is not possible to shoot or trap.

The Amboseli wildebeeste is such a population which cannot be shot or trapped because of existing by-laws governing the management of Game Resrves. In view of this, I adapted the visual method for assessment of condition, hopefully that it will be invariably fairly accurate.

The lumbar region of wildebeeste was used in the estimation of condition. The criteria used here was based on the depressions in the lumbar region and the protrussions of the tubar-coxae and tubar ischii. These two bones together with the regression of gluteal muscles and prominence in the lumbar depression are distinct anatomical features which enables one to assess the seasonal trend in fat reserves in an animal.

Riney (1960) describes these anatomical changes clearly on deer and has the rating of good, medium, or poor condition. In my case of identifying condition, a photographic key of various conditions of wildebeeste was developed (Refer to Plates I (a), (b), (c) and (d)) and used in the field. Condition was assessed for both male and female wildebeeste. Results are presented in the form of histogram (Fig. 19).

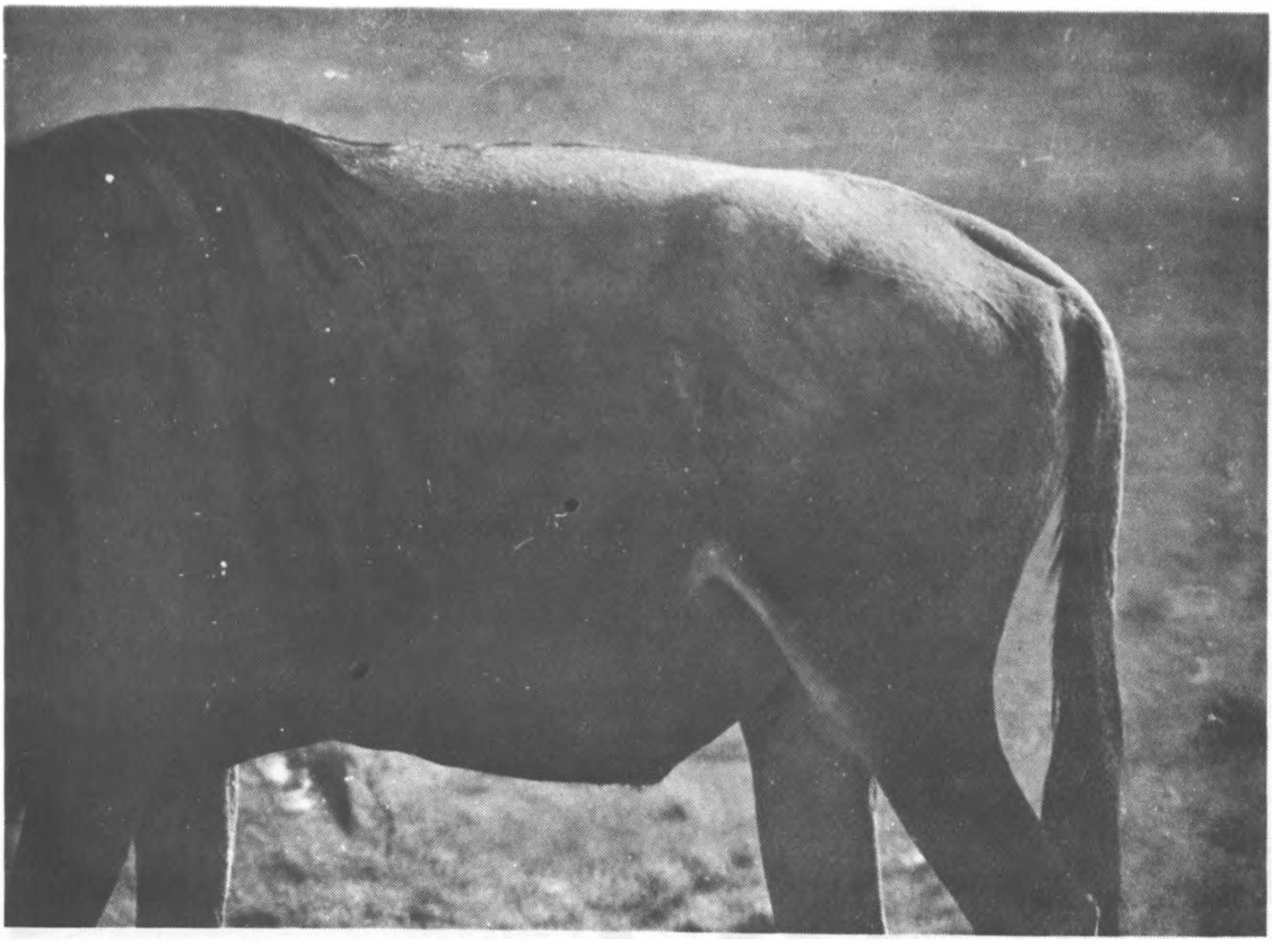


Plate 1(a) (above) shows Good condition rating.

Plate 1(b) (below) shows Fair condition rating.

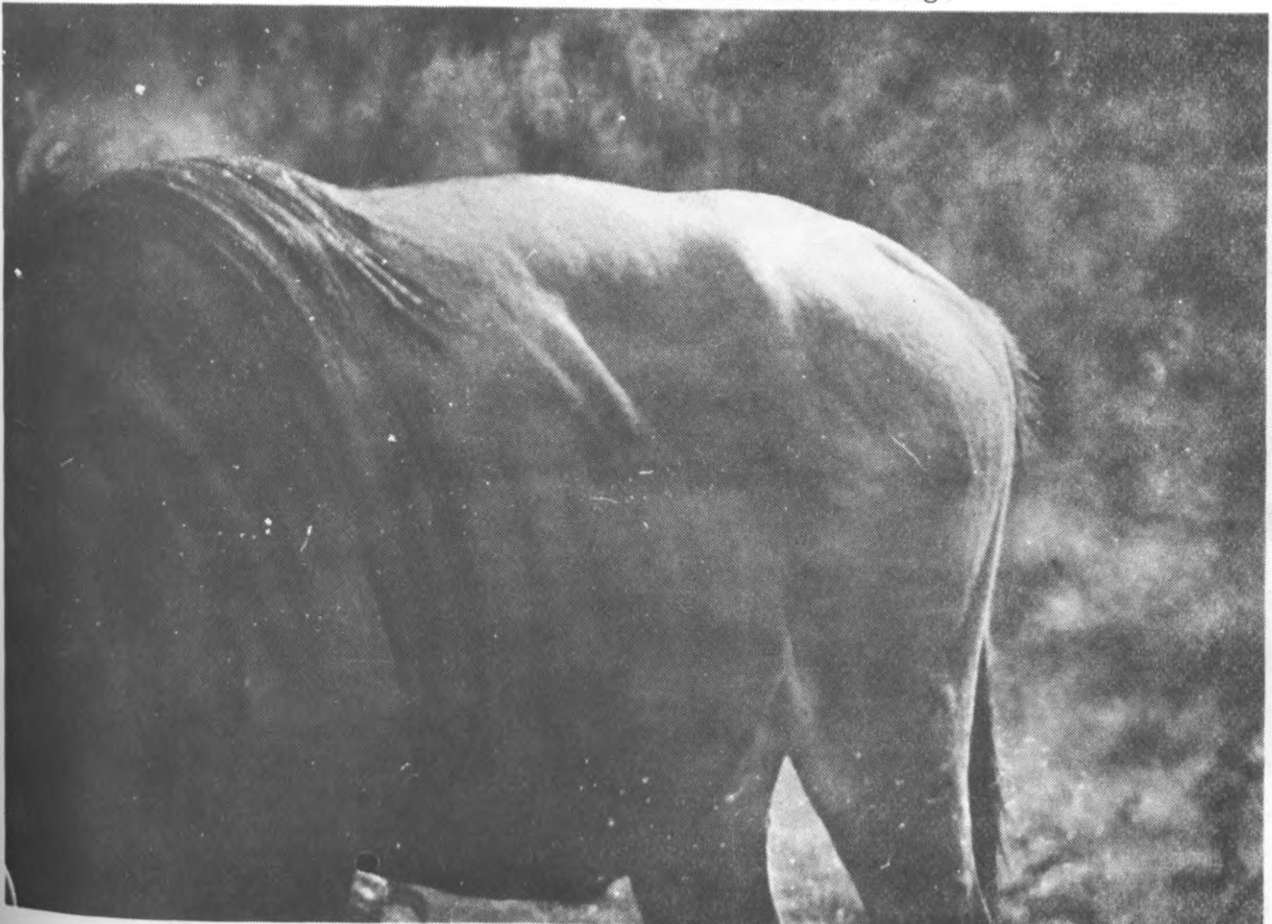
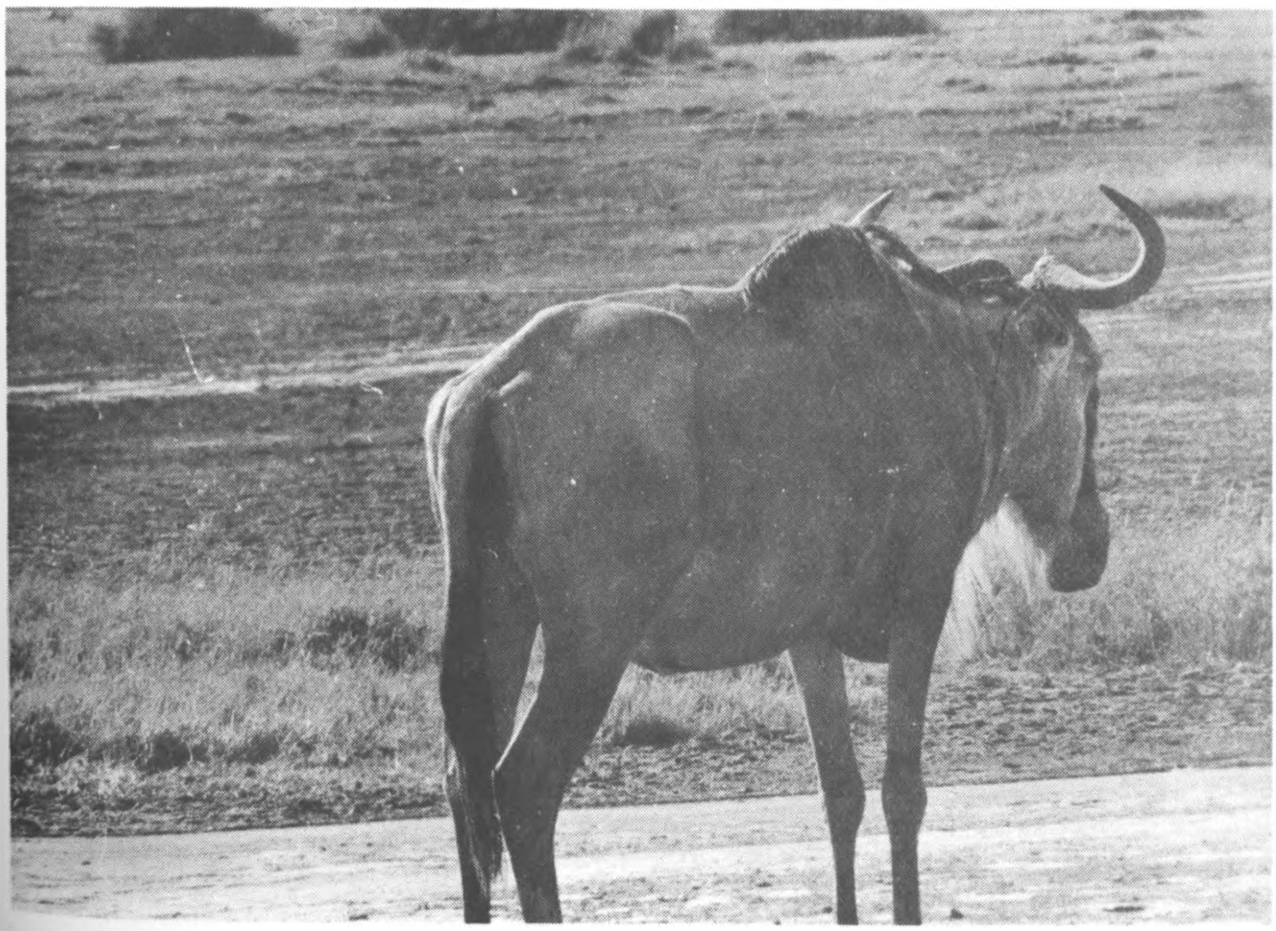


Plate 1(c) (above) shows Poor condition rating.

Plate 1(d) (below) shows very Poor condition rating.



RESULTS

8.1 Primary productivity: The annual net primary productivity of major grasslands was calculated using the following formula:

$$N.P.P. = \sum_{i=1}^{n} (B_i - W_{i-1})$$

where N.P.P. = net primary productivity
B_1 = biomass above the ground inside the exclosure at a time t_1.
B_i = biomass inside the exclosure after a time t_i.
W_i = biomass outside the exclosure at a time t_i.

Net primary productivity was calculated from the data on biomass of standing crop in kg/ha/annum.

C. dactylon grassland	=	8044.0 kg/ha/annum.
S. marginatus grassland	=	1019.8 kg/ha/annum.
S. spicatus grassland	=	718.3 kg/ha/annum.
S. homblei grassland	=	400.0 kg/ha/annum.

The seasonal changes in productivity of these grassland is illustrated (Ref. Fig. 17). The results quite clearly indicate that of all the major grasslands in the basin, *C. dactylon* was the most productive. This was obviously related to their ecology, as discussed in this thesis (Ref. Chapter I, Sect. 2.3) rainfall distribution, (Fig. 4) and grazing intensity discussed under "Utilization of Pastures" (Ref. Page 49).

8.2 % Leaf: Stem: Sheath ratio: Figs. 18a, b, c and d show the seasonal changes in the percentage composition

FIG. 17 Seasonal Primary Productivity of major grasslands in the basin.

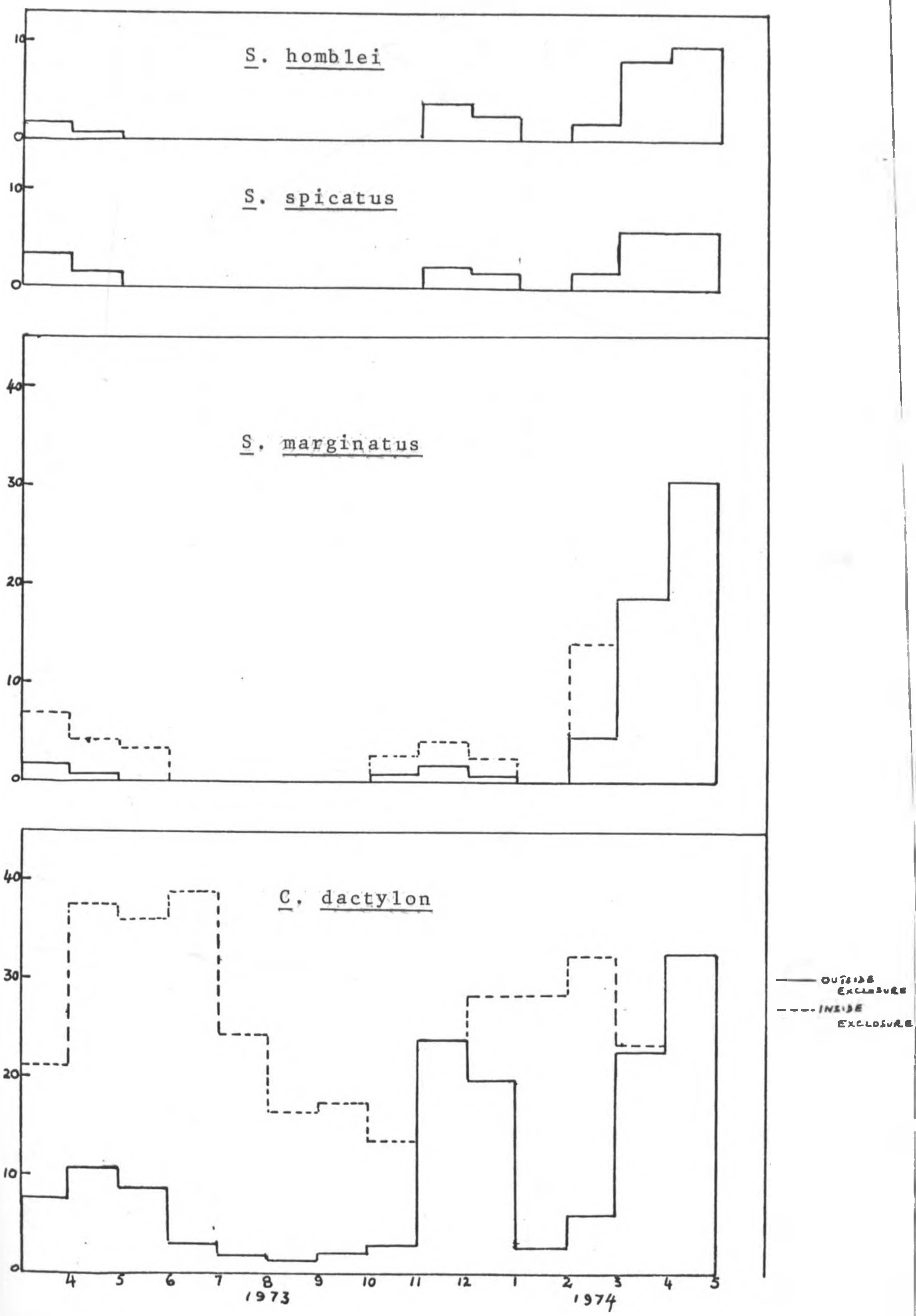
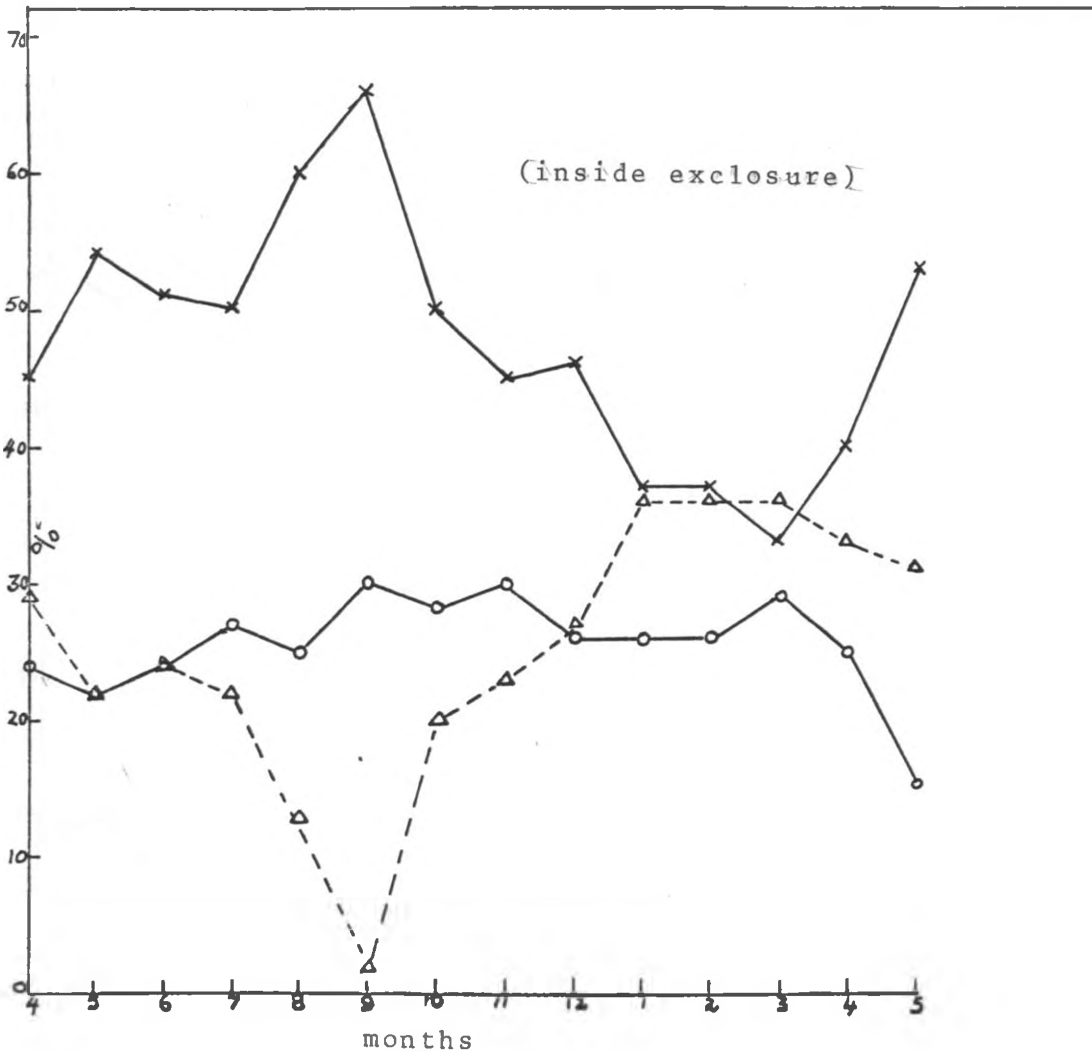


FIG.18a Leaf-stem-sheath composition of C



. dactylon grassland in and outside exclosure

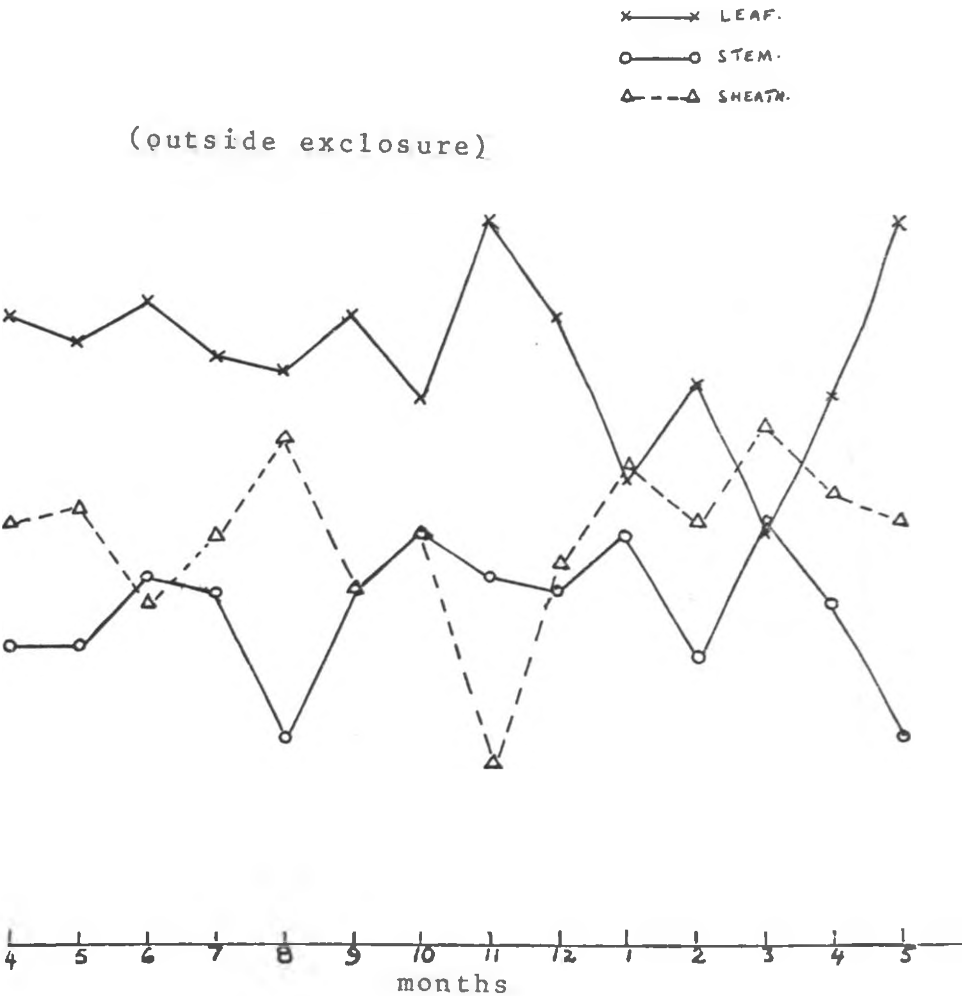
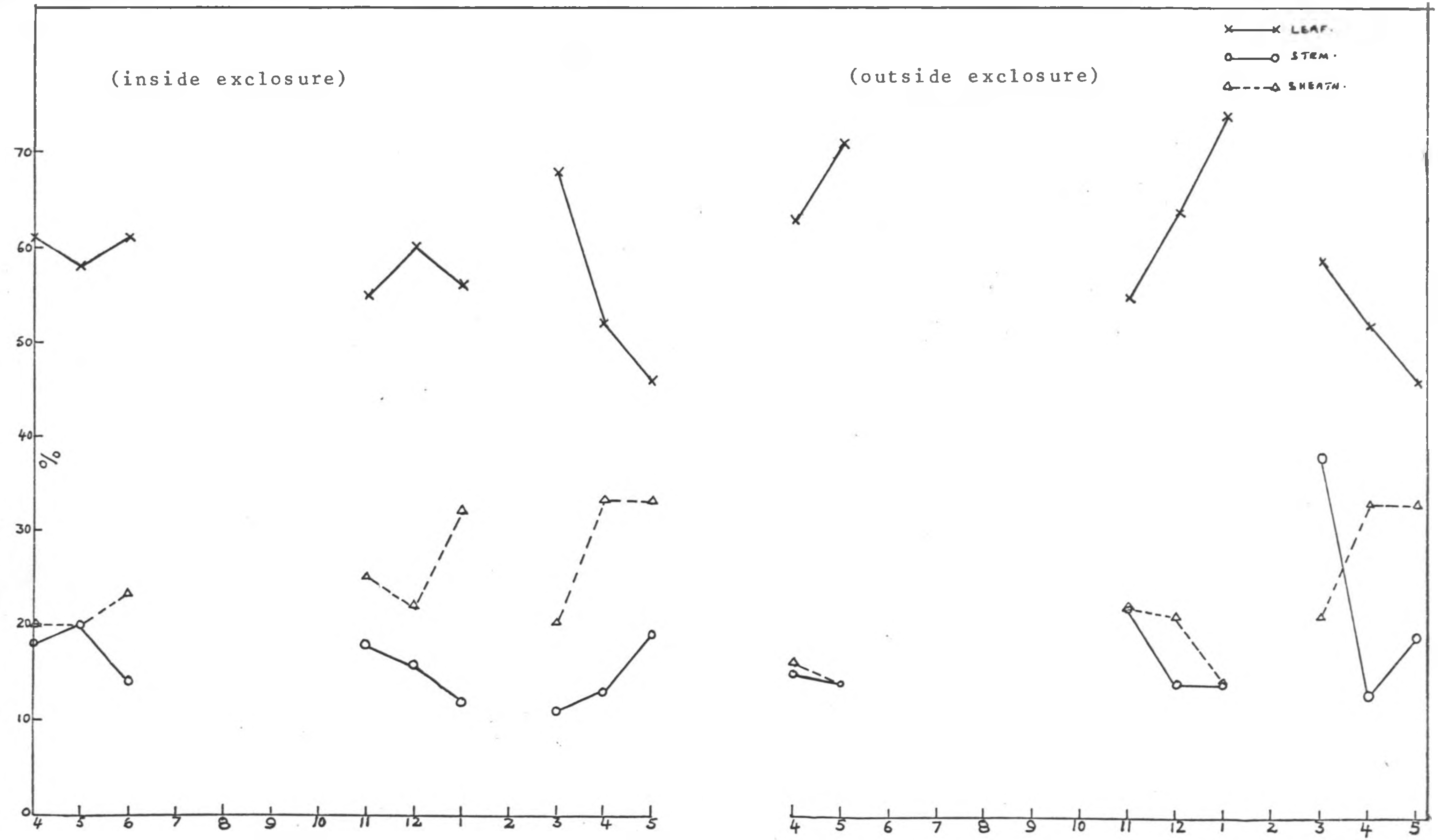


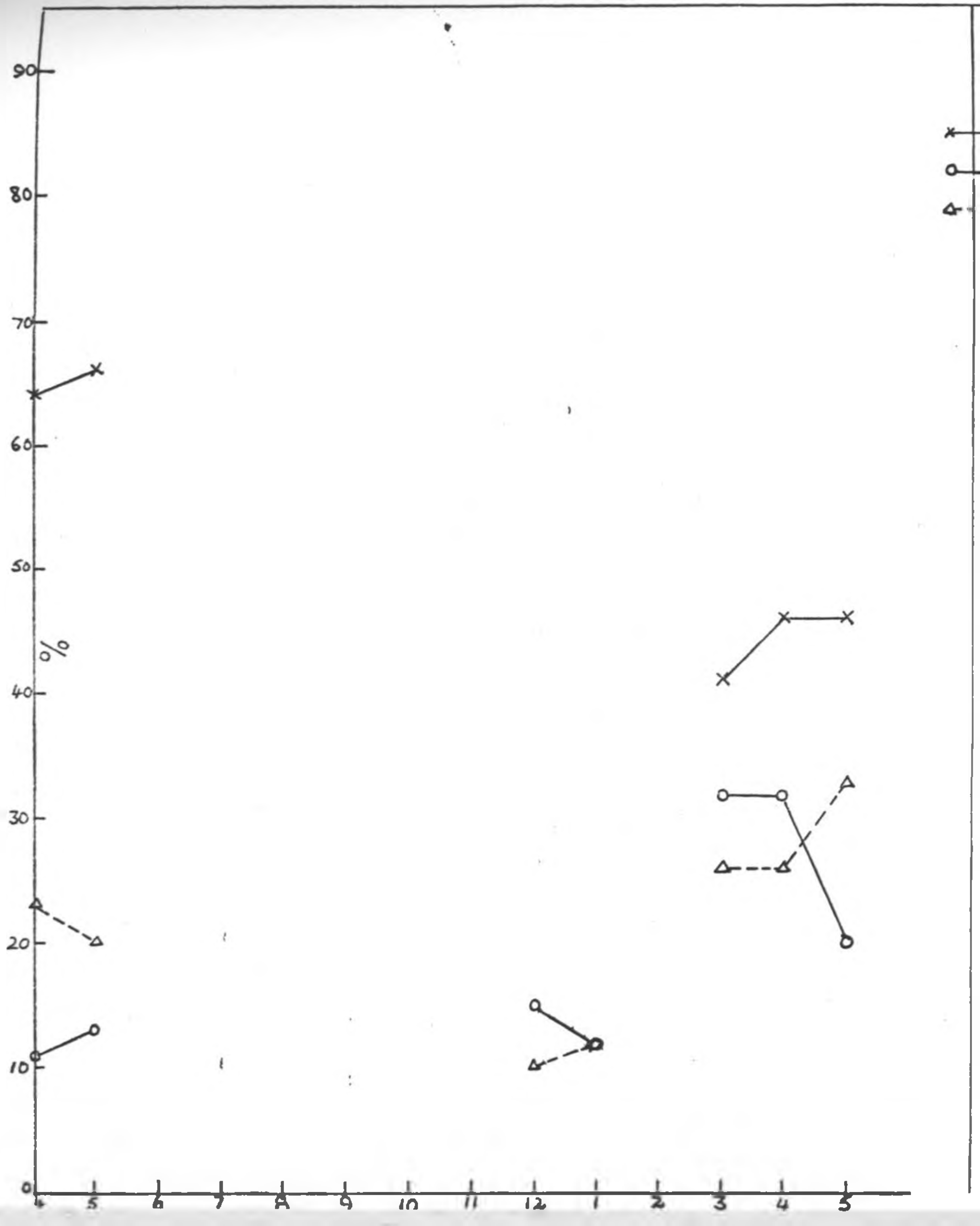
FIG. 18b   Leaf-stem-sheath composition of S. marginatus grassland in the basin.



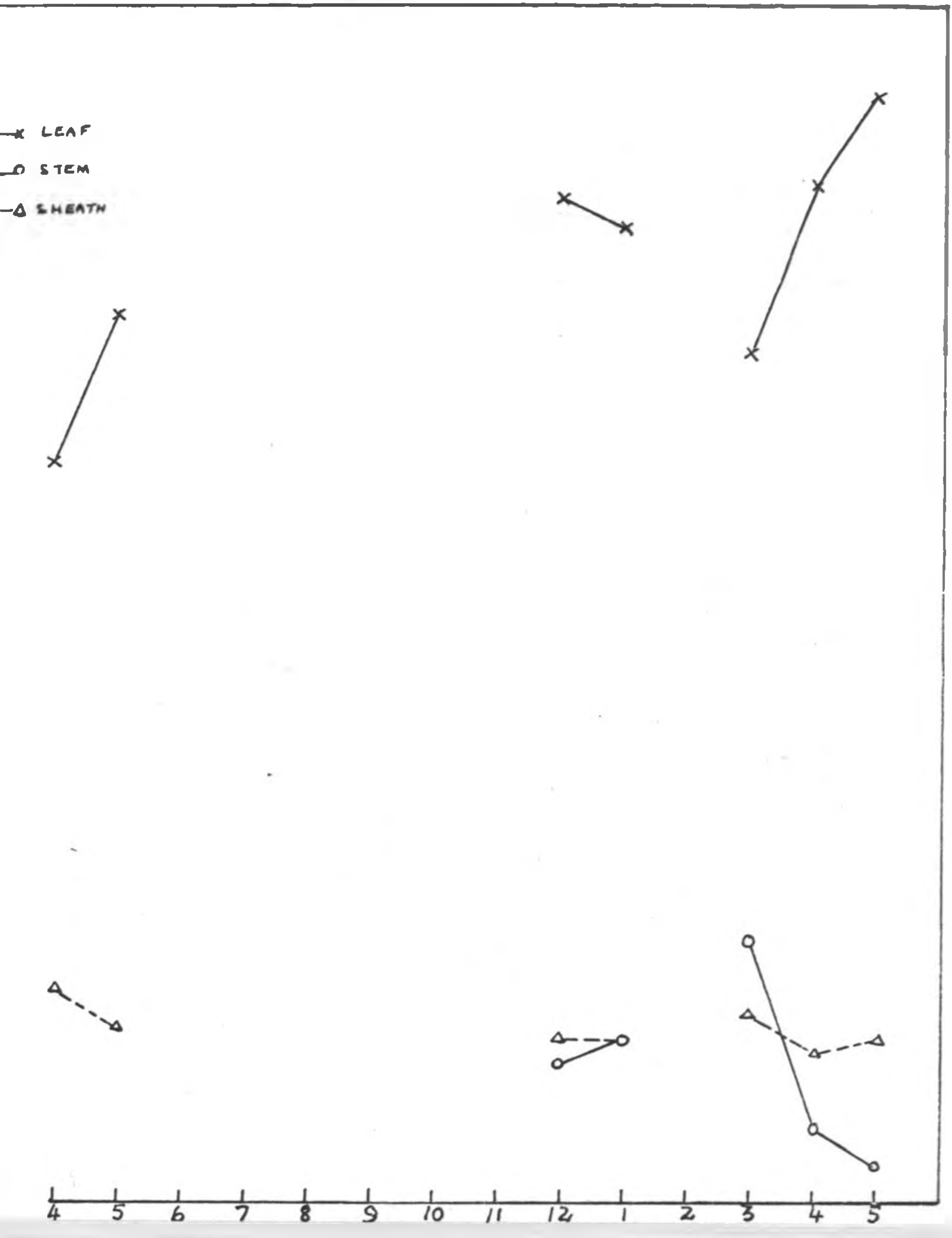
FIG, 18c and d

Leaf-sheath-stem composition of *S*, *spicatus* and *S*. *homblei*.

FIG.18c S. spicatus



FIG,18d S. homblei



of leaf, stem and sheath in each of the major grasslands in the basin. The discontinuity in lines in the case of Figs. 18b, c and d indicate that there was no growth taking place in these grasses at times indicated. If there was any grass at all it was either in clumps or too short to be clipped. And in the case of Figs. 18c and 18d, there was no significance differences in weight of grass in and outside the exclosures. This may indicate either these grasslands were hardly grazed or if there was any grazing at all very little. Results of primary productivity of these grasslands namely S. spicatus and S. homblei and in the case of S. marginatus only during the dry season confirm that there was little or no grazing on them. A clear picture of utilization of these pastures is discussed under "grazing calendar" (Sect. 9.1, Chapter II). Fig. 18a of C. dactylon show that there was continuous growth throughout the year, the significance of this is discussed under Section

8.3 Crude protein and crude fibre: Seasonal changes in crude protein and crude fibre values of the major grasslands are shown in Table 6.

Data for crude protein and crude fibre values was analysed for the whole plant. The figures in the table may appear relatively high compared to similar work done on Kenya grasses (Dougall, 1963a). These differences may be attributed to a number of factors:

(i) Sampling error - it was possible that organic matter and legumes,considered to be the richest source of protein (Dougall, 1963a) may have been included in the material for chemical analysis.

TABLE 6 Seasonal changes in crude protein/crude fibre values in the basin

		4	5	6	7	8	9	10	11	12	1	2	3	4	5
	% C.P.	16.90	17,06	14,00	12.69	14,03	14,66	15,75	24,50	19,25	17,06	15.75	11.75	12,95	13.45
C. dactylon	% C.F.	30.17	27,06	27,39	27,94	26,77	25,85	27.45	25,93	26.66	27.46	28.65	24,07	28.90	29.70
	% C.P.	20,56	15.75	-	-	-	-	-	16,19	14,00	11.56	11.32	12.82	12.25	12.44
S. marginatus	% C.F.	22,10	28.68	-	-	-	-	-	24,88	25,24	24.89	25,32	21.49	31.75	31.34
	% C.P.	14,32	12.83	-	-	-	-	-	17.53	17,06	16.19	-	10.21	12,63	13.31
S. spicatus	% C.F.	18,23	27.73	-	-	-	-	-	24,73	25.31	24.00	-	22.91	24.93	28.29
	% C.P.	16.52	17.92	-	-	-	-	-	-	25.38	27.56	-	12.95	13.50	17.31
S. homblei	% C.F.	28.71	26,72	-	-	-	-	-	-	21.18	20.46	-	27.90	28.80	22.93

A number of samples of the same grass were needed to be analysed to determine the mean value, and that too over a continuous period of time.

(ii) The stage of growth - the value of crude protein and crude fibre will vary with the growth stage of the plant. In this case no consideration was given to the growth stage of the plant. For example, C. dactylon is a high water grass, and as a result of grazing pressure, there was regeneration of new growth, and therefore most likely this may have contributed to high values of crude protein and crude fibre.

(iii) Area of sampling - the differences may also be attributed to area of sampling, e.g. type of soil and possibly salinity of the basin may have been a contributing factor in the results being high.

It was however important to analyse the crude protein and crude fibre values of these major grasses to be able to determine whether preference for a particular pasture by wildebeeste, is motivated by the nutritive digestibility.

8.4 Distributions: Monthly distribution of wildebeeste in the basin shown on a grid pattern appear in the Appendix (i - xiii). Actual numbers of wildebeeste observed and counted were inserted in the approximate grids. The open map with grids superimposed on the actual vegetation map (Fig. 3, Chapter I) was very instrumental in determining the utilization of pastures and the grazing calendar in the basin.

Since cattle concentrated in the basin at the peak of the dry season, observations showed that distributions of both wildebeeste and cattle on the limited grazing areas were inseparable. In this case, it was not intended to show cattle distribution in the basin throughout the dry season, and only one typical dry season cattle distribution is given (Appendix xvi). It will however, be noticed that in the case of cattle, only estimated numbers are indicated.

UTILIZATION OF PASTURES

The seasonal use of alkaline and secondarily induced pastures (Chapter I, Sect. 2.3 - 2.3.3) by wildebeeste was facilitated by the initial use by zebra Equus burchell (Gray). Zebra have been observed (Pers. Obs.) to move into the basin earlier than wildebeeste. This was usually at the end of the rainy season when the vegetation in the basin was lush, with a high leaf/culm table (Ref. Table 7). The vegetation was mature and in most cases ungrazed because a large proportion of animal community was in the wet season ecosystem during the rainy season (Fig. 4, Chapter I).

And while, as explained above zebra are distributed on the alkaline and secondarily induced pastures, elephants Loxodonta africana (Blumenbach) and buffaloes move directly into the swamps (Pers. Obs. and Western, 1973). Thus the use of swamp pasture by wildebeeste and cattle was apparently facilitated by the initial use by elephants and buffaloes.

As the dry season advances, zebra were found grazing in association with wildebeeste and Thomson's gazelles Gazella thomsonii (Gunther) progressively utilizing moving into the swamp pasture regarded as a reserve pasture. However at the peak of the dry season concentration was on mainly C. dactylon, with constant browsing of S. consmilis by both wildebeeste and cattle. Browse is used here to show that because S. consmilis was a tall beach grass, wildebeeste and cattle could not eat its leaves unless they raised their necks to something over one metre, the average height of S. consmilis.

Cattle started moving into the basin at the peak of the dry season when the alkaline pastures were dry,

TABLE 7 Leaf Table of major grasslands in the basin

		1	2	3	4	5	6	7	8	9	10	11	12	1	2	3	4	5
	LEAF (CM)	10.5	10.7	4.5	3.5	8.2	4.8	4.5	3.8	4.0	3.5	4.8	3.0	2.5	3.2	6.8	16.2	27.5
C.dactylon	CULMS	25.9	24.5	12.2	6.5	18.9	11.3	6.5	5.8	8.6	6.1	5.3	4.3	5.1	6.8	12.8	46.2	52.5
	LEAF	5.2	4.5	2.8	2.5	3.0	2.6	2.0	2.0	2.0	2.0	2.3	2.7	2.2	2.0	2.7	6.8	20.3
S.marginatus	CULMS	26.5	23.3	-	-	-	-	-	-	-	-	-	9.7	4.1	-	10.3	30.8	52.6
	LEAF	2.4	2.0	1.2	1.3	1.4	1.0	1.0	1.0	1.0	1.0	1.3	1.4	1.0	1.1	2.4	3.0	3.5
S.spicatus	CULMS	15.8	12.3	6.1	4.3	7.3	-	-	-	-	-	6.3	9.6	-	-	16.3	18.5	20.8
	LEAF	2.6	2.1	1.5	-	-	-	-	-	-	-	1.4	1.2	-	1.0	2.3	3.8	6.4
S.homblei	CULMS	17.3	15.1	6.8	-	-	-	-	-	-	-	5.5	3.0	-	-	8.2	16.8	25.8

and in most cases grass was mature, dry and in clumps, except for C. dactylon which was green, and although mature, was usually with graze being a high water table grass. A change in the leaf table heights was an indication that other grasslands had been utilized or were subject to drought conditions and if there was any grass at all, the small heights made it difficult of the grazing animal community with reference to wildebeeste, not to utilize them.

Grazing conditions during the dry season were changing so fast that the grazing community were limited to either C. dactylon, or the swamps. A very interesting situation which was not followed closely was that zebra and wildebeeste increased their grazing time, and infact zebra conspicously continued grazing nearly the whole night. At this time of limited food resources, cattle displace wildebeeste from the available grazing area, usually C. dactylon grassland.

Elephants and buffaloes continued utilizing the swamps throughout the dry season although elephants browsed on the A. xathophloea trees. The initial utilization of swamps by elephants and buffaloes was governed by the height of sedges and presence of water. In places where the sedges had been grazed low, cattle, wildebeeste and Thomson's gazelle would move into these areas.

However, the grazing sequence of wildebeeste and cattle in the basin is described under grazing calendar.

9.1 Grazing calendar: This describes the grazing sequence of wildebeeste and cattle in the basin in relationship to seasonal occupancy of the pastures

(Ref. Distribution Maps, Appendix i - xiii). In fact it is a detailed aspect of the whole study on pasture use to answer the following questions:-

(i) whether pasture use in the basin is conditioned by rainfall?

(ii) whether the relative proportion of leaf, sheath and stem in the pastures a factor in pasture use?

(iii) whether quality and digestibility are also factors in the over all pasture use?

January and February, 1973: The vegetation in the basin was lush, with mature ungrazed grass. A number of water-holes were still filled with water. The lake bed was wet.

A number of territorial wildebeeste males and few small herd sizes of 10-15 were distributed on the higher planes of the basin. This was probably an indication that there was plenty of grazing area outside the basin.

However, as the period changed, wildebeeste moved into the basin and distribution was mainly on the open alkaline grasslands especially on S. marginatus. Few herds of wildebeeste were observed to graze in open A. xathophloea woodlands where the ground cover is mainly C. dactylon grass. There was progressive movements into the depressions and on the fringes of the swamps where the main grass was C. dactylon.

As an illustration of wildebeeste occupancy of pastures in the basin, occupancy for the month of February 1973 (Ref. Map in Appendix ii) show that 20% of wildebeeste population were grazing on S. marginatus, 6% on S. spicatus, 2.2% on S. homblei, 22.5% on C. dactylon, 15% on swamp pasture, 7.5% on the Lake (mainly sedges and S. consmilis), 17.5% in the woodlands, and 4% on other grasslands like O. jaegeri or in just in open bare areas.

March and April 1973: As the dry season advanced, occupancy build up was on mainly C. dactylon, swamp pasture and on the fringes of the dry lake bed and especially around lake couch. Grazing area was becoming limited and movements was towards the depressions with C. dactylon and towards the swamps. The use of these areas was not only because of availability of graze but also the presence of water was an added attraction. The alkaline grasslands were at this time dry and if there was any vegetation at all, it was mature, in clumps and with no leaf, and therefore unsuitable for wildebeeste. Cattle utilized similar areas, but in considerable numbers. The herd size of wildebeeste increased with the dry season.

May 1973: During the months of March and April there was some rain (Fig.4, Chapter I) enough to cause new growth of grass, and this resulted in the dispersal of wildebeeste and cattle from the basin. Only a few herds of wildebeeste were left scattered in the basin (Ref. Map, Appendix v). There was none grazing in the swamps. Grazing at this time was on the high planes of the basin.

June - October 1973: After the rains when wildebeeste moved into the basin, grazing was towards the swamps and finally concentration was mainly on C. dactylon and on swamp pastures. This continued from the months of June to October 1973 when there was a little rainfall. Cattle occupance was mainly on C. dactylon. However, observations showed that wildebeeste and cattle preference was similar and grazing was limited to these two pastures, although grazing was done on the lake mainly the sedges and S. consmilis grassland. There was very little utilization in the woodlands except for the western side of the study area where the distribution of smaller swamps and shed from heat attracted wildebeeste and cattle. Wildebeeste if found grazing in these areas were displaced by cattle.

These were critical months in the basin because, this is the peak of dry season, and there was continuous increase in biomass density /km^2 in the basin as the food resources continued to be limited. An indication of limited food resources was shown by the high mortality in cattle within the entire Amboseli ecosystem, Western and local residents (personal communications).

November and December 1973: There was short spell of rainfall for these two months. Wildebeeste were distributed within the basin and some moved to graze in high areas of the basin or completely outside the basin. Compared to the month of October 1973, 45% of wildebeeste which had utilised the basin dispersed to the wet season ecosystem.

January and February 1974: Within a short time after wildebeeste moved out of the basin, concentration started to build up in the basin. The situation was different from occupancy of 1973, and wildebeeste and cattle moved directly into the swamp pasture, C. dactylon and on the fringes of the dry lake bed. It appeared that the November-December rains were not enough to effect the growth of alkaline grasslands.

If there was any growth at all, either it was grazed down or dried out before animals moved into the basin. Data on population shows that there was an increase of over 50% of wildebeeste and cattle population in the basin, all concentrated in either the swamps or on C. dactylon grassland. Available grazing area had not changed which had limited as the dry season advanced. There was little rain during these months, but not enough to effect any vegetation growth.

March 1974: Fig. 4, Chapter I shows that there was good rainfall during the month of March 1974. The situation in the basin changed, from dry, almost semi-arid to lush and green vegetation. This coincided with the calving peak in wildebeeste. And a large proportion of the entire grazing community dispersed from the basin. An indication that there was little use of the basin was shown by the increase in leaf and culm heights (Ref. Table 7) and a drop in wildebeeste population (Refer to Table 2a, Chapter II)

9.2 Herbage intake: Having discussed seasonal pasture use in the basin (Ref. Sec. 9.1), it was important to estimate offtake of herbage by the grazing herbivores in the basin. Results of herbage intake was based on the date from primary productivity, indicating what was available to the grazing herbivore, and the biomass of grass sampled outside the exclosure. The difference in biomass of grass in the exclosure and outside was the amount of herbage consumed. Fig. 17 clearly illustrates these differences except for S. spicatus and S. homblei which had very lettle differences in weight that calculations of herbage would not indicate any meanful results. But however, there was some grazing on these swards as discussed (Sect. 9.1). I therefore decided to calculate herbage intake of C. dactylon and S. marginatus grasslands which were important to the grazing community in the basin apart from the swamp pasture. There were technical difficulties in setting up exclosures in the swamp for estimation of herbage intake.

Usually intake is calculated using the following criteria as explained above:

Intake = biomass of herbage inside exclosure - biomass outside exclosure.

However, this formula may either under or over estimate herbage intake, and therefore Linehan et. al., (1952) proposed a correction formula used in the calculation of herbage intake.

Intake = (a-b) x Log(c) - Log(b)/Log a - Log b

a = Biomass of herbage outside exclosure previous month

b = Biomass of herbage outside exclosure following month

c = Biomass inside

Therefore intake of S.marginatus was 916.40 kg/ha/annum as compared to 1019.8 kg/ha/annum, (Ref. Sect. 8.1) available to the grazing herbivore, whereas intake of C. dactylon, was 7744.80 kg/ha/annum of herbage compared to 8044.0 kg/ha/annum available to the grazing herbivore in the basin.

9.3 Grazing efficiency: Results on primary productivity and herbage intake are very important in the management of the habitat and the food resources available to the grazing herbivore (Eadie, 1969). The efficiency of pasture use of mainly these two pastures can therefore be assessed as follows:-

$$\text{Grazing efficiency} = \frac{\text{Herbage intake}}{\text{Pasture production}} \times 100$$

In the case of S. marginatus grazing efficiency was 96.28% and C. dactylon 89.93% based on the above data.

9.4 Changes in vegetation; Western and Van Praet (1973) have shown that salinity in Amboseli is the main casue of changes in the basin. They conclude that the dying A. xathophloea trees are being replaced by a bush S. monoica resistent to salinity. The results of A. xathophloea analysis are shown in Table 8. Observation from the data indicate that:

1. There was a progressive increase in the number of dead trees from the edge of the basin (Transect 5) to the centre of the basin (Transect 1 and 2). There was a similar increase in the number of clumps of S. monoica (S. monoica was found to be inversely correlated with A. xathophloea based on my data ($r = -0.95$ $p < 001$).

2. The basin edge woodlands transects 4 and 5 showed that the area suffered least loss of trees and as tabulated (Table 8) there was regeneration of young A. xathophloea. This area (Transect 4 and 5) is outside the stock free area in the centre of the basin.

These findings confirm the results of Western and Van Praet (1973) that essentially salinity increases from the centre of the basin to the edge of the basin. The fact that A. xathophloea are dying and being replaced by S. monoica is illustrated by reference to Plates 2a and 2b taken in the basin during the period of study 1973.

TABLE 8 *A. xathophloea* Tree Evaluation

TRANSECT.	*A.xathophloea* Alive	Fallen	Dead	*Sueda monoica*	*A. tortilis*	Young *A.xathophloea*	Comments
1	3	37	14	195	-	-	One alive *A.xathophloea* tree fell on 23.10.73. There was grass as an undercover.
2	14	39	20	218	1	-	*A. tortilis* and *A.xathophloea* which were alive had been debarked by elephants. No grass as an undercover.
3	5	70	26	358	2	-	One *A.xathophloea* tree which was alive fell on 15.9.73. There was no grass except during the rains.
4	56	6	2	40	-	8	All alive *A.xathophloea* trees had been debarked by elephants, and only a few young branches had been broken off.
5	44	10	6	6	1	75	The main grassland here was *C. dactylon*. Few trees had been debarked by elephants.

Plate 2a (above) notice the bare saline areas and the sueda monoica bush wíthin the woodland.

Plate 2b (below) notice the dead, fallen A. xathophloea trees. Some of the trees near to the camera showed signs of drying possibly as a result of salinity.

9.5 Ecological density: As a reflection of pasture use in the basin, the densities of wildebeeste and cattle are presented in Table 9 based on the numbers (Table 2 and 2a) and the available grazing area. Of the total area of the basin, only 68% was utilized for grazing during the wet months, but reduced to 45% during the peak of the dry season. The results therefore show seasonal fluctuations in density/km^2 in respect to the area which was available for grazing. The densities are particularly high during the dry season months June to November, an indication that grazing area was becoming restricted as the dry season advanced. This may also indicate that of the available grazing area, wildebeeste and cattle may have had similar grazing preference. However, data from primary productivity (Fig. 17) and habitat use (Ref. to Grazing calendar in this chapter) indicate that grazing was infact restricted to *C. dactylon* grassland and the swamp pasture.

TABLE 9 - Ecological density of the available grazing area

	1973											1974		
MONTHS	1	2	3	4	5	6	7	8	9	10	11	12	1	2	3
Wildebeeste	1	8	12	13	2	8	13	21	21	23	10	9	20	20	10
Cattle	-	20	23	25	10	52	54	71	85	110	50	27	88	110	44

CONDITION OF WILDEBEESTE

In the previous sections of this Chapter, I have demonstrated that grazing area in the basin was becoming restricted with advancement of the dry season. It was therefore important as discussed (Sect. 7.5, ChapterIII) to relate the physiological response, in terms of seasonal trend in fat reserves of wildebeeste and cattle to the limited food resources.

The results of condition of wildebeeste (Fig. 19) for both male and female illustrate that there was a gradual deterioration of condition from good to very poor condition. Assessment of fat reserves when wildebeeste move into the basin show that 10% females and 20% males were in good condition. At the middle of the dry season, in the months of July, August and September 1973, 5% females and 8% males were in good condition. At the end of the dry season, when calving started, none of the females were in good condition. 83% were in poor condition and 11% were in very poor condition. In males, 2% in good condition, 56% in poor condition and 2% in very poor condition.

While there was deterioration in the condition of wildebeeste, there were high incidences of cattle die-offs not only within the basin, but in the entire Amboseli ecosystem. Over 40% of cattle population were considered to have died in the entire Amboseli ecosystem - (Western personal communication). Few observations were however made on wildebeeste die-offs (Ref. Sect. 4.4, Chapter II).

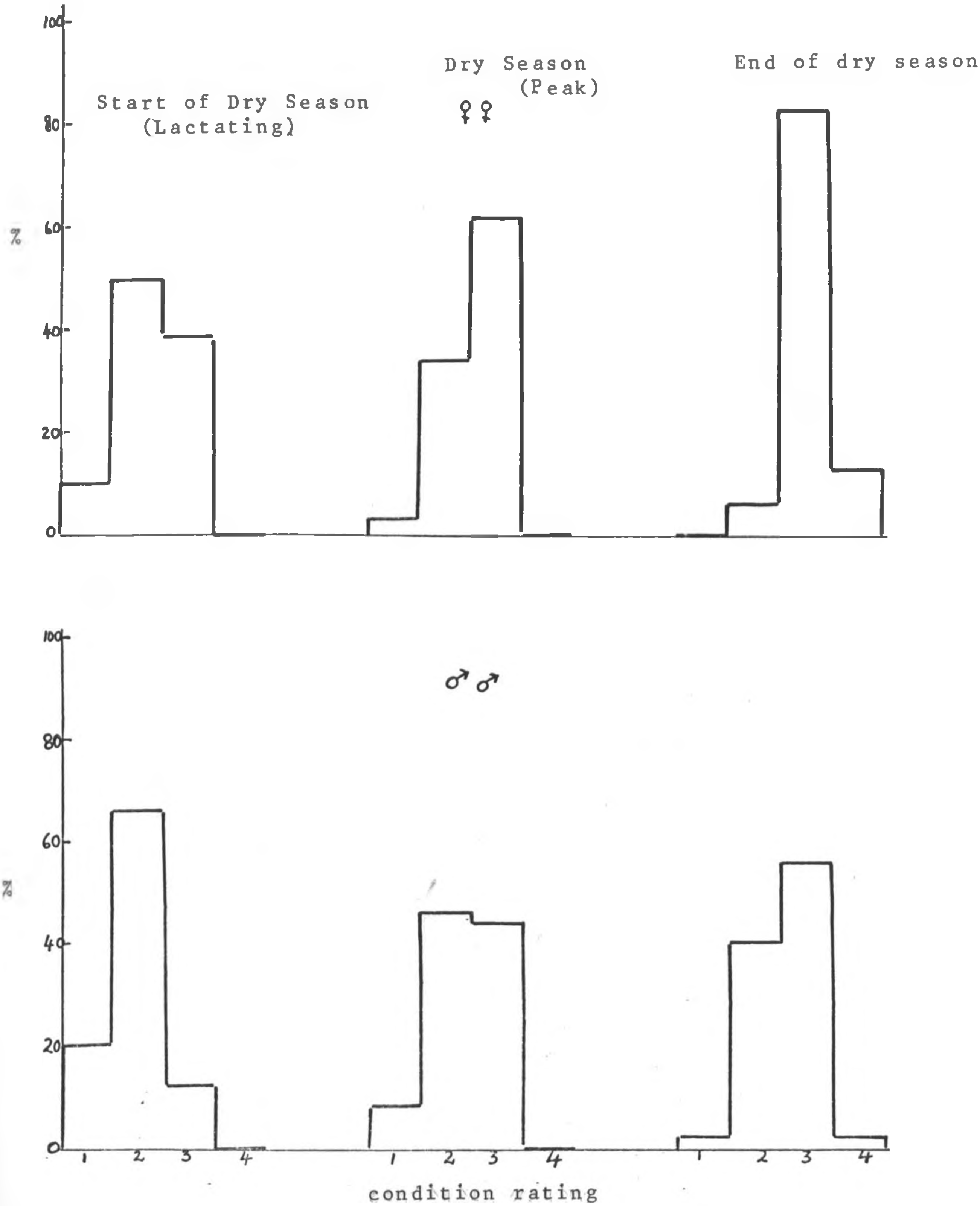
Possibly other than disease, it was clear that cattle may have possibly died because of starvation as a result of limited food resources.

FIG, 19 Seasonal condition of wildebeeste in the basin, where

1	=	condition	rating	as	Good
2	=	"	"	"	Fair
3	=	"	"	"	Poor
4	=	"	"	"	Very Poor.

FIG, 19 Seasonal condition of wildebeeste in the basin, where

1	=	condition	rating	as	Good
2	=	"	"	"	Fair
3	=	"	"	"	Poor
4	=	"	"	"	Very Poor.


Start of Dry Season (Lactating)
Dry Season (Peak)
End of dry season
♀♀
♂♂
%
100
80
60
40
20
0
1 2 3 4
condition rating

INTERSPECIFIC COMPETITION

Far from these physiological changes in wildebeeste and cattle die-offs in response to limited food resources and any other adversity, it was possible that either wildebeeste or cattle may have been grazing at the disadvantage of each other. Both wildebeeste and cattle were observed to graze on C. dactylon grassland and swamp pasture at the peak of the dry season. And although quality measurements were not performed in the case of swamp pasture, it was assumed that C. dactylon grassland was a better pasture than the swamp pasture. This assumption was supported by a number of factors:

(i) C. dactylon was productive all the year round including the dry season (Ref. Fig. 17).

(ii) There was continuous grazing on this sward resulting in new growth. And since it is a high water table grassland (Ref. Chapter I) it was likely to continue producing new growth even during the dry season. This is one of the qualities of good grassland. The grassland was leafy as well as being of high production over a prolonged season of the year (Raymond 1948, and William 1950). Consequently there was high concentration of wildebeeste and cattle on this sward at the time of stress (Refer to Grazing Calendar, ChapterIII).

(iii) Fig. 18 shows that there was more leaf on this sward than any other major grassland in the basin during the dry season. It was therefore possible that since grazing herbivores tend to select for leaf than stem (Arnold 1962, Gwynne and Bell 1968) both cattle and wildebeeste could have been selecting for leaf than stem from this sward.

(iv) Table 6 supports the fact that of the major grasses in the basin, C. dactylon was a high quality grass at the time of stress during the months of August, September and October 1973. Bogdan (1958) recognised that C. dactylon was one of the valuable grasslands to grazing herbivores during the dry season.

Lamprey (1963) showed that grazers tend to eat the same grass species in the same proportions if they feed in the same grassland type. This was possibly true in the basin when wildebeeste and cattle were feeding on C. dactylon grassland. This may have been true because cattle were observed to 'displace' wildebeeste from C. dactylon grassland, and no other explanation could have been given other than selectivity was similar for both cattle and wildebeeste. It was also observed that at the peak of the dry season, the wildebeeste changed their feeding strategy. Although data was not collected on activities, it was observed that wildebeeste sometimes grazed at night and very early in the morning before cattle moved into the basin. Usually cattle were directed to the Masai 'bomas' in the evenings and it was at this times that wildebeeste moved into C. dactylon grassland for grazing. In most cases following the 'displacement effect', wildebeeste were either in bare areas standing or grazing on poor pastures like S. cosmilis or on dry mature grasses. This displacement effect was only achieved when cattle moved into the basin on C. dactylon grassland where wildebeeste were usually grazing.

Sinclair (1970) has stated that if an encroaching species A, incidentally ate an amount of food in passing through the habitat of B, where food was limited, then species B will be competing with species A for that resource. In the basin cattle were observed to encroach and 'displace' wildebeeste from _C. dactylon_ grassland; it is quite true that competition for food between cattle and wild ungulates is a recurring subject for discussion (Field et. al., 1973) and even within wildlife ungulates (Sinclair, 1970).

For competition of food resources to be taking place between the competitors, certain conditions must be operating:

(i) Similarity in the requirements of the resource
(ii) Limited food resources

Rogerson (1966) has shown that the energy requirements for cattle and wildebeeste were relatively similar e.g. the digestibility coefficient of wildebeeste was close to that of cattle and the proportion of food utilized as metabolisable energy, 50.8% was similar in both cases. Similarly the utilization of metabolisable energy for maintenance, 82% of wildebeeste was similar to that of cattle.

In the basin I have demonstrated that food resources were limited evidenced by high incidences of cattle die-offs, and the gradual deterioration in condition of wildebeeste, particularly at the peak of the dry season. Both wildebeeste and cattle were in most cases concentrating on _C. dactylon_ grassland, and possibly both had similar selectivity for plant parts. It was therefore possible that cattle and wildebeeste were competing for the same resource at the time of stress.

DISCUSSION

Amboseli basin has a bimodal distribution rainfall (Fig. 4, Chapter I) the long rains of March-May, and the short rains of November and December. In discussing pasture use in the basin (ChapterIII), wildebeeste and cattle were observed to concentrate in the basin only during the dry months. They would disperse from the basin in the rainy months. It then appears that either the concentration or the dispersal mechanisms were in response to some ultimate factors caused by seasonal changes. These ultimate factors were: availability of food resources, seasonal availability of water and seasonal drought conditions. This infact is the case when considering pasture use in the basin during the dry season.

And although these conditions also prevailed in the basin during the rainy months, grazing herbivores dispersed. It was likely that dispersal from the basin was probably because the wet season ecosystem was offering better pasture in terms of growth stages and hence good quality as argued by Gwynne and Bell (1968) and Bell (1969). And since the dry season grazing resulted into limited food resources (Sect. 9.5, Chapter II) it was likely that dispersal from the basin was because of superabundance of food resources in the wet season ecosystem. It is thus clear as a result of seasonal changes, a mechanism is created by which grazing animal community evens out grazing pressure from the basin to allow rest period for basin grasslands to be utilized in the next dry season. It is therefore invariably clear that the seasonal use of the basin grasslands was conditioned by rainfall.

The pattern of pasture use in the basin was shown to be facilitative as discussed by a number of ecologists, e.g. Vesey-FitzGerald (1960), Gwynne and Bell (1968) and Bell (1969). However, in the basin temporal and spartial sequence of grazing was created for the animals to survive through the prolonged dry season.

It was most likely that the pattern of pasture use in the basin was governed by a number of factors: growth stage and maturity of grass (Table 7) quality (table 6) and availability in terms of productivity (Fig. 17 and Sect. 8.1, Chapter III). And if it is true that grazing ungulates select for leaf in preference to stem or sheath as argued by Arnold (1962), Gwynne and Bell (1968) and Bell (1969), then leaf, stem and sheath analysis of grazed pastures (Fig. 18) and occupancy data (Sect. 9.1, ChapterIII) support the argument that wildebeeste and cattle grazing in the basin was in response to the proportion of leaf, stem and sheath in the pastures. Wildebeeste and cattle would move into pastures with more leaf than either stem or sheath governed by time and space. A number of other factors have been known to influence animal preference for species of grass, e.g. presence of silica bodies, as suggested by Field (1968), fibre content and mechanical properties of grass suggested by Gwynne (unpublished). These latter factors probably explain the fact that S. spicatus and O. jaegeri grasslands were hardly grazed by wildebeeste and cattle (Sect. 9.1, ChapterIII). This was also supported by their physical structure (Sect. 2.3.1, Chapter I).

There are evidence that when wildebeeste moved into the basin occupance was mainly on S. marginatus with progressive increase in use of C. dactylon and the swamp pasture. In fact as the dry season progressed, wildebeests, followed by cattle showed increased occupancy on C. dactylon. Both these grasslands have been recognised as high quality grasses favoured by grazing herbivores (Bogdan, 1958). And far from factors mentioned above, preference for these two species seemed to be apparent in the basin.

As the dry season advanced, it became apparent that both wildebeeste and cattle were responding to the changes in the available grazing area. Certainly the size of grazing groups increased and grazing was in most cases restricted to sedges and C. dactylon. But of these C. dactylon was probably a better pasture and hence increased grazing.

Apart from increased grazing groups, a marked phenomena in response to the available grazing area, was a change in the condition of wildebeeste (Ref. Fig. 19). The overall seasonal trend in fat reserves for both male and female wildebeeste decreased as the dry season progressed. There were however marked differences in condition of both sexes. Probably this was expected because of seasonal physiological demands of each sex. For example during the rut, the male was in a reasonable good condition compared to the female. Condition of pregnant female progressively fell either because of poor nutrition or has to cater for the foetous as well as its own energy requirements. On the other hand lactating females were generally in poor condition. Far from these expected reaction to nutritional changes, it was possible that wildebeeste were reacting to climatic variations and may be disease as well. It was not possible to evaluate condition during the rains, however, it was assumed that with new growth in vegetation, presumably condition index improved.

Due to differences in physiological demands of each sex, it was observed that pregnant females were segrated from the males. The pregnant females were generally distributed on better pasture in this case mainly C. dactylon and the males on the lake grazing on the sedges mainly C. laevigatus. However, this was not always the case, but this suggested some form of response on the part of male wildebeeste the limitation of available grazing area. They were however, fewer males in areas which were grazed by females.

Another very marked reponse to the changes in available food resources was the 'displacement effect' demonstrated by cattle to wildebeeste. This was observed mainly on C. dactylon grassland. Wildebeeste were generally displaced on poor pastures. This was an indirect form of competition. A number of arguments have been discussed in the general use of the word 'competition' by ecologists (Andrewartha and Birch, 1954) and in my case I have used it to mean the sharing of a limited resource by grazing herbivores at the disadvantage of one or both of them. I this case cattle were sharing the available grazing area at the disadvantage of wildebeeste. However, one may argue that cattle were dying in great numbers whereas minimal numbers of wildebeests died, and therefore it should be wildebeeste competing with cattle for the limited resource. On the other hand if we believe that cattle were dying presumably as a result of starvation, and hence a mechanism of population regulation, then cattle were competing with wildebeeste in the basin for the limited food resource. Possibly cattle were dying density-dependently. It has long been a problem to demonstrate competition between livestock and wild game (Field et.al., 1973) or for that matter within wild game

(Lamprey 1963, Talbot 1966, Gwynne and Bell 1968 etc. although Sinclair (1970) has demonstrated competition between wildebeeste and buffalo in the Serengeti National Park. Competition between wildebeeste and buffalo in the basin was probably avoided because of different niches utilized by these two species of animals.

There were also evidences that wildebeeste were responding to changes in the available food resources possibly as a result of displacement effect by cattle, it was noticed that they changed their feeding strategy. Wildebeeste were noticed to graze in evenings and sometimes at night after cattle had been moved away to the bomas. This was evident from occupancy data since cattle were utilizing similar niches with wildebeeste. Arnold (1962) has however demonstrated that grazing in sheep was performed at night as a result of limited food resources and Jewell (personal communication) contended that ungulates continued grazing at night in response to possibly limited food resources. I realise the inadequacy of raw data to support my argument that wildebeeste grazed at night in response to limited food resource but based on personal observations, this could probably have been the case in the basin at the peak of the dry season.

Optimum utilization of some of the basin grasslands by grazing herbivores was indicated by grazing efficiency of 96.28% on S. marginatus and 89.93% on C. dactylon grasslands.

Bias and Errors: There were a number of biases and errors in determining pasture use on the basis of distributions, primary productivity, quality of grasslands, and changes in the vegetation. Some of the biases and errors have been discussed in the thesis.

(i) Distributions:- It was possible that there were some bias in placing correctly grids occupied by wildebeeste and cattle. This was particularly so in the open grasslands which had no features other than roads. Consequently there must have been an error in determining the boundaries of various grasslands.

(ii) Primary productivity:- In determining primary productivity more than one exclosures could have been placed in each grassland as a measure of avoiding bias. But one was faced with a situation where the basin being a major tourist attraction, some of the exclosure would have been interfered with or somehow carried away by the local residents - Maasai. In some areas like the swamps it was a matter of technicalties. May be the exclosure could have been large enough to have more samples, but again the basin being a small area, one would have been faced with obstructuon or may be the exclosures would have been destroyed by large herbivores like elephants. Biases in calculating herbage intake could probably have avoided by moving exclosures more frequently in the grasslands at different times. But in this case the area of study could have created a problem in itself.

It was possible for mechanical biases from the physical difficulty, of clipping to a low level comparable to grazing of wildebeeste or cattle. In a majority of cases clipping gives higher estimate of intake although in this thesis a correction factor was used in the calculations (Sect. 9.2, Chapter III).

A normal decline of herbage weight following maturity (clipped outside at the height of dry season) was a loss of forage that may have falsely been attributed to grazing and hence a possibility of error in the calculations of herbage intake.

(iii) Quality:- The biases and errors as regards crude protein and crude values were briefly discussed in the thesis (Sect. 8.3, Chapter III). The biases and errors are attributed largely due to sampling techniques. More samples of grasses were needed from which a mean value could have been determined to avoid biases.

(iv) Changes in vegetation:- It was difficult to expect any marked changes in vegetation of Amboseli basin in 15 months of study work. And although efforts were made to determine this aspect of habitat ecology, it was inaccurate to rely wholly on mortality of A. xathophloea and S. monoica as indicators of habitat changes in the basin. There were changes in the grass species composition possibly as a result of grazing intensity, stampeding by vehicles, salinity of the basin and these factors needed to be evaluated to determine the form of habitat changes in the basin. The use of satellites has been known to be an accurate method of determining vegetation changes. Possibly this is an aspect that needs further attention in the basin.

(v) Condition of wildebeeste:- Personal judgement of whether wildebeeste was in good or very poor condition must have contributed to the bias in the assessment of condition. The advantage of this method have been discussed in this thesis (Sect. 7.5, Chapter III). Perhaps another bias in this visual assessment of fat reserves was that no consideration was attached to the age of the animal. Possibly disease, other than response to limited food resources could have been a contributing factor in the bias in the assessment of condition.

CHAPTER IV

GENERAL DISCUSSIONS AND CONCLUSIONS

It should now be apparent from previous discusssions that density-dependent factors were probably operating on wildebeeste and cattle populations. There are suggestive evidences that this was the case in the basin. The results on incidences of mortality by predation, or even by disease on wildebeeste,and cattle by starvation were probably induced by density-dependent factors.

The evidence available (Chapter II) indicated that there were some seasonal biases in wildebeeste mortality. It was indicated that increase in mortality during the dry season was related to the increase in density of both the prey and predator (Sect. 4.4, Chapter II). The main predator was observed to be lion. Data on mortality therefore suggest that mortality on wildebeeste was operating density-dependently.

Differential mortality, heavier on males than females is suggested by the results, and this seems to be apparent in other wildebeeste populations e.g. Talbot and Talbot (1963), Watson (1967) and Hirst (1969). It is not however, understood whether this was circumstantial on the part of predator or prey, however, Klein (1969) on differential mortality in deer suggests that this was usually the case when populations outgrow their food supply, and they either stagnate or decrease in number. This could probably be the case in the basin as evidenced by limited food supply (Chapter III).

The other evidence of operational density-dependent factor was suggested by incidences by cattle die-offs during the 1973-74 drought (Fig. 4, Chapter I). Due to limited food resources, it was probable that cattle were dying because of starvation.

Varley (1969) however, argues out that starvation has a variety of effects on population dynamics that may not be density dependent. He sights cases of available food supplies are different in different seasons and hence incidences of starvation are not density dependent, but produces big population changes which are not related to density. In the basin, there were incidences of starvation related to the population density and the available food resources resulting into cattle die-offs. While it is true according to Varley (1969) seasonal changes bring about variations in food supply, certainly incidences of catastrophic mortality may be a 'key factor' in determining population changes.

Fig. 15 in Chapter II suggests quite clearly that there were high incidences of juvenile and adult mortality in the Amboseli wildebeeste. It is quite possible there would be yearly recurring fluctuations in juvenile and adult mortality and these would result in the population regulation of Amboseli wildebeeste.

One particular criterion has been used in this thesis to suggest wildebeeste response to limited food resources. This is evidenced in Chapter III and illustrated with reference to Fig. 19. Results on mortality however, suggest that only 2.6% of recovered carcasses were considered to have probably died of starvation.

These examples as suggested in this thesis probably indicate that density-dependent factors were operational in the basin as a measure of population regulation.

Thus when cattle or for that matter livestock are barred from using the basin, and with the changing conditions of available food resources, wildebeeste population will probably be regulated density-dependently to reach an equilibrium balance.

The main conclusions emerging from this thesis based on data collected for 15 months are: Population fluctuations in the basin are governed by rainfall and food supply, There are evidences of density-dependent factors operating on population regulation of wildebeeste and cattle,

Management: Having discussed the relationship between wildebeeste, cattle and the vegetation changes in the basin, a reasonable approach to management policy in the basin would be in the conservation of the habitat. I would recommend the following steps to be taken:-

i, A strict control in the number of vehicles using the basin at any one time. Probably the authorities concerned should introduce organised game viewing whereby visitors on arrival in the park use park vehicles large enough to accommodate a number of visitors. This may be a source of revenue for park, Visitors or tour operators will be required to hire the vehicles.

ii, Number of roads in the basin should be limited and clearly defined, Strict by-laws should therefore be passed for drivers of the vehicles to keep to the roads,

iii, Further building of lodges and hotels in the basin should be stopped, This is because the present two main lodges at Ol Tukai might end up like a small town and with present increased labour force working in the lodges, it is probable that there would be a rise in human population around that area, This may not present the atmosphere for a park in natural surroundings.

iv. Evidence of swamp pollution should be investigated and if there are any, measures taken to remedy the situation, Swamps are in fact the life of Amboseli wildlife populations.

v. Feasibility surveys should be done within the basin for a possible re-routing water from the swamp to more drier areas of the basin. Hopefully, this will induce continuous vegetation growth during the dry season.

vi. More ecological surveys should be directed towards habitat research in terms of production, quality and results related to animal use. It may not be a bad idea to conduct research into introducing a grass species resistant to saline conditions but suitable for grazing.

But since these habitat changes are cyclic as suggested by Western (1973), may be the best management policy would be non-interference, hopefully that the right vegetation conditions will some day emerge as evidenced by seasonal use of the basin (in this thesis).

REFERENCES

ANDREWARTHA, H.G., and BIRCH, L.C. (1954) The distribution and abundance of animals. Univ. of Chicago Press, Chicago and London.

ANDREWARTHA, H.G. (1964) Introduction to the study of animal populations. 2nd Ed. Methuen. London.

ARNOLD, G.W. (1962) Factors within plant associations affecting the behaviour and performance of grazing animals - Grazing in Terrestial and Marine environments (Ed. by D.J. Crisp) pp. 133-154. Blackwells. Oxford & Edinburgh.

BAILEY, N.T.J. (1959) Statistical methods in Biology E.L.B.S. edition. Printed in Great Britain.

BELL, R.H.V. (1969) The use of herb layer by grazing ungulates in the Serengeti - Animal populations in relation to their food resources (Ed. by A. Watson) pp. 111-123. Blackwells. Oxford & Edinburgh.

.... GRIMSDEL, J.R., Van LAVIERE, L.P. and SAYER, A.J. (1973) Census of the Kufue lechwe by aerial stratified sampling. E. Afr. Wildl. J. 11: 55-74.

BOGDAN, A.V. (1958) A revised list of Kenya grasses. Nairobi Government Printers.

BOULIERE, F. (1965) Densities and biomass of some ungulate populations in Eastern Congo and Rwanda, with notes on population structure and lion ungulate ratio. Zoo. Afr. 1: 199-207.

CHILD, G. (1972) Observations on wildebeeste die-offs in Botswana. Arnoldia 315: 1-73.

COWLISHAW, S.J. (1951) The effect of sampling cages on the yields of herbage. J. Brit. Grassld. Soc. 6: 179.

DEEVEY, E.S. (1947) Life tables for natural populations Quart. Rev. Biol. 22: 283-314.

DOUGALL, H.W. (1960a) Average nutritive values of Kenya feeding stuffs for ruminants. E. Afr. Agric. For. J. 26(1): 119-128.

.... (1963a) Average chemical composition of Kenya grasses, legumes and browse. E. Afr. Wildl. J. 1: 120.

ELTON, C., and MILLER, R.S. (1943) As ecological survey of animal communities with practical system of classification habitats by structural characters. J. Ecol. 42: 460-496.

ESTES, R.D. (1966) Behaviour and life history of wildebeeste (Connochaetes taurinus Burchell). Nature. London 212: 999-1000.

FIELD, C.R. (1968b) Methods of studying the food habits of some ungulates in Uganda. Proc. Nutr. Soc. 27: 172-177.

.... HARRINGTON, G.N., and PRATCHETT (1973) A comparison of the grazing preferences of buffalo (Syncerus caffer) and Ankole cattle (Bos indicus) on three different pastures. E. Afr. Wild. J. 11: 19-29.

FRASER, A.F. (1968) Reproductive behaviour in ungulates. Academic Press. London and New York.

GAUEHLEY, G. (1966) Mortality patterns in mammals. Ecology 47: 906-918

.... (1970) Fat reserves of Himayalan Thar in New Zealand by season, sex, area and age. N.Z. Jr. Sc. 13(2): 210-219.

GLOVER, J., DUTHIE, D.W., and DOUGALL, H.W. (1960) A table of estimates of nutritive values of ruminant feeds. E. Afr. For. J. 26: 117-118.

GRIMSDELL, J.J.R. (1973) Age determination of the African buffalo (Synceros caffer Sparmann) E. Afr. Widl. J. 11: 31-53.

GWYNNE, M.D. and BELL, R.H.V. (1968) Selection of vegetation components by grazing ungulates in the Serengeti National Park. Nature. London 220: 390-393.

GWYNNE, M.D. (Unpublished) Variation in the tensile strength of the leaves of some East African rangeland grasses. 2nd East African Wildlife Symposium.

HIRST, S.M. (1969) Predation as a regulating factor of wild ungulate population in Transyaal low veld nature reserve. Zoo. Afr. 4: 199-231.

JARMAN, P.J. (1974) Personal communication.

JEWELL, P.A. (1974) Personal communication.

JOLLY, G.M. (1969a) Sampling methods for aerial census of wildlife populations. E. Afr. Agric. For. J. 34: 46-49.

.... (1969b) The treatment of errors in aerial counts of wildlife populations. E. Afr. Agric. For. J. 34: 50-55.

KERWIN, M.L. and MITCHELL, G.J. (1971) The validity of wear-age technique for Alberta pronghorn. J. Wildl. Mgmt. 35: 743-747.

KLEIN, D.R. and OLSON, S.T. (1960) Natural mortality patterns of deer in south-east Alaska. J. Wildl. Mgmt. 24: 80-88.

KLEIN, D.R. (1970) Food selection of North American deer and their response to over-utilization of preferred plant species. Animal populations in relation to food resources. (Ed. A. Watson) pp. 25-46. Blackwells. Oxford and Edinburgh.

KRUUK, H. and TURNER, M. (1967) Comparative notes on predation by lion, leopard, cheetah and wild dog in the Serengeti area, East Africa. Mammalia 31: 1-27.

RINEY, T. (1955) Evaluating condition of free ranging red deer (Cervus elaphus) with special reference to New Zealand. N.Z.J. Sc. & Tech. 36 Sec. 13(5): 429-483.

.... (1960) A field technique for assessing physical condition of some ungulates. J. Wildl. Mgmt. 24(1): 92-94.

SADLEIR, R.M.F.S. (1969) The ecology of reproduction of wild and domestic mammals. Mathuen & Co. Ltd., London.

SERGEANT, D.E. and PIMLOTT, D.H. (1959) Age determination moose from sectioned incissor teeth. J. Wildl. Mgmt. 13: 315-321.

SEVERINGHAUS, C.W. (1949) Tooth development and wear as a criteria of age in white tailed deer. J. Wildl. Mgmt. 13: 195-216.

SINCLAIR, A.R.E. (1970) Studies on the ecology of East African buffalo. D. Phil. Thesis. Oxford University.

.... (Unpublished) On age determination of Serengeti wildebeeste.

MITCHELL, B. (1967) Growth layers in dental cement for determining the age of red deer. J. Animal Ecol. 36: 279-293.

NORTON-GRIFFITHS, M. (1973) Counting the Serengeti migratory wildebeeste using two stage sampling. E. Afr. Wildl. J. 11: 135-149.

PENNYCUICK, C.J. and WESTERN, D. (1972) An investigation of some sources of bias in aerial transect sampling of large mammal populations. E. Afr. Wildl. J. 10: 175-191.

PETRIDES, G.A. and SWANK, W.G. (1965) Population densities and range carrying capacity for large mammals in Queen Elizabeth National Park (Uganda). Zool. Afr. 1: 209-225.

RAYMOND, W.F. (1948) Evaluation of herbage for grazing. Nature. Lond. 161: 937-938.

ROGERSON, A. (1966) The utilization of metabolisable energy by wildebeeste. E. Afr. Wildl. J.4: 149.

.... (1968) Energy utilization by eland and wildebeeste. Symp. Zool. Soc. Lond. 21: 153-161.

TALBOT, L.M. and TALBOT, M.H. (1963) The wildebeeste in Western Masailand. East Africa Wildl. Monogr. 12: 1-88.

TALBOT, L.M. (1964) The concept of biomass in African wildlife research. Mammalia 28(4): 613-619.

VESEY-FITZGERALD, D.F. (1960) Grazing succession among East African game animals. J. Mammal. 41: 161-172.

.... (1965) The utilization of Natural pastures by wild animals in the Rukwa Valley. Tanganyika E. Afr. Wildl.J. 3: 38-48.

.... (1969) The utilization of buffalo in L. Manyara National Park. E. Afr. Wildl. J. 7: 131-145.

.... (1974) Utilization of grazing resources by buffaloes in the Arusha National Park. E. Afr. Wildl. J. 12: 107-134.

VARLEY, G.C. (1969) The concept of energy flow applied to a woodland community - Animal Populations in relation to food resources.(Ed. by A. Watson) pp. 389-405. Blackwells. Oxford & Edinburgh.

SINCLAIR, A.R.E. and DUNCAN, P. (1972) Indices of condition in tropical ruminants. E. Afr. Wildl. J. 10: 143-149.

SMITH, N.S. (1970) Appraisal of condition estimation of East African ungulates. E. Afr. Wildl. J. 8: 123-129.

SLOBODKIN, L.B. (1961) Growth and regulation of animal populations. Holt. Rinehart and Winsconsin. New York.

SPINAGE, C.A. (1967) Ageing the Uganda defessa waterbuck (Kobus defessa ugandae Neumann). E. Afr. Wildl. J. 5: 1-17.

.... (1973) A review of age determination of mammals by means of teeth with special reference to Africa. E. Afr. Wildl. J. 11: 165-187.

STEWART, D.R.M. (1966) Technique for studying the food preferences of grazing herbivores. Ph.D. Thesis. University of East Africa.

LAMPREY, H.F. (1963b) Ecological separation of the large mammal species in Tarangire Game Reserve. Tanganyika E. Afr. Wildl. J. 1: 63-92.

.... (1964) Estimation of large mammal densities, biomass and energy exchange in the Tanganyika Game Reserve and Masai Steppe in Tanganyika. E. Afr. Wildl. J. 2: 1-46.

LAWS, R.M. (1952) A new method for age determination in mammals. Nature. Lond. 169: 972-973.

LINEHAN, P.A., LOWE. J., and STEWART, R.H. (1952) The output of pasture and its measurement. J. Brit. Grassld. Soc. 7: 73.

LOWE, W.P.W. (1967) Teeth as indicators of age with reference to red deer of known age from Rhum. J. Zool. Lond. 152: 137-153.

MACFAYDEN, A. (1957) Animal ecology. Aims and methods. Sir Issac Pitman & Sons. London.

MILNER, C. and HUGHES, R.E. (1968) Methods for measurement of primary production of grassland. I.B.P. Handbook 6. Blackwells. Oxford & Edinburgh.

MITCHELL, B. (1963) Determination of age in Scottish red deer from growth layers in dental cement. Nature. Lond. 198: 350-351.

WATSON, R.M. (1967) The population ecology of wildebeeste (Connochaetes taurinus albojubatus (Thomas)) in the Serengeti. Ph.D. Thesis. University of Cambridge.

............, (1969) Reproduction of wildebeeste (Connochaetes taurinus albojubatus (Thomas)) in the Serengeti Region and its significance to conservation. J. Reprod. Fert. Suppl.6: 287-310.

.... (1969) Aerial photographic methods in census of animals. E. Afr. Agr. For. J. 34: 32-37.

WESTERN, D. (1973) The structure, dynamics and changes in Amboseli ecosystem. Ph.D. Thesis. University of Nairobi.

.... and Van PRAET, C. (1973) Cyclical changes in the habitat and climate of an East African ecosystem. Nature. Lond. 241: 106-106.

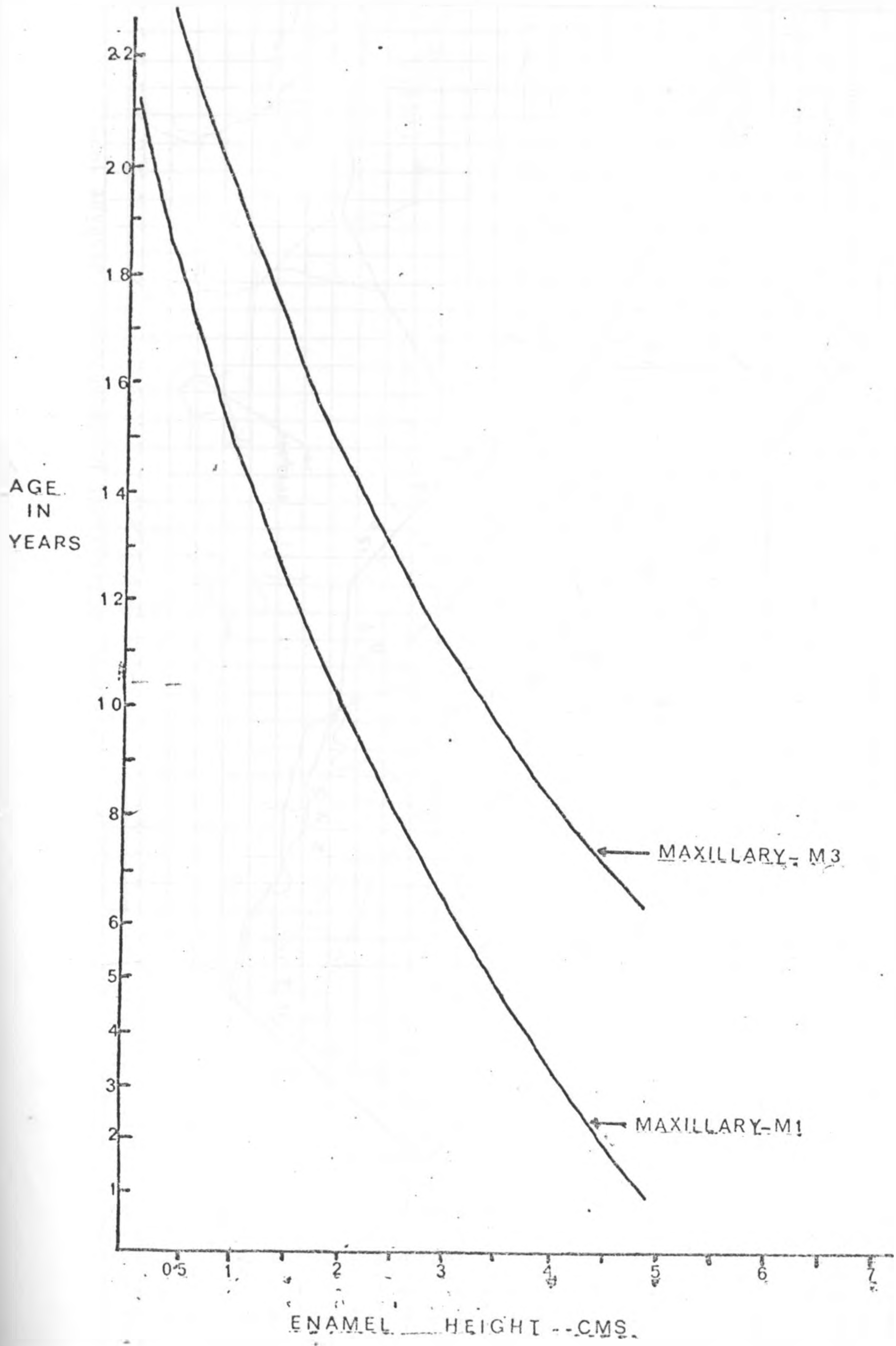
WILLIAMS, D. (1950) Quality in Grasslands. Nature. Lond. 166-760.

WILLIAMS, L.A.J. (1967) The Kilimanjaro Volcanic Rocks of the Amboseli area Kenya, Ph.D. Thesis, University of East Africa.

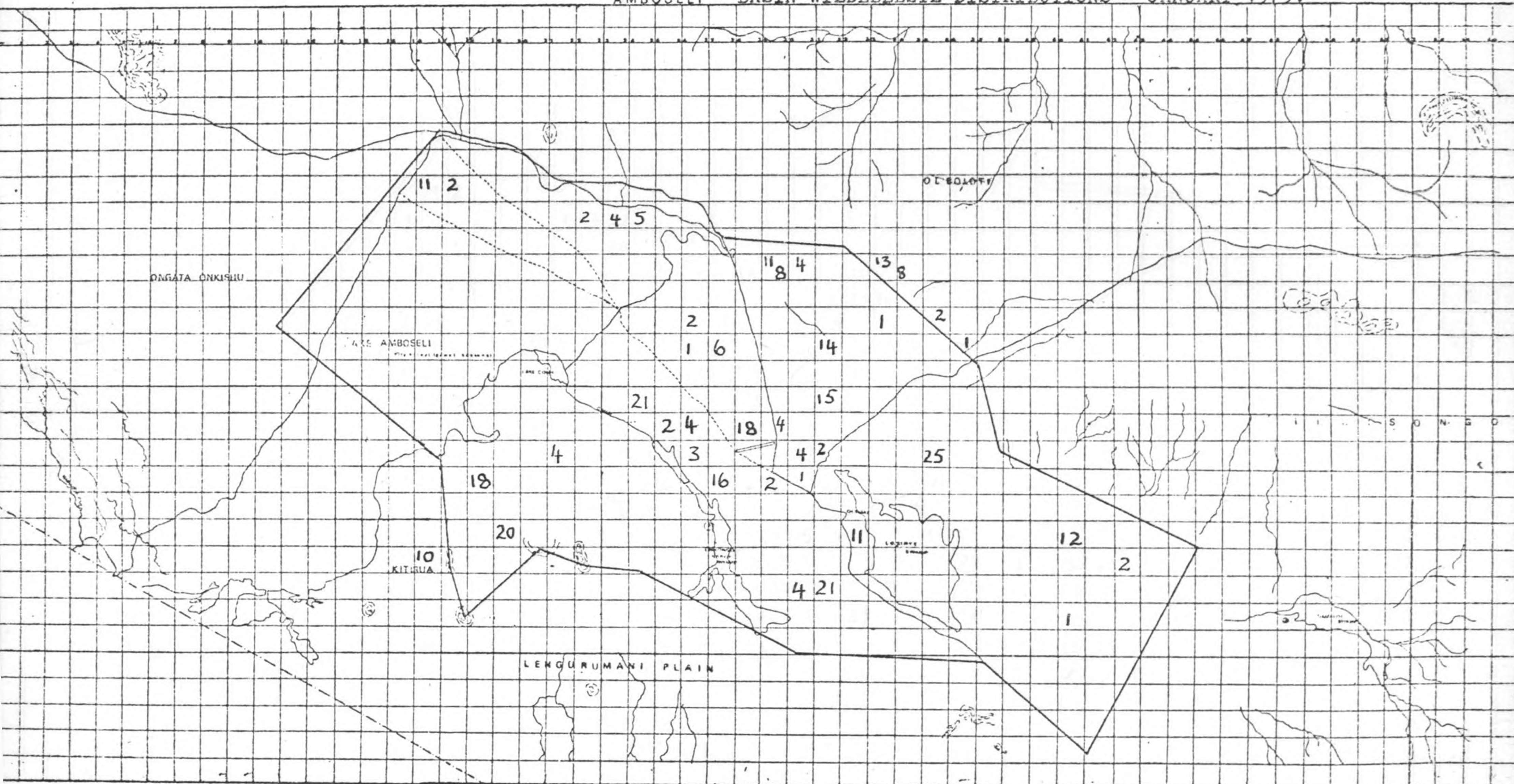
WYNNE-EDWARDS, V.C. (1962) Animal dispersion in relation to social behaviour. Oliver and Boyd. Edinburgh and London.

A P P E N D I C E S

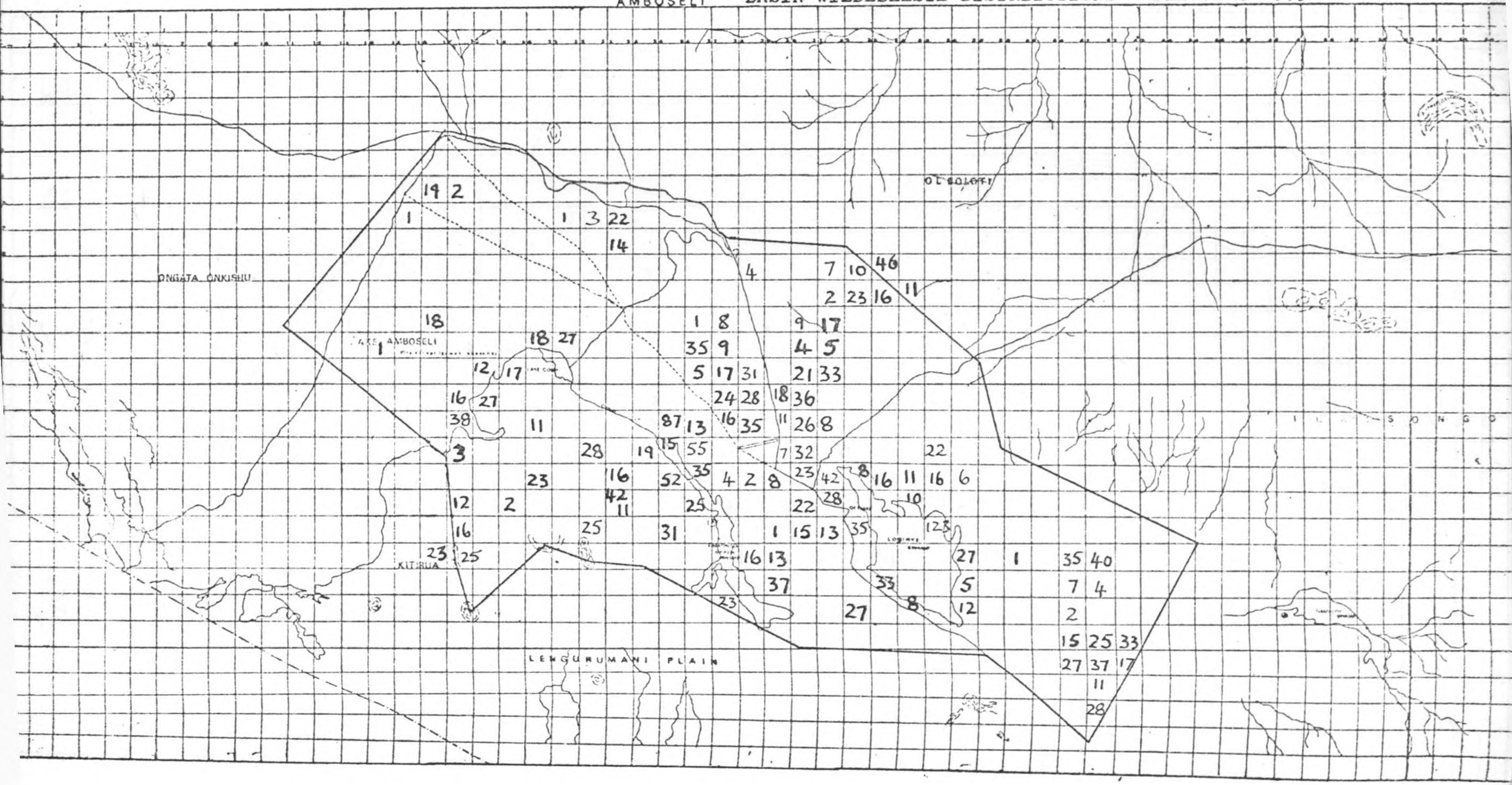
WILDEBEESTE AGEING
(SINCLAIR'S METHOD)



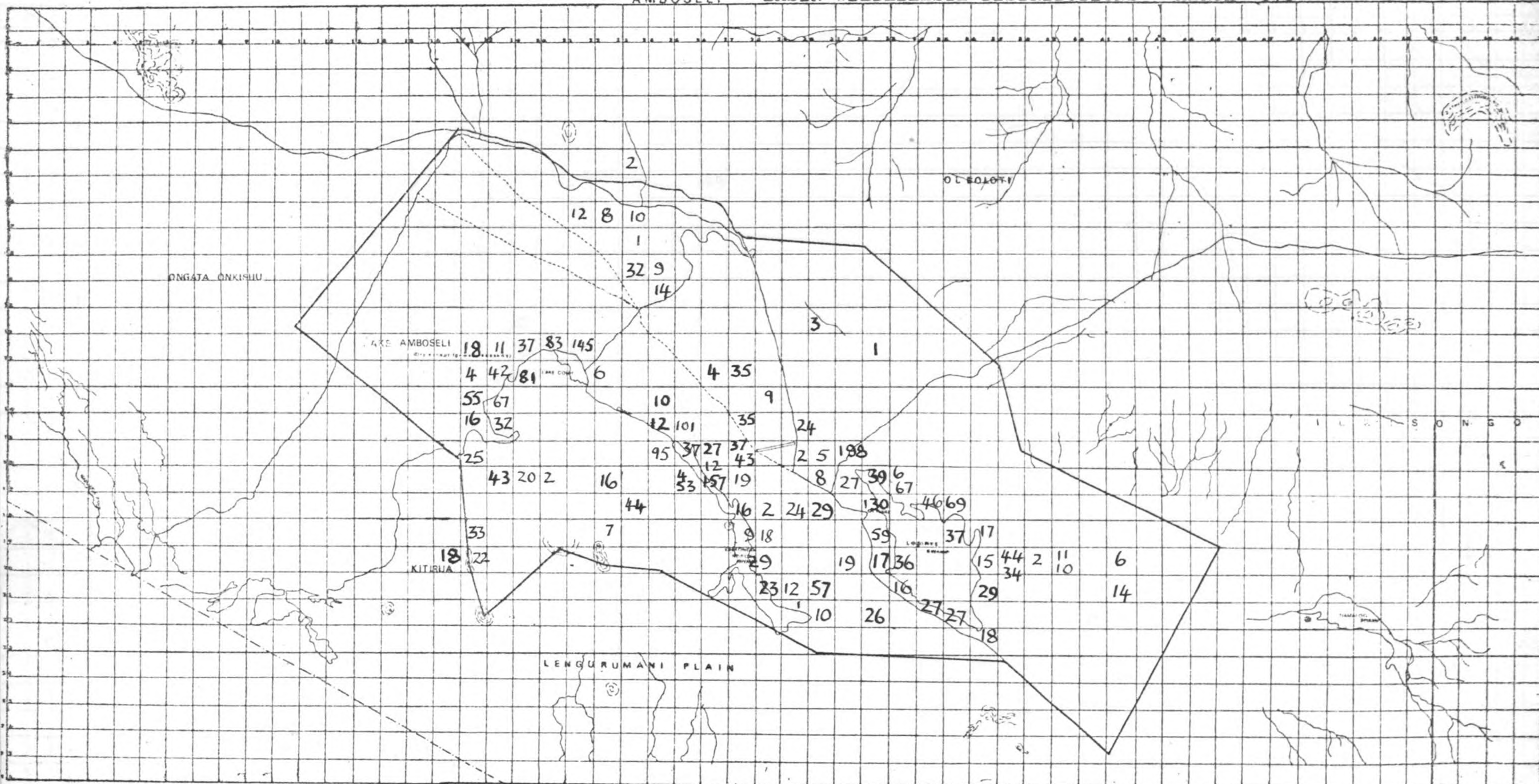
AMBOSELI - BASIN WILDEBEESTE DISTRIBUTIONS - JANUARY 1973.



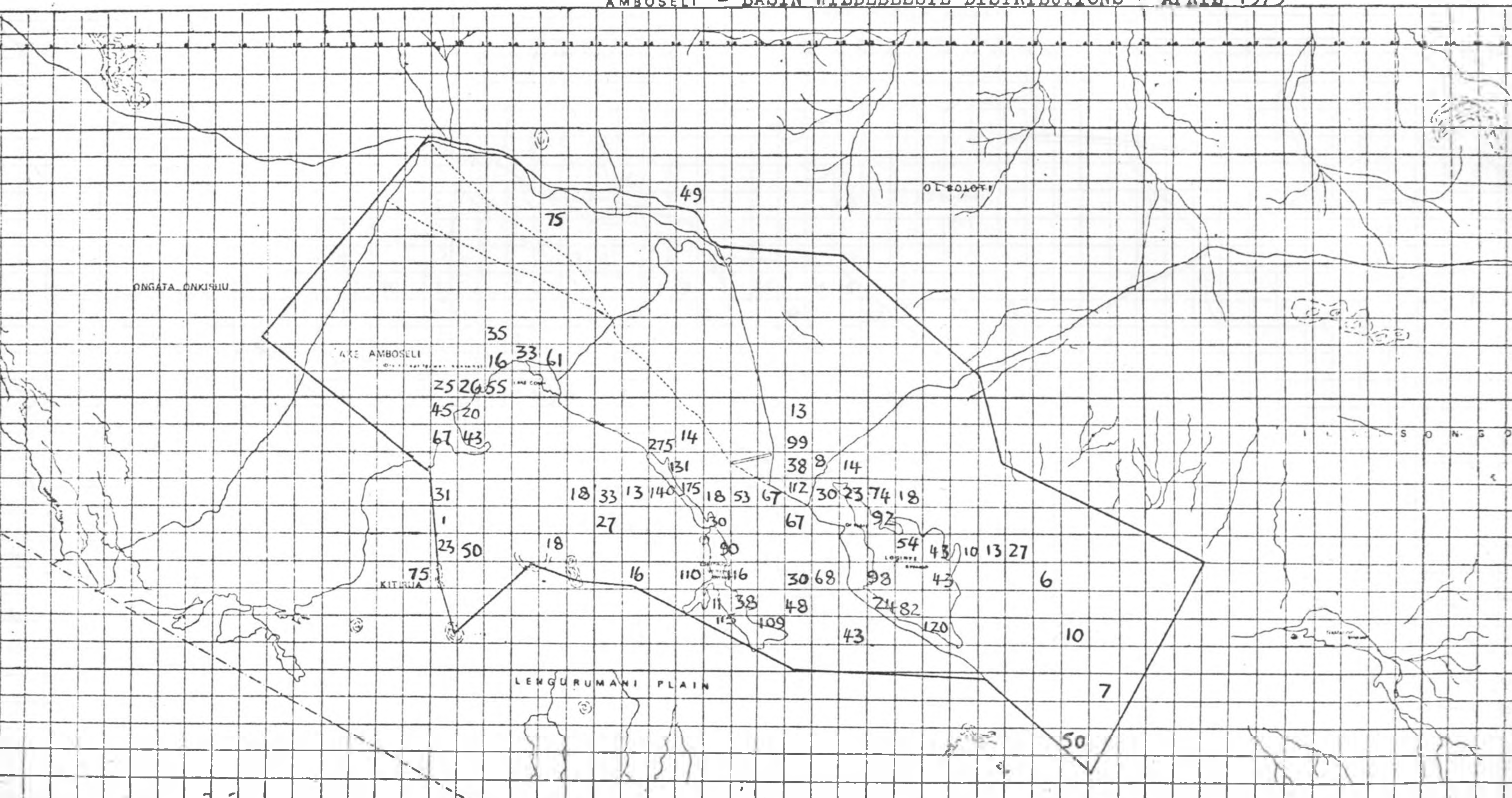
AMBOSELI - BASIN WILDEBEESTE DISTRIBUTIONS - FEBRUARY 1973



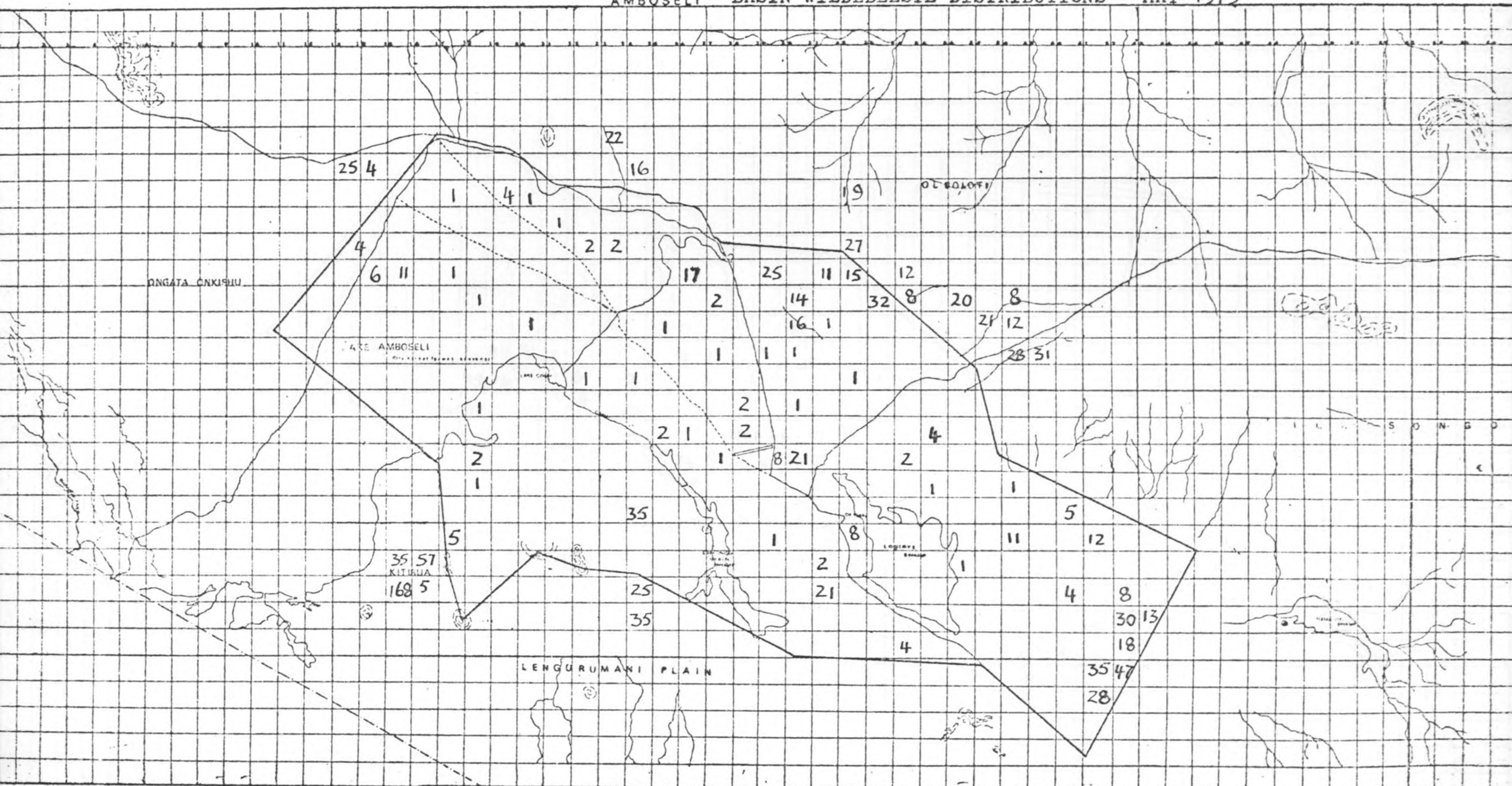
AMBOSELI - BASIN WILDEBEESTE DISTRIBUTIONS - MARCH 1973



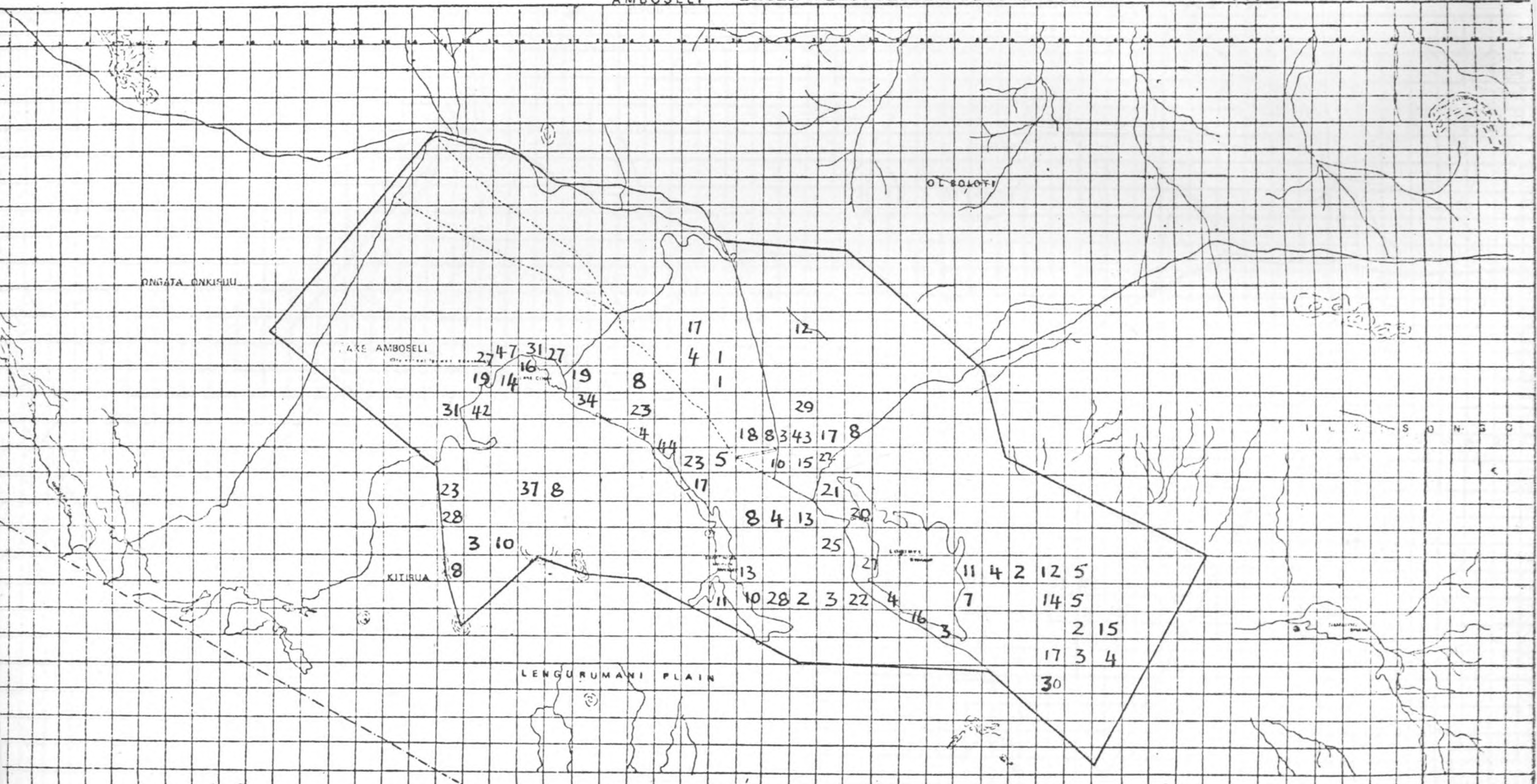
AMBOSELI - BASIN WILDEBEESTE DISTRIBUTIONS - APRIL 1973



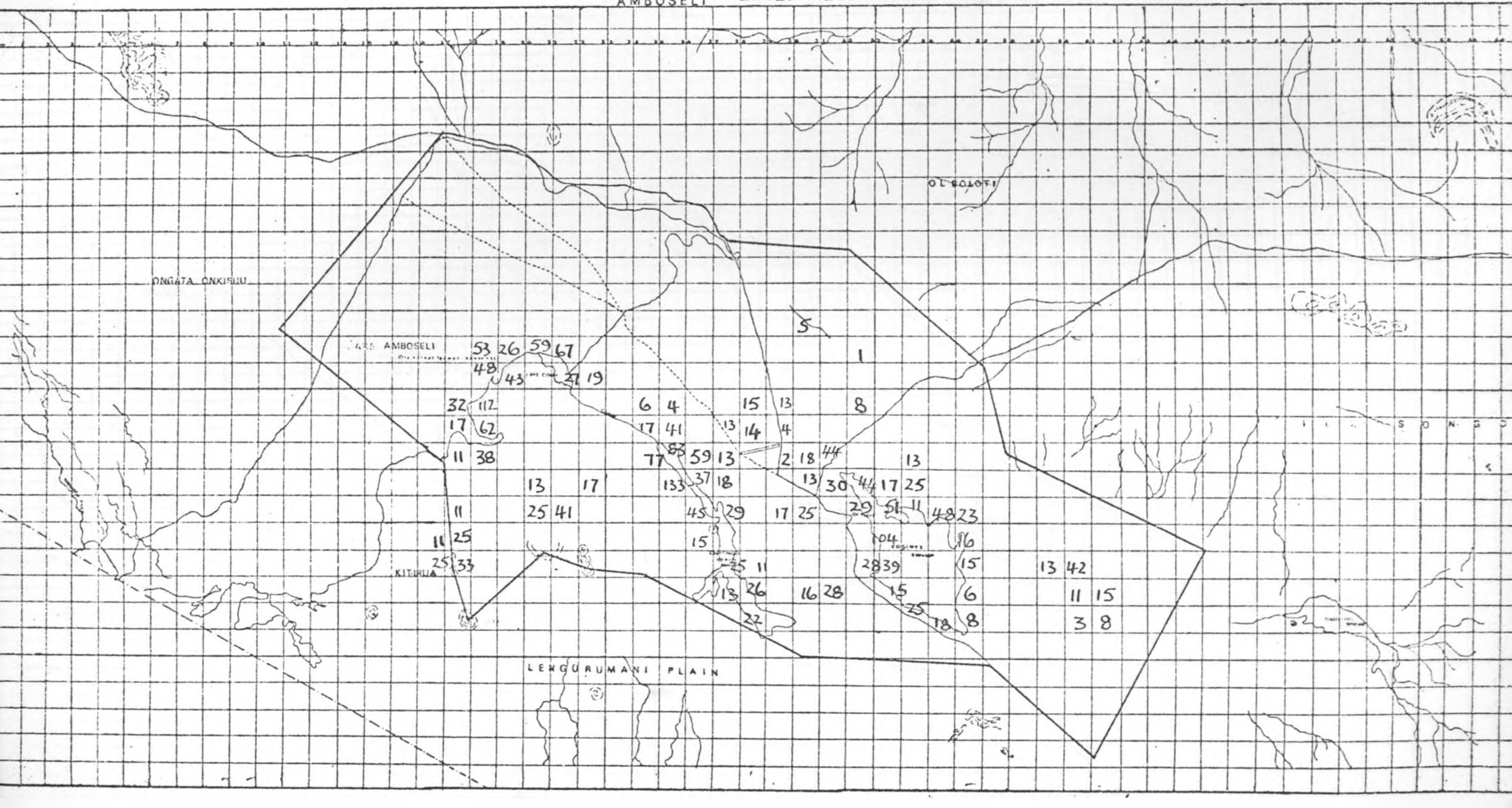
AMBOSELI - BASIN WILDEBEESTE DISTRIBUTIONS - MAY 1973



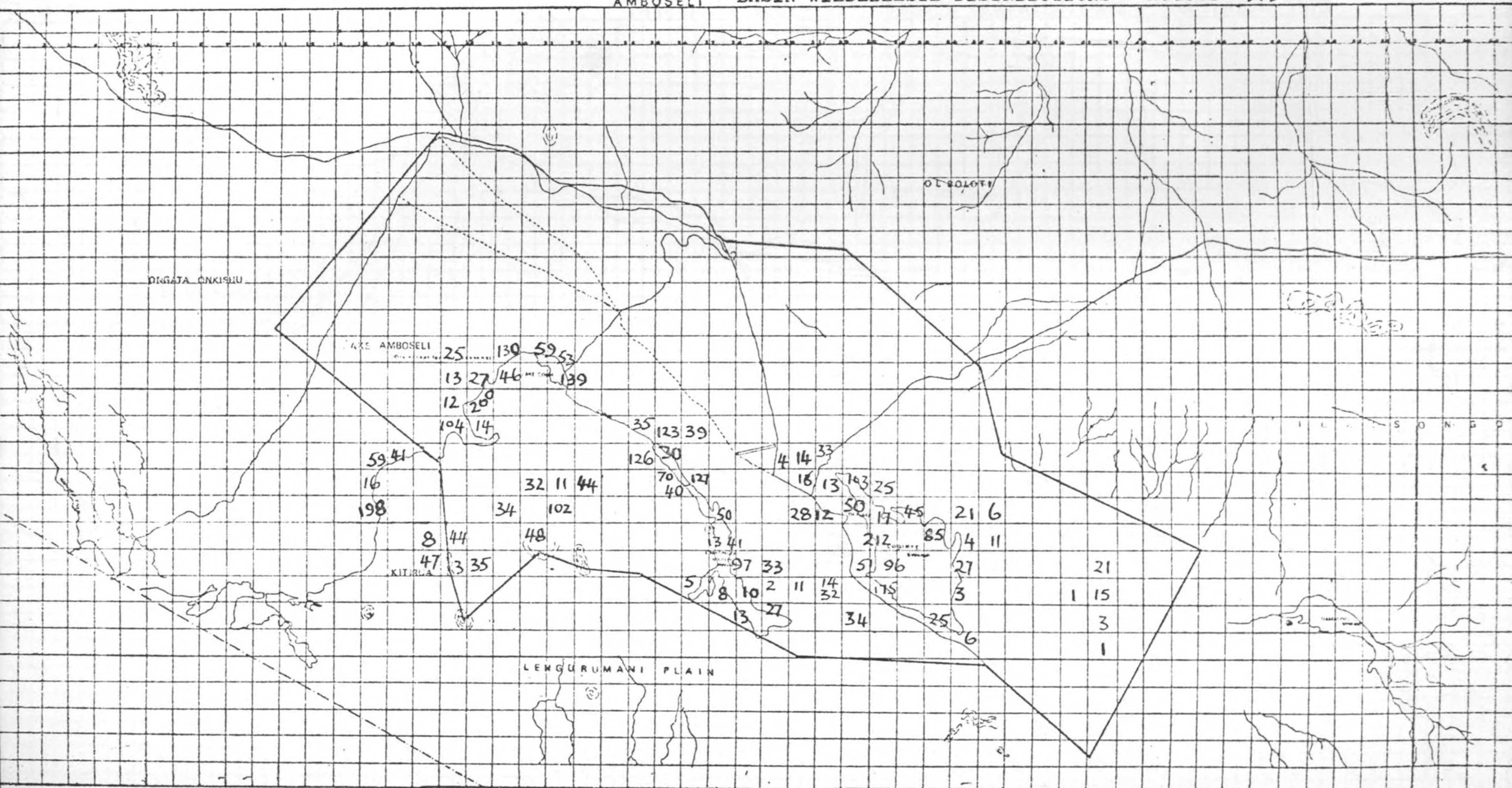
AMBOSELI - BASIN WILDEBEESTE DISTRIBUTIONS - JUNE 1973



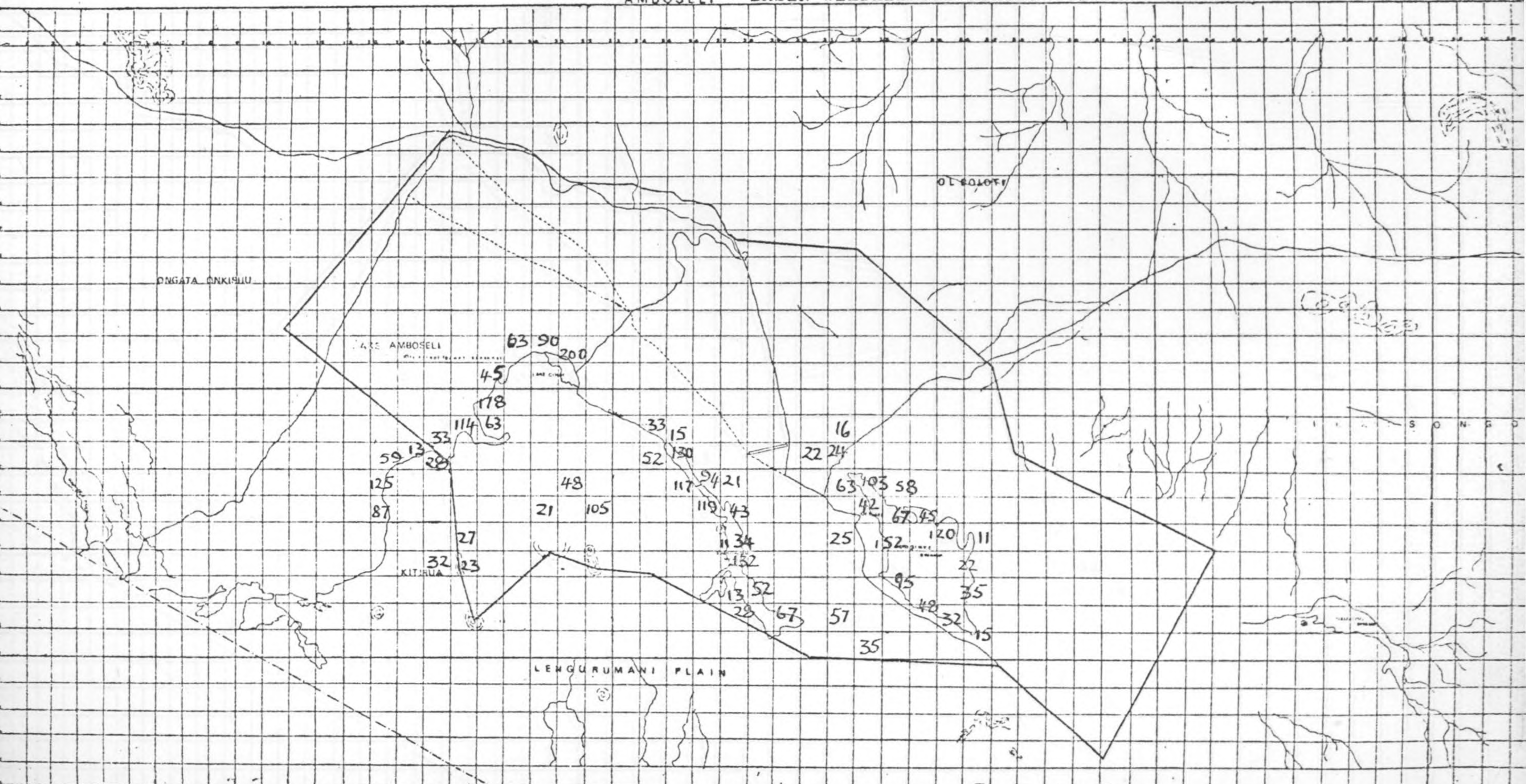
AMBOSELI - BASIN WILDEBEESTE DISTRIBUTIONS - JULY 1973



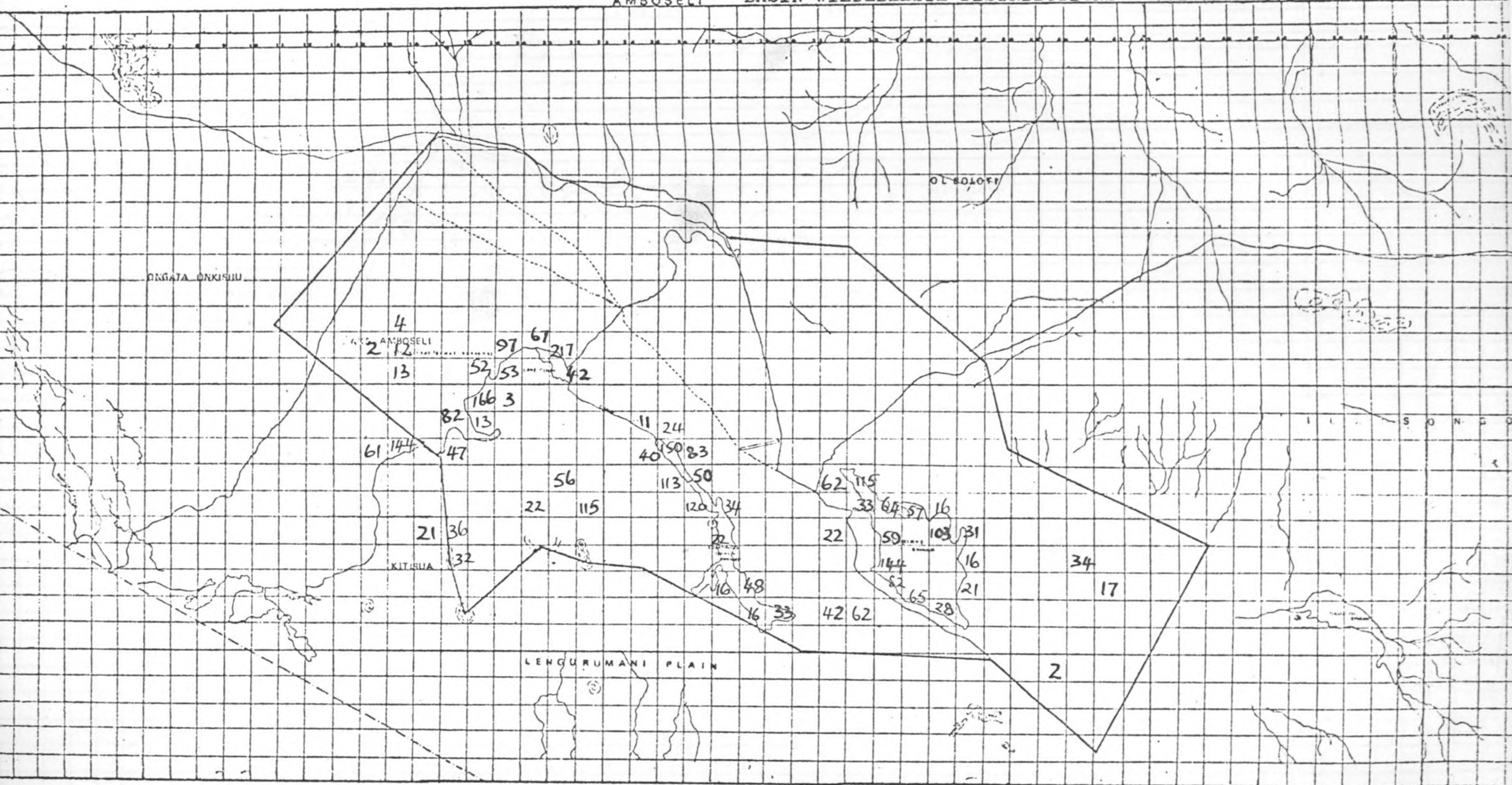
AMBOSELI - BASIN WILDEBEESTE DISTRIBUTIONS - AUGUST 1973



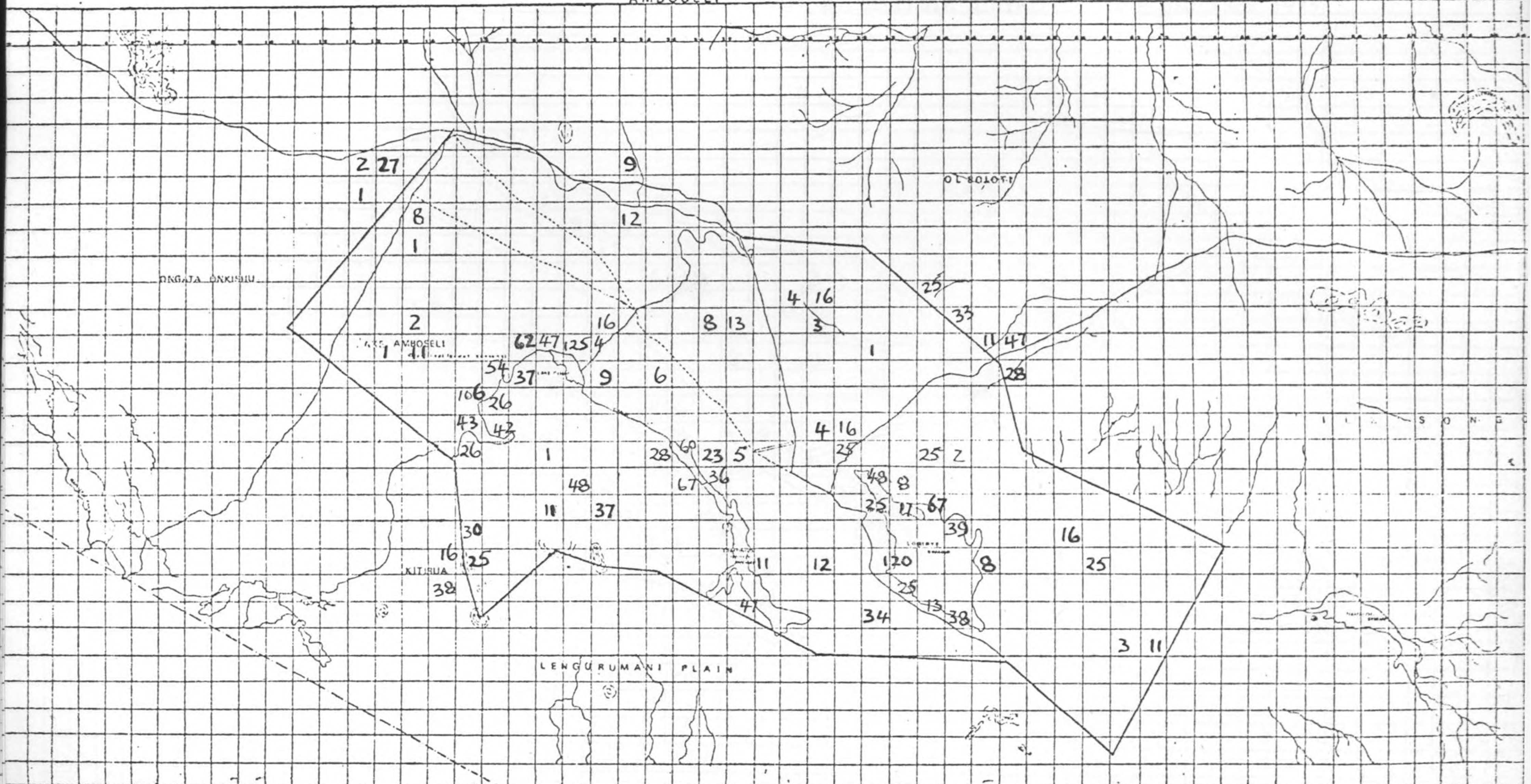
AMBOSELI - BASIN WILDEBEESTE DISTRIBUTIONS - SEPTEMBER 1973



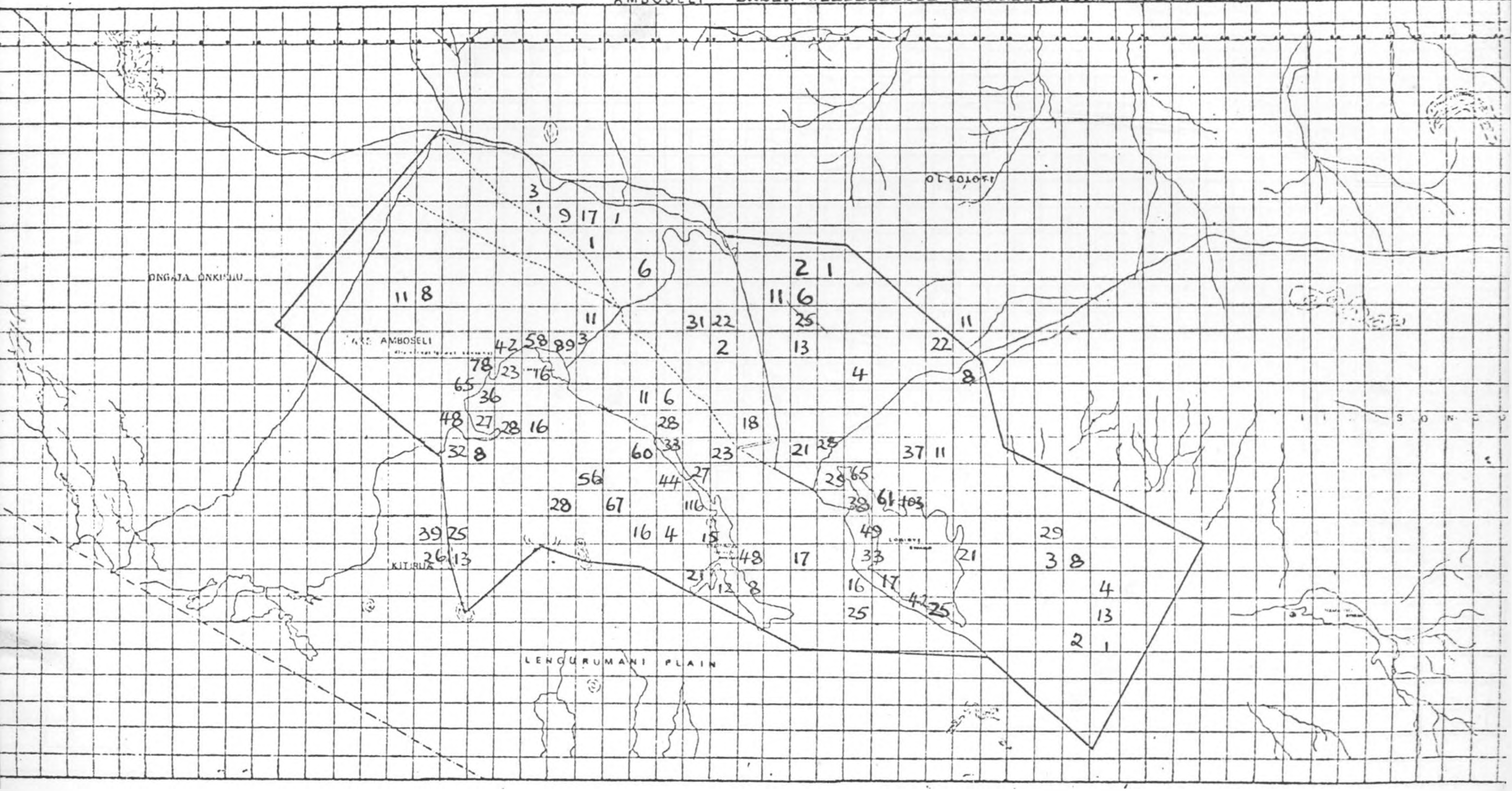
AMBOSELI - BASIN WILDEBEESTE DISTRIBUTIONS - OCTOBER 1973



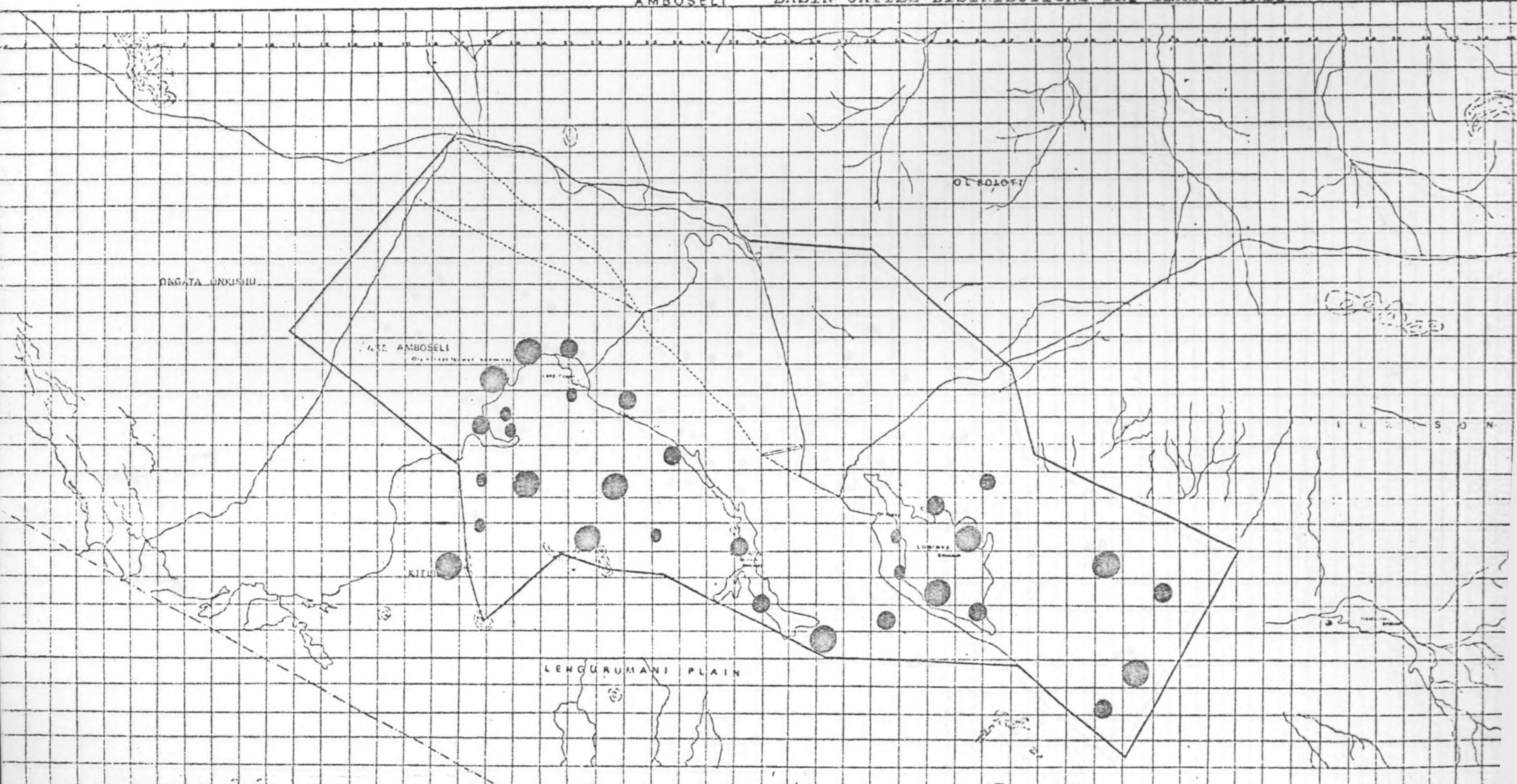
AMBOSELI - BASIN WILDEBEESTE DISTRIBUTIONS - NOVEMBER 1973



AMBOSELI - BASIN WILDEBEESTE DISTRIBUTIONS - DECEMBER 1973

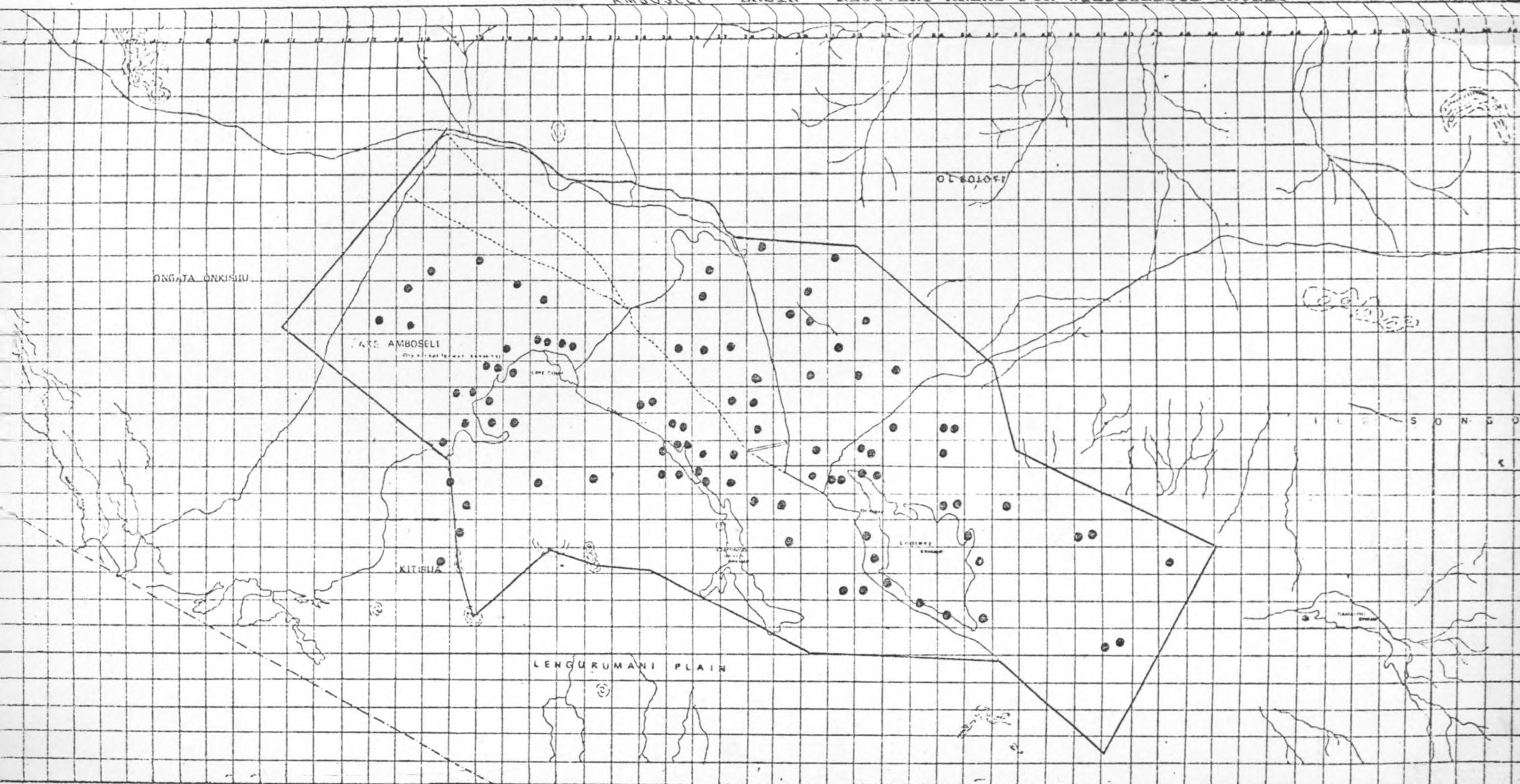


AMBOSELI - BASIN CATTLE DISTRIBUTIONS DRY SEASON ONLY



KEY -
> 1000
500 - 1000
100 - 250

AMBOSELI - BASIN - RECOVERY AREAS FOR WILDEBEESTE SKULLS



KEY - ●● Frequent recovery areas
● Less frequent recovery areas.