

ERRATA AND ADDENDA

p.4.	1.22	For Sinclair (1972) read Sinclair & Gwynne (1972)
p.15.	1.9.	For 'aribtrarily' read 'arbitrarily'
p.22	1.27	For 'montly' read 'monthly'.
p.27	1.3	Add 'to calculate biomasses <u>are</u>
p.40	1.2	For 'ITCA' read 'ITCZ'.
p.43	1.4	For 'Griffiths (1967)' read 'Griffiths (1972)'
	1.18	For 'Dury (1968)' read 'Dury (1964)'.
p.54	1.2	'...were collected. They were identified by....'
p.83	1.11	For 'YZ' read 'Y2'.
p.84	1.11.	For 'lenth's' read 'lengths'.
p.95	1.25	For 'morality' read 'mortality'.
		Add '....in the plains, <u>and</u>
P.100	1.9	For 'rhinosceros' read 'rhinoceros'.
	1.26	For 'park' read 'plains'.
p.101	1.14	Add 's = total number of species'.
	1.28	For 'herbivores' read 'herbivore'.
p.106	1.24	For 'indentical' read 'identical'.
p.109	1.29	For 'than' read 'that'.
p.113	1.18	Add 'the effect <u>of</u> the extra animals'.
	1.23	Add ' <u>shown</u> by each species...'
p.123	1.8	For 'thos' read 'those'.
p.124	1.30	Remove '....indicating <u>a</u> higher
p.132	1.3	For 'west' read 'wet'
p.138	1.11	For 'Kiley-Wothington' read 'Kiley-Worthington'.
p.144	1.8	For 'It' read 'Its'.
p.154	1.15	Add 'to increase <u>the amount</u> of sheath...'
p.170	1.24	For 'lenth's' read 'lengths'.
p.180	1.21	Add ' <u>and</u> as the weights'.
	1.8	For 'along' read 'alone'.
	1.19	For 'neccessary' read 'necessary'.
p.181.	1.14	For 'nutritions' read 'nutritious'.
p.186.	1.25	For 'is' read 'in'
p.188.	1.17	Add 'TDN = total digestible nutrients'.
p.190.	1.4	For 'for' read 'of'
	1.18	For '0.5' read '0.25'.
p.191.	1.22	For 'Table 9.2' read 'Table 10.2'
p.201	1	For 'adaption' read 'adaptation'.
	1.14	For 'Table 10.5' read 'Table 10.6'.
p.216	1.26	Should read 'when solar radiation is highest, but air temperatures are still increasing'.
p.233	1.21	For 'Clawson and Meyer' read 'Meyer and Clawson'.
p.236	1.1	Add ' <u>adequately described</u> with....'
p.255	1.3	Add 'in the file NNPCOM was made, <u>for some variables</u> were clearly unlikely.....'
p.257	1.20	Remove 'lateritic soil types'.
p.258	1.8	For 'has' read 'had'.
p.267	1.20	For 'herbivores' read 'herbivore'.
p.273	1.5	Add 'Watson's (1967) data...'
p.274	1.23	For 'separate' read 'separated'.
p.278	1.16	For 'produtivity' read 'productivity'.
p.279	1.15	For 'nutritional' read 'nutritional'.
p.280	1.11	For 'reseves' read 'reserves'.
p.285	1.8	Add 'only started <u>in</u>'

Table 12.2 Title: remove 'on condition variance'.
 Tables A.12.1
 and A.12.2. Add 'on p 333'
 p.339 1.28 For 'possible' read 'possibly'.

Add to Bibliography:

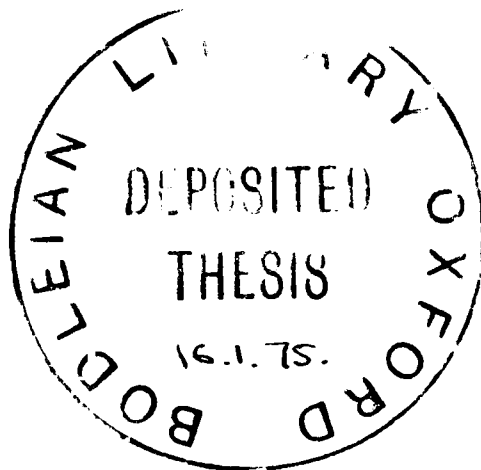
AEFTAT-UNESCO: (in prep.) Vegetation map of Africa
 1:5,000,000.
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 E.Afr. agric. for. J. 36 195-199

The feeding ecology of Coke's hartebeest,
Alcelaphus buselaphus cokei Günther
in Kenya

by

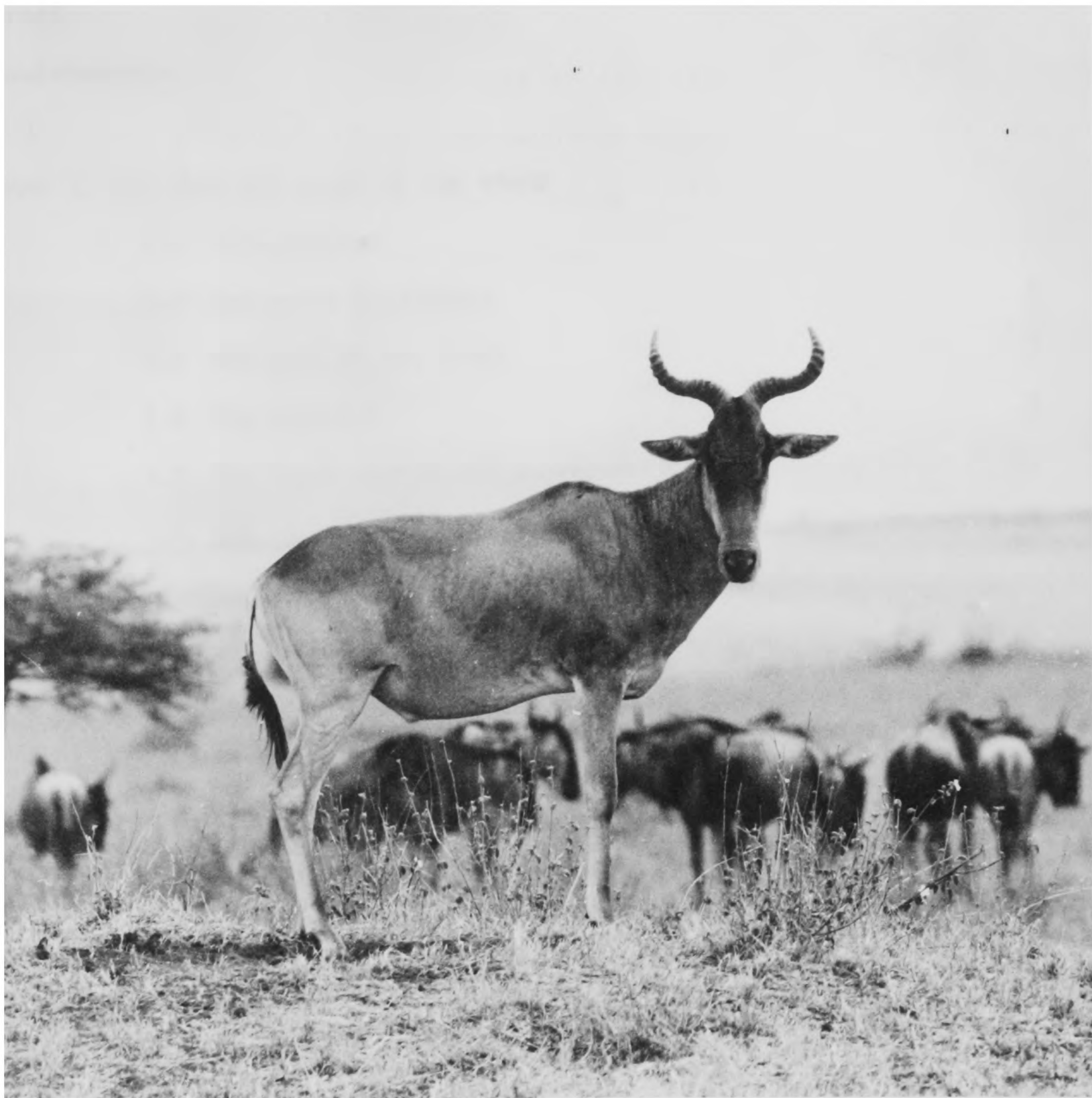
Mark Rangeley Stanley Price

A thesis submitted for the degree of
Doctor of Philosophy
at the University of Oxford



September 1974

Pembroke College
Oxford



Frontpiece. Adult male Coke's hartebeest, Alcelaphus buselaphus cokii
Gunther.

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Abstract.

Despite a wide distribution through Africa, the genus Alcelaphus has been little studied. The aim of the work described here was the study of a population of Coke's hartebeest in the Athi Plains of Kenya, which included the Nairobi National Park. It was designed to complement existing information on the species' behaviour and to examine the interactions between the hartebeest and their food supply. The approach, both in the field and subsequently, is also described in Ch.1. In Ch.2 I describe the methods which are referred to frequently through later chapters. These include the field methods of counting and ageing hartebeest, the location of study areas and the sampling of vegetation, the measurement of rainfall and the collection of specimen animals. The organisation of the resulting data and their analysis are described.

Descriptions of the Athi Plains are few. Their geology and topography are outlined in Ch.3, while Ch.4 concerns their climate, with the emphasis on rainfall as the most important seasonal parameter. The vegetation of the Nairobi Park and the rest of the plains is then described (Ch.6) at the level of the vegetation zones for the whole plains (1850 km²) and of vegetation types for the study areas. The Nairobi Park is shown to have a very varied vegetation despite its small size (114 km²).

In Ch.6 the sizes and distributions of the populations of hartebeest and other numerous herbivores are described from aerial censuses over the plains and ground counts in the park. This establishes that the density of hartebeest in the park is 6.6 times that of the plains. The latter population also contains significantly fewer adult females and young above the age of 1 month. The hartebeest in the plains show very minor population movements compared to either wildebeest or zebra, and

exchange with the park population is infrequent. Using information theory methods, Ch.7 serves to define the niche of the hartebeest in relation to those of other herbivore species, and to compare the structure of the communities of the two areas. The herbivore community of the plains also includes cattle, sheep and goats. The results of this ground-work confirm the sedentary existence of the hartebeest population, but show it to occupy a relatively wide variety of vegetation zones through the year, occupying many vegetation types and tolerating a broad range of grass standing crops. Compared to other species, the hartebeest shows a very marked seasonal occupation of vegetation types in the park, but this is not apparent in the plains. The same methods are extended to measure the similarity between species' distributions, and the cases of high overlaps are examined using published information on the feeding habits and diets of the species. Considerable ecological separation can be inferred between all species-pairs except between hartebeest and zebra in the park in the dry season, and between hartebeest and cattle in the plains in the wet season. The distributions of the latter pair in the dry season, also, suggest their ecological equivalence.

In Ch.8, starting Part II, I describe the hartebeest's diet and its seasonal changes from the analysis of rumen contents. The hartebeest grazes exclusively. Its diet is described in terms of its content of grass parts, rather than grass species, amongst which Themeda triandra is shown by various sources to be predominant. The effects of the differential digestion of these parts in the rumen are reversed by applying a correction factor based on specific gravity (Appendix 12) to obtain the diet proportions. In the wet season the proportion of leaf in the diet is higher than in the sward, while the less nutritious stem is under-represented. When the leaf in the sward has been depleted in the dry season, the hartebeest no longer exercise any dietary selection.

Comparison of these results with those published for zebra show that the parts taken by the 2 species are very different in proportion, and I conclude that this would result in their ecological separation even when feeding together. On the other hand, contemporary evidence on cattle diets, also from the Athi Plains, shows them to be taking the same diet as the hartebeest, and evidence is presented that Themeda is also frequently eaten by cattle. Their coincident distributions are paralleled by similarities in their rumen morphology and bacteriology, with both classified as the only "bulk roughage grazers" in the Athi Plains community.

The method developed for the correction of grass part proportions in the rumen to those in the diet allows the daily dry matter intake to be calculated from the weight of dry matter in the rumen (Ch.9). Intake varied between 26 and 87 g/kg.W^{0.73}.day in the dry and wet seasons respectively, through the effect of the water content of the food on its specific gravity and subsequent behaviour in the rumen. The calculated variation in intake with the succulence and quality of the food is consistent with experimental observations on the factors controlling the intake of coarse feeds by domestic ruminants. The calculated intakes are similar to those of 42 and 34 g/kg.W^{0.73}.day of an experimental hartebeest and sheep, respectively. A regression method for predicting the hartebeest's intake under field conditions from the faecal nitrogen content is developed.

In Ch.10 the dry matter intake is converted into the intakes of protein and energy, and the gain to the hartebeest of selective feeding is calculated. Selection appears capable of increasing the digestible crude protein intake by 50%. The calculated intakes are compared with maintenance standards for domestic ruminants and are shown to have fallen below the maintenance levels in the dry season of September 1972.

Calculation of the intakes uses information from a feeding trial with hartebeest and sheep, whose intakes were also measured. The experimental hartebeest's metabolisable energy intake was $51.5 \text{ kcal/kg.W}^{.73} \cdot \text{day}$, which was considerably lower than the measured metabolic heat production of $116.1 \text{ kcal/kg.W}^{.73} \cdot \text{day}$ of another tame animal. The metabolisable energy intake of the sheep of $45.1 \text{ kcal/kg.W}^{.73} \cdot \text{day}$ suggests that the lower metabolic rate may be more correct, and further supporting evidence is presented.

Chapter 11 is the first of 3 chapters in which the hartebeest's energy expenditure is considered. The daily activity patterns are described from day and night observations in the wet and dry seasons. Little seasonal variation in the regime of 3 feeding periods at nearly equal intervals through 24 hours was apparent. The total times spent feeding was 2 hours shorter at 8.6 h/24h in the dry season than the wet. About half of this reduction was made up by an increase in the time spent walking, associated with the need to visit water sources in the dry season. Further observations showed that males drank every 3 days, females every 2 days. The energy cost of this activity was almost the same in both seasons at 52% greater than the basal metabolic energy expenditure.

The use of energy for growth and the deposition of body reserves is considered in Ch.12. The shot animals showed that full adult body weight is not reached until the fourth year, after which weight appears to decline immediately. Using a photographic method the external condition of territorial males was shown to depend on the rainfall over the previous 4 months. Non-territorial males were always in significantly better condition. The shot hartebeest were characterised by very small kidney fat reserves which showed no seasonal variation. Marrow fat varied seasonally, as did the weight of a selected muscle, representing the protein reserves of the body. The latter also changed through age, parallelling the changes in total body weight. The significance of these

findings is discussed in the light of the low fat content of tropical ungulates, the hartebeest's slow growth rate and its possible adaptiveness.

The small surpluses of energy ingested by the hartebeest and the small body reserves lead to a discussion of the female reproductive pattern (Ch.13). First breeding occurs in the fourth year. Calving occurs in every month of the year. The timing and size of the birth peaks allow the conclusion that nutrition and female condition are the ultimate and proximate factors influencing reproduction. The adaptiveness of this system to a fluctuating, equatorial environment is discussed.

In Ch.14 the utilization of the resources of food and water of the park are considered. The hartebeest's seasonal use of the vegetation, mentioned in Ch.7, is described, and is shown to be clearly defined and predictable. The data necessary for a causal analysis of the grazing cycle were not available. The quantity of standing water in the park study area is shown to depend on the rainfall over the previous 2 months. Only under exceptional conditions does animal use make significant inroads in to the water resources. Comparing this study area with those in the plains, the abundance of water in the park is due to the construction of dams rather than to any greater water-retaining capacity. In the dry season, the hartebeest aggregate around the remaining water sources. This provides evidence additional to that in Ch.11 that the hartebeest conserve energy by reducing their activity when experiencing sub-maintenance intakes in the dry season. The significance of this to the distribution of the hartebeest in the plains is discussed.

In the final discussion (Ch.15) the ecology of the hartebeest is compared with those of several other species. Most notably, the hartebeest differs from the related wildebeest by being more sedentary, eating a poorer quality diet, growing more slowly, reaching sexual maturity later, but calving as often as conditions allow, followed by a high calf survival rate. In their "opportunistic" reproduction and

prolonged mother-offspring bond, the hartebeest resemble some of the desert marsupials. The relationship between cattle and hartebeest is considered in more depth. Their ecological equivalence (Chs.7,8) is shown to lead to their competition both through exclusion on the part of the cattle, and exploitation for the same food. The hartebeest is the competitively inferior species, and their density and lower proportion of young animals in the plains are identified as the results of this interaction. Archaeological and historical evidence confirms that similar habitat selection by Bos spp. and Alcelaphus spp. has occurred over a long time throughout the African continent. Finally, the reasons for the predominance of the hartebeest in the park since 1961 is discussed, and it is concluded that the high densities observed in 1971-72 were not unusual in historical times. The management practice of burning the park's vegetation has allowed further increases in numbers, while the large numbers of cattle in the plains have caused the reverse.

Acknowledgements

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Dr. R. Abel taught me how to use a bomb calorimeter. S. Spencer wrote several computer programmes, while Dr. P. Griffiths had the patience of a saint while I was learning to interact with the ICL 1906A computer. Mrs. B. England typed almost all of this thesis. I am most grateful to all these people.

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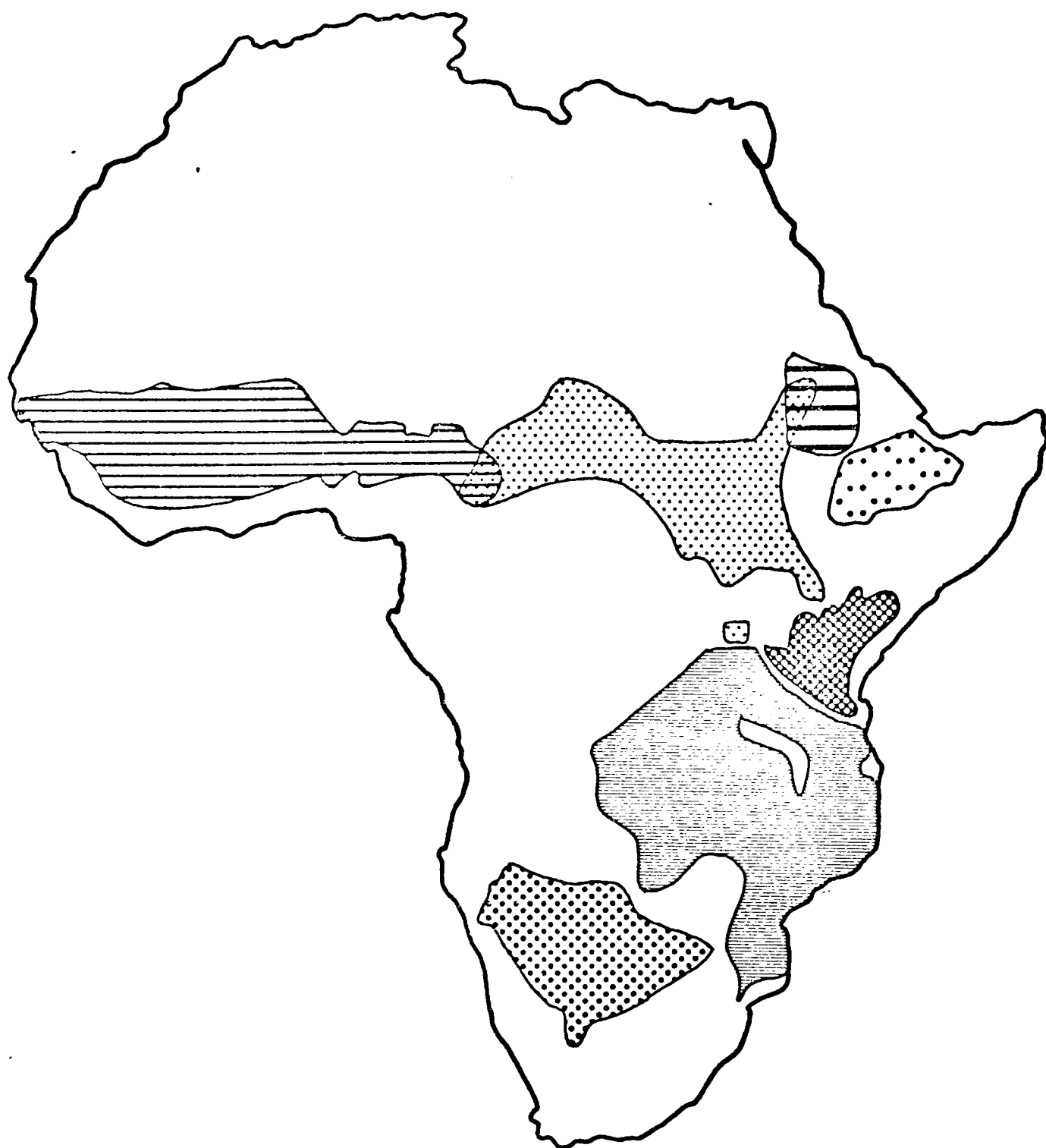
Chapter 1.

THE AIMS AND SCOPE OF THE STUDY

1.1 Introduction

Over the last 15 years the large mammal fauna of East Africa has been the subject of much research. The level of research effort has varied from long-term studies of whole ecosystems, carried out for the most part by research institutes to the occasional survey of large areas. Within this body of research, three types of study can be distinguished by their scope and methods. The first is the survey and description of large areas and their mammals (Lamprey 1963, Harris 1972, Western 1973), or the analysis of local communities (e.g. Bell 1969). The second type is the study of single species. This autecological approach is more intensive, and may depend less on observation only for collecting information. The scale of the project may allow some experimentation (Wyatt 1969, Field 1970). The third approach is an ecophysiological one to the adaptations of animals to their environments. In East Africa, the most striking adaptations are to the extreme conditions of high temperatures and heat stress, which are often associated with water shortage (e.g. Taylor and Lyman 1967, Schoen 1972, Finch 1972 a, b). These investigations are more experimental, and often must be conducted under unnatural, but controllable, conditions indoors. This may create difficulties of extrapolation to the wild situation.

These three types of study form a hierarchy with the community, or synecological approach at the top as the most extensive. The results of each generate predictions and hypotheses about the ecology or behaviour of species at the other levels, and in this sense they are not different. The study described here was conceived as the study of a single species, but, as will become clear, a more complete picture was possible by considering the physiology of the individual and the ecology of the population



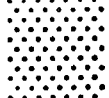
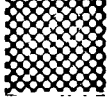
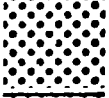
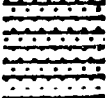
-  Alcelaphus buselaphus major, Western hartebeest
-  A.b. lelwel and A.b. jacksoni, Lelwel and Jackson's hartebeest
-  A.b. tora, Tora hartebeest
-  A.b. swaynei, Swayne's hartebeest
-  A.b. cokei, Coke's hartebeest
-  A. lichtensteini, Lichtenstein's hartebeest
-  A. caama, Cape or Red hartebeest
-  intergrades

Fig.1.1. The distribution of living hartebeest species, subspecies and intergrades, from Sidney (1965).

in the context of the community.

1.2 The genus Alcelaphus

Coke's hartebeest Alcelaphus buselaphus cokei Gunther (Frontispiece), known in East Africa as the kongoni, is one of 5 extant subspecies of the hartebeest, Alcelaphus buselaphus (Sidney 1965). These forms have a broad east-west distribution across the African continent (Fig. 1.1). A.b. cok^ei is the most southern race and is replaced by Lichtenstein's hartebeest, A. lichtensteini, in northern Tanzania. In turn, this is replaced by A. caama, the Cape or red hartebeest of South Africa.

The genus Alcelaphus has received little serious study, and information on the West African subspecies is very scanty. Bolton (1973) has reviewed the distribution and status in Ethiopia of A.b. lelwel, A.b. tora and A.b. swaynei. Aging criteria have been developed for Lichtenstein's hartebeest in Zambia (Mitchell 1965), and herd structure and movement in the same population have been described (Dowsett 1966). The feeding habits of the Red hartebeest (van Zyl 1965) and their reproduction (Skinner et al. 1973) have been studied in small populations, which may not be representative of the species.

Coke's hartebeest alone of the genus Alcelaphus has been studied in some depth in East Africa. It is included in the community studies of Lamprey (1963, 1964), Harris (1972) and Western (1973). The feeding ecology, habitat selection and reproduction of a population in the Rift Valley of Kenya have been studied (Blankenship and Field 1972, Field and Blankenship 1973), but by far the most important work is that of Gosling (1969, 1974). His study was concerned with the ecological significance of male hartebeest behaviour in the Nairobi National Park in Kenya. This work also included descriptions of the hartebeest's vegetation utilization, movements and reproductive ecology. Despite this study, Coke's hartebeest, which like all the hartebeests with the exception of Lichtenstein's, inhabits open plains (Dorst and Dandelot 1970) has been the

subject of little research. This is surprising for it is still widespread in Kenya (Stewart and Stewart 1963), and contrasts with the numerous studies on another East African alcelaphine, the wildebeest (e.g. Watson 1967, Estes 1969, Bell 1969, Talbot and Talbot 1963, Pennycuick 1974).

1.3 The aims of the study

The main objective of the study was to investigate the feeding ecology of the hartebeest in terms of its diet and nutrition. This was combined with continuing the study made by Gosling between 1966 and 1968 in the Nairobi National Park, and assessing the effects on the population of the management policies of the National Parks authorities. Within these objectives, four main themes can be defined:

1. To explain why the hartebeest is the most abundant large herbivore in the Nairobi Park on a year-round basis. The question "Why are there so many hartebeest?" is frequently asked by visitors and park staff alike. Their high numbers are a relatively recent phenomenon (Foster and Kearney 1967), which suggests that their increase has been associated with changes in the ecology of the park. If so, were the changes natural or due to management practices? The answers to these questions could provide basic information against which future changes could be monitored and the outcome of new management policies predicted.
2. To complement the behavioural work of L.M. Gosling by looking at the ecology of the hartebeest in the same area. In addition, the same techniques for counting, ageing, recognition of individual animals and description of the vegetation were used to detect changes in the park and the hartebeest population in the period since his study. The most notable difference between the two study periods was their climate. Rainfall in each of the years 1966-68 was higher than the long-term average (Gosling 1974), while the years 1970-72 were each drier than average (see below).

3. To investigate the interactions between the hartebeest and their food supply, and the changes through time of these interactions.

The diets of many East African herbivores have now been described in terms of the type of plant and the species eaten, and in some cases, the parts of the plant in the diet. Apart from this last information, the hartebeest is no exception in this respect (Stewart and Stewart 1970, 1971, Casebeer and Koss 1970, Field and Blankenship 1973).

By comparison, the nutrients obtained by wild herbivores as a result of their diet selection have been studied far less. This situation has arisen for a variety of reasons. First, although the factors which determine how much a ruminant eats under laboratory conditions have been the subject of many investigations (e.g. Campling, Freer and Balch 1961, Blaxter, Wainman and Davidson 1966), the relationships between a free-ranging herbivore and the sward, from which it harvests its food, have received less attention. The complexity of these relationships has been described by Eadie (1970) on upland pastures. from the point of view of sheep production. In their low level of management and their seasonal production, the East African grasslands are similar.

For a grazer, all the grass above ground may be potentially edible, but different plant species and parts of the same species have widely different food values (Raymond 1969). Grazers can increase their nutrient intake above the mean level of the sward by selective feeding (Arnold 1966, Sinclair 1972), but the extent of this selection is governed by the sward structure (Arnold and Dudzinski/Allden and Wittaker 1970, Stobbs 1973a, b). The same structure will not be optimum for all animal species.

Because of this ability to feed selectively, it is difficult to measure the point at which a food supply becomes inadequate for even one species. This contrasts with situations in which food occurs as discrete items, and the responses of animals to the changing abundance of prey can be followed (e.g. Goss-Custard 1970).

For all animals the nutrient intake is the product of the amount of dry matter eaten and its nutrient concentration. But, unlike other animals, if a ruminant switches to a lower quality diet, a constant nutrient intake is less easy to maintain by increasing the amount eaten. In the laboratory the intake of roughage diets is determined largely by the bulk properties of the food, rather than by the requirements of the animal, to which intake is then adjusted (Blaxter 1962). Field evidence shows that a sub-maintenance plane of nutrition can result from the inadequate intake of poor quality food, rather than through its absolute shortage (e.g. Eadie 1970, Gwynne and Morton Boyd 1970). Similarly, under more extreme conditions of natural food shortage, animals die of apparent starvation, but their rumens are not reported to be empty (Klein 1968, Child 1972, Keep 1973, de Graaff et al 1973, Hillman pers. comm. 1974). This is further evidence of the complexity of the interactions between sward structure and its food value, herbivore intake and their nutritional status.

Apart from the reasons above, information on the intake of herbivores is essential for any calculation of the carrying capacity of an area (if the amount of food available can be measured), or of the energy flow through it. The food intake of free-grazing domestic animals is usually measured by indirect methods (van Dyne 1968), but even these may not be practical for use with wild herbivores. In current models including these parameters, the intakes of wild ruminants are either based on percentages of the live-weight, chosen by analogy with domestic species (Harris and Francis 1972) or of some proportion of the weight of the rumen contents of a freshly-killed animal (Petrides and Swank 1965, Moen 1973). A more critical means of estimating intake for the hartebeest was also an objective of this work. The nutrient intake could then be calculated and compared with the known requirements of domestic species (A.R.C. 1965, Elliott and Topps 1963, 1964). Once this is done, aspects of the herbivore's growth, condition and reproduction can be investigated in terms

of the effects and implied effects of any seasonal variation in the intake and nutritional status of the population.

For this last purpose, some means of defining the seasons was necessary. In the arid parts of East Africa, rainfall is a "driving" variable (Harris and Francis 1972) by virtue of its effect on plant growth and, hence, food quality for herbivores (Braun 1974), and its influence on animal distribution, reproduction etc. Thus, measurement of rainfall and some means of defining the seasons were important aspects of this study, and most data are presented in a seasonal context.

4. Today the ecological literature abounds with reports of measurements of the energy flow through whole ecosystems, between two or more trophic levels or through single species. Application of the concepts and methods associated with this branch of ecology (e.g. Ryszkowski and Petrusewicz 1967) to large mammals are few. They are mostly concerned with converting existing figures or estimates of primary production and animal numbers into energy standing crops and flows (Lamprey 1964, Petrides and Swank 1966, Buechner and Golley 1967, Phillipson 1973). Compared to this community or population approach, studies of energy flow at the level of individual large mammals and, then, their populations are almost non-existent. The work of du Plessis (1972) on the blesbok is a notable exception in the tropics.

During the study two tame hartebeest were available for measurement of their metabolic rate and digestive efficiency. As an estimate of the hartebeest's food intake under field conditions was obtained, calculation of the energy flow through the hartebeest was feasible. Here, information on only the daily energy intake and its expenditure by an "average" adult hartebeest is considered. The results of Finch (1972a, b) on the hartebeest's heat exchange with the environment under seminatural conditions cover another aspect of its energetics. Extrapolation of the energy relations of the individual to the population is beyond the scope of this work.

1.4 The approach

To investigate the hartebeest's abundance in the park, a comparative approach was used, taking advantage of a natural experimental situation. Geographically, the park is part of the Athi Plains. The two areas share the same volcanic origin and physiography (Ch. 3), and on a gross scale the same climatic patterns and vegetation (Chs. 4 and 5). On the other hand, the area of the park is only 6.5% of the area of the relevant part of the Athi Plains, yet its density of hartebeest is 6.6 times greater (Ch. 6). The difference in densities has been examined in terms of the fine structure and resources of the two areas and the ways in which they are managed and exploited. In the plains, the Maasai continue their traditional pastoralism based on cattle, sheep and goats, while the Nairobi Park has been managed as a National Park since 1946. This has included the development of roads for visitors, the construction of dams and, since 1968, rotational burning of the vegetation. Except where the sizes of the two areas and their different animal densities demanded different sampling techniques, the value of this situation was maximised by using the same procedures of data collection in both.

At the beginning of the study, the only information on the ecology of the hartebeest in this area was the results of total monthly counts of the large mammal species in the Nairobi Park (Foster and Kearney 1967, Foster and Coe 1968, Foster and McLaughlin 1968). The total information on the hartebeest in the plains were the results of aerial censuses (Stewart and Zaphiro 1963, Modha 1969), but these provided only population size estimates, without information on the patterns of distribution. The first year's field work had to be extensive to provide a base-line knowledge from which hypotheses concerning the population and its behaviour could be developed. This resulted in a feedback to the original sampling methods, to determine, in turn, the nature and design of subsequent data collection.

In the first year this approach involved total counts of the hartebeest in the park, assessment of their population structure and their year-round pattern of vegetation utilization. Aerial censuses were made over the plains, to map their distribution and estimate their population size. The procedure is described in more detail in Ch. 6, but the censuses were flown along regularly-spaced transects across the plains (p.80). The transects were straddled by a total of 76 "blocks" drawn on a 1:50,000 map. Information on habitat selection and utilization was obtained by visiting the block along each transect which the flight showed to have the highest number of hartebeest. One block was sampled from each transect. In this way data were collected on approximately 50% of the estimated population from only 10 blocks arranged along a north-south axis across the plains and covering only about 15% of the total area.

This sampling was done every two months for a year, covering a wide range of climatic conditions. Visiting areas of high hartebeest density over this period enabled familiarisation with the area, the identification of its component vegetation associations and their utilisation by the hartebeest and other large herbivores. As a result, 6 study areas were delimited in the plains, and one comparable area was defined in the park. All were chosen to be sampled repeatedly in the second year.

This sampling design had two advantages over the previous one. First, information from the same sites on each occasion allowed more powerful analysis than did the same amount of information collected at different sites on each occasion. Second, an aerial census was no longer necessary to locate the areas of high hartebeest density for ground-sampling.

The information collected was correspondingly more detailed. Whereas in the first year, vegetation utilization by the hartebeest was recorded as their presence in broad categories such as open grassland, riverine bush or scrub grassland, it was subsequently described in terms of plant associations ("vegetation types" Ch. 5). The emphasis on the type of

information collected also changed. For example, in the first year the distance between each herd of hartebeest and individuals of other species was recorded. Subsequently for this study, this information was considered to be less valuable than knowing which species shared the vegetation types used by the hartebeest, and this was then recorded.

A parallel switch from the extensive to the intensive approach was made in the study of individual hartebeest. For the first 12 months specimens were shot at the rate of 2 or 3 in each month with the aim of detecting seasonal variations in their body condition, parasite levels, rumen contents etc. This frequent sampling was then replaced by taking larger samples in 4 months of contrasting conditions. Spacing the samples at 2 - 3 month intervals amplified the observed variations, and the larger sample size enabled some statistical validation of the results.

The change of emphasis mentioned above was one result of a conclusion reached at the end of the first year. By then, certain aspects of the hartebeest's ecology appeared strikingly different from those of other species in the same community. Moreover, apart from differences in the density of the hartebeest in the park and the plains, the relative proportions of the herbivore species in the two areas were not the same. This led to the conclusion that any description of the hartebeest's ecology would be deficient if the species was studied in isolation. Therefore, the minimum information necessary for comparison of the numbers and distribution of other species with those of the hartebeest was collected in the 7 study areas. The methods used are described in Chapter 2, and the species included in this in Chapter 7.

In calculating the energy flow and assessing the adequacy of the hartebeest's nutrient intake, liberal use has been made of the literature on domestic ruminants. The sciences of animal physiology and production are largely concerned with determining the amount which animals eat, and the fate and efficiency of utilization of nutrients. Because

of this, the nutritional factors which affect the growth rate, the age of puberty, the post-partum interval and reproductive success are the subjects of a voluminous literature. For the same reasons, the minimum dietary requirements and metabolic rates of domestic ruminants are well known. These are all important aspects of wild ruminant ecology but are extremely difficult or impossible to measure under natural conditions. A basic premise, therefore, of this thesis is that animal production science can provide wildlife ecology with useful concepts and specific information. This view is now used in the study of North American deer (Moen 1973, Geist 1971) but has scarcely influenced the study of tropical, wild ruminants.

Nonetheless, extrapolation from domestic to wild ruminants must be judicious, and justification for doing so is given where possible in this thesis. As a general rule, the results of work on temperate-climate cattle are not applied to the hartebeest if the results of an equivalent study on cattle in the tropics are available. Although cattle have existed in Africa for at least 3,000 years (Payne 1964), the validity of comparing wild, indigenous antelopes with domesticated, exotic species may be questioned. On the other hand, much of the physiology of cattle, sheep and goats is common to ruminants generally (Phillipson 1961), and there is little reason, on the meagre evidence available (e.g. Rogerson 1968), to think that wild species are fundamentally different. Indeed, there is good reason to suggest that if an exotic species shows a particular adaptation to arid conditions, such as the increased retention and recycling of nitrogen, the adaptation will be present and perhaps be even better developed in an indigenous species. For present purposes, the same physiological processes are assumed to occur in all ruminants, but no calculations are made on the basis of any hypothetical, superior efficiency or adaptation of either wild or domestic species.

1.5 The study period and subsequently

Field work started in September 1970 to anticipate the arrival of the short rains (described further in Ch. 4) of October and November. These rains failed almost completely in this year, so that the long rains of April 1971 were the first effective rain for a year. Consequently, near-drought conditions prevailed during the first 5 months of the study. As there was no green grass, plant identification and vegetation mapping were impossible, and work in the Athi Plains was delayed until January 1971. The possibility that the distribution and behaviour of the hartebeest under these conditions were not typical of more normal years was appreciated.

The delay also meant that less time was available for the intensive sampling of the 6 study areas of the plains. These were censused only 3 times, in March, June and September 1972, chosen to represent contrasting seasons. Of these months, March was equivalent to a "medium-dry" season following heavy rain in December 1971 and some in February 1972. June was the height of the wet season with heavy rain in that month and in May. By September, conditions were typical of the dry season. Equivalent sampling was done, in the Nairobi Park in the 12 months between November 1971 and October 1972. Field work finished in November 1972.

The total rainfall at Nairobi airport in each of the years 1970-72 was less than the long-term average of 786.7 mm (E.A.M.D. pers. comm.):

1970	603.5 mm
1971	738.4 mm
1972	644.0 mm

Thus, the hartebeest was studied in a relatively arid period. During 1973, rainfall was again very low, culminating in the complete failure of the short rains of that year. By early 1974 large numbers of cattle and wild herbivores were dying of starvation throughout the Athi Plains. Approximately 90% of the hartebeest in the park died (Hillman pers. comm.

1974). Qualitative information about the relative mortality suffered by the different species is used in the final discussion. The mortality of hartebeest has inevitably meant that the question "Why does the Nairobi Park have so many hartebeest?" has been recast as "Why did the Nairobi Park have so many hartebeest?" and it has been expanded to "What will the composition of the herbivore community be as it recovers over the next few years, and can this be altered by deliberate management policies?"

1.6 The structure of the thesis

The content and organization of this thesis describes the feeding ecology of the hartebeest in the context of the ecology of the community. Because the second year's data were more detailed, and were collected with more specific aims, most of the first year's results are excluded. The results of the aerial counts, some information from the first shot animals and the results of total counts in the park are exceptions in this respect.

The thesis is divided into two parts. After a description of the methods used in the field (Ch. 2), much of the first part is devoted to a description of the geography and topography of the area (Ch. 3), its climate (Ch. 4) and its vegetation (Ch. 5). This lengthy diversion from the hartebeest was unavoidable for two main reasons. First, no detailed study of the Athi Plains or their herbivores preceded this work. Therefore, the basic descriptions of the area did not exist. In particular, 25 studies have been made in the Nairobi Park over the last 15 years (Western 1973), yet none has produced a vegetation map or analysis of its herbivore community. Hopefully, some of the necessary, basic information will now be available to other workers. Second, this information is highly relevant to the aims of the study. Comparison of the resources of the park and plains and the description of animal distributions required information on their vegetation cover, their relative capacities to retain water etc. It will become clear that the geological structure

of the area is a significant factor in the hartebeest's ecology.

The remainder of Part 1 is concerned with the large herbivore community of the Athi Plains ecological unit. The population sizes of the main herbivore species in the park and the plains, and the structure of the hartebeest population in the two areas are considered first (Ch. 6). This is followed by an analysis of the structure of the herbivore community in which the species are compared in terms of their habitat tolerance, measured in various ways. Interspecific relationships are investigated by assessing the similarity between species in their habitat selection. This measures the ecological separation and defines the hartebeest's ecology relative to those of other species. It also shows from which species, and under what conditions, the hartebeest is ecologically least separate.

Part 2 is concerned specifically with the hartebeest's feeding ecology. The diet, its selection and seasonal variation are treated first (Ch. 8), followed by calculation of the amount eaten each day in different months (Ch. 9). In Chapter 10, their nutrition under field and experimental conditions is described, and their metabolic rate is estimated. The next three chapters are concerned with the expenditure of energy. In Chapter 11 their activity is described and its energy cost calculated, while Chapter 12 concerns their growth and body condition. The hartebeest's reproduction is considered in Chapter 13, in terms of their reproductive capacity and the factors which influence the timing of their breeding. Their feeding behaviour is returned to in Chapter 14 where the pattern of seasonal utilization of the food resources in the Nairobi Park is described. Finally, in Chapter 15, the ecology of the hartebeest is discussed and compared with those of other species, and the factors which determine the different densities in the Nairobi Park and the Athi Plains are discussed.

Chapter 2

METHODS

2.1 Introduction

The means by which information was collected in this study can be divided conveniently into two groups. One group consists of the methods used throughout the field-work for such sampling as ground counts, the distribution and habitat selection of animals, and vegetation description. As the results of these procedures are used in various places throughout this thesis, a description of these methods is given in this chapter. Similarly, a large amount of information was amassed by these methods, and the means by which it was stored, accessed and manipulated are also described here.

The second group of methods used for data collection and analysis ^{is} ~~are~~ more specific to certain aspects of the work described here, and they are detailed in the appropriate places in this thesis. The division between the two groups of methods is not absolute. Certain subjects, such as the shooting of sample animals, are described here, broadly, in terms of the selection of individuals and their collection. The techniques for taking information from the carcasses appear later.

It was clear from the start of the project that the large mass of information to be collected on the distribution and habitat selection of the hartebeest and other species could only be analysed by computer. To a certain extent this determined the design of subsequent data collection methods. If field data needed no further preparation or calculation after being taken before the information was ready to be stored in the computer (e.g. herd composition), it was recorded in duplicate on computer coding sheets in the field. Cards were then punched from these original sheets, checked for punching errors, and were then ready to be entered.

This method had the advantage of saving time, but with the possible disadvantage that variables taking continuous values (e.g. grass height) had to be coded in to categories, entailing a potential loss of accuracy. In actual fact, the programme eventually used to analyse these data was able to code such values (p. 27), but as many such parameters were estimated rather than measured (p. 20), codification probably avoided giving the information a spurious accuracy.

Some of the variables such as the degree of trampling of the vegetation had arbitrarily defined values. Such information only served a descriptive function, and is not used in any quantitative analysis in this work. The methods of its collection are included here only for the sake of a complete description of the vegetation sampling procedures.

2.2 Data collection

Age classes and the ageing of hartebeest

On all ground counts, hartebeest were classified in to one of 4 age classes: adult, subadult, juvenile or newly-born. The 3 categories for the immature animals are the results of combining 7 age groups distinguished by Gosling (1974) on the basis of male horn development. Observation of known-aged animals allowed an absolute age span to be attached to each class. Newly-born calves have no horns. As these erupt in the 4-5 th week of life, this age class covers the period from 0-1 month.

Juveniles were defined as those animals whose horns had erupted but which were still straight when viewed from the front or in profile. As horn curvature starts between 10 and 12 months of age, the total of newly-born calves and juveniles is considered a reasonable approximation of the number of animals less than one year old in the population. From the point at which the horns start to curve to when the first and second curves are complete and the tips of the horns are maximally separate, the animal is a subadult. As full adult horn conformation is reached at 24 months, the subadults are equivalent to yearlings. The appearance of the first

and second curves in females may precede that of males by up to 2 months (Gosling loc. cit.). Immature animals were not sexed on counts, but the difference in the course of development is so slight that for the purposes of this study I considered the male age class divisions to be applicable to the population.

The numbers of adult males and females were recorded separately, making a total of 5 sex/age classes. It is important that "adult" as used throughout this thesis refers to animals which have attained maximum horn development, but not necessarily maximum body size or sexual maturity. This distinction is returned to in Chapter 12.

The ageing of dead hartebeest was possible using the methods devised by Gosling (loc. cit.). Essentially, the pattern of tooth eruption and wear of immature animals was correlated with their horn development, to which an age could be attached (above). The adult horn shape was reached as the second permanent molar (M2) was erupting. By assuming an equal rate of eruption for M3, the full adult dentition was calculated to be present when the animal was 3-4 years old. The extent of the subsequent attrition of M3 was correlated with the period since full eruption. This tooth was calculated to decrease in length by 0.25 cm during each arbitrary age class. The similarity of the wear patterns of the hartebeest and waterbuck (Spinage 1967) and wildebeest (Watson 1967) allowed a one year interval to be assigned to each wear class. Thus M3 length provided an estimate of the age of the hartebeest older than 3-4 years.

The location of study areas

At the beginning of the study, the Athi Plains were divided into 76 blocks of approximately equal size. Natural features, most notably river courses, were used as boundaries. This aided their location on the ground and ensured that impassable escarpments or river beds did not lie in the blocks. A selection of these blocks ^{was} ~~were~~ visited after each aerial census of hartebeest (p. 8).

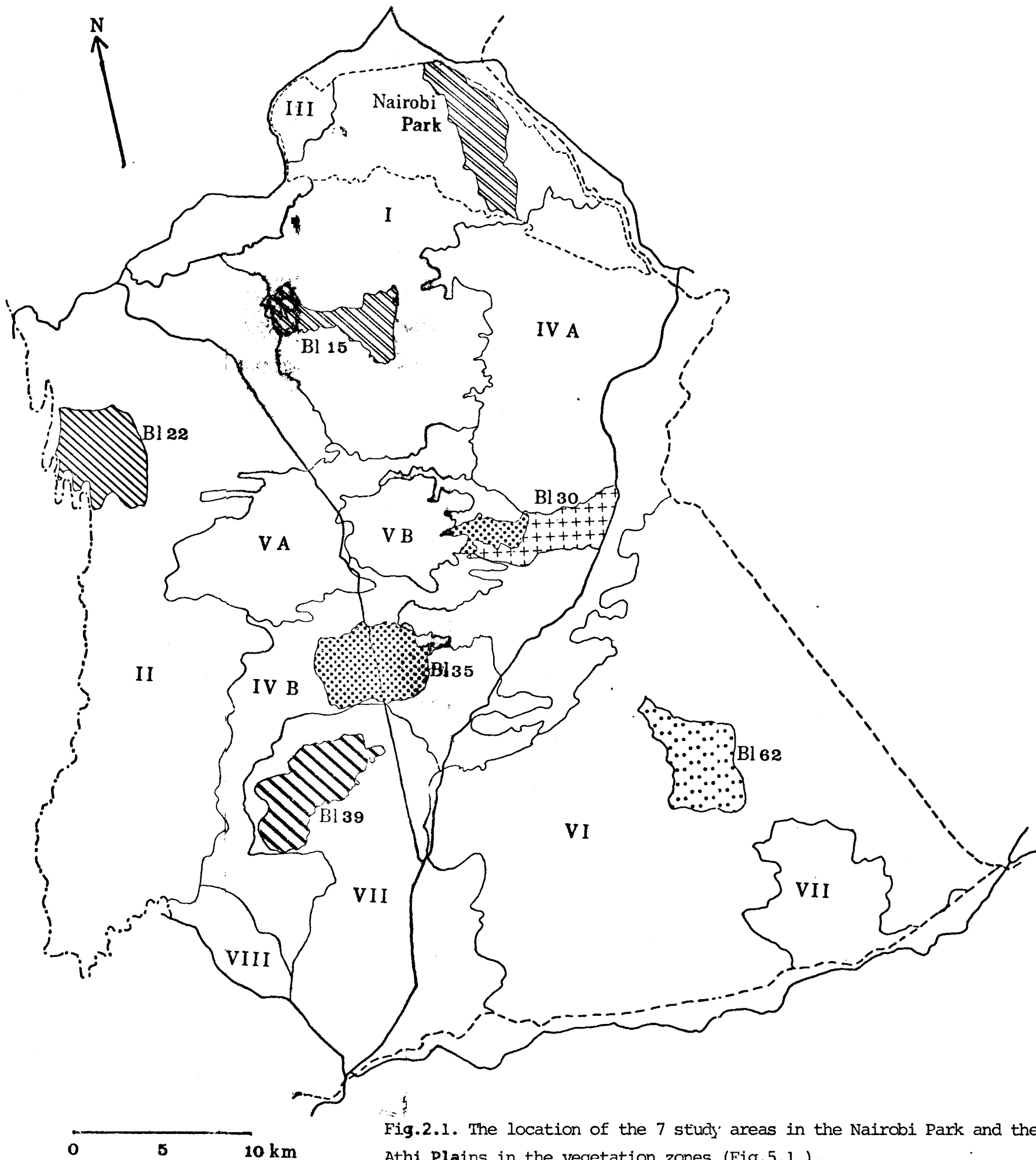


Fig.2.1. The location of the 7 study areas in the Nairobi Park and the Athi Plains in the vegetation zones (Fig.5.1.).

In the second year, 6 of these blocks, with some slight increases in size, were selected for repeated sampling. Three considerations influenced their location:

1. Between them they represented the main geological/vegetation divisions of the Athi Plains.
2. They supported high densities of hartebeest either always, sometimes or never.
3. Their mutual arrangement would allow monitoring of the seasonal patterns of animal distribution and movements which the aerial flights had indicated.

An area of similar size in the park was defined. This area was chosen to include a wide variety of vegetation types and for its high density of hartebeest. In these respects, it was not typical of the park as a whole. Fig.2.1 shows the 7 study areas in their vegetation zones (p.50).

The vegetation of each block was described in terms of vegetation types, which were mapped (p.54). The field map of each block was divided by a grid system of numbered 1 x 1 km squares. This enabled animals, water sources etc. to be located. In the park study area, where a grid of finer scale was required, the squares measured 400 x 400 m.

Ground counts and sampling

Apart from the areas covered by the Whistling Thorn, Acacia drepanolobium, the plains are open and hartebeest are easily visible. Much of the area occupied by the hartebeest in the park is accessible even in the wet season by virtue of its dense coverage of roads and tracks. Its total area of 114 km^2 could nearly be covered in a total count of hartebeest during the daylight hours of one day. The time spent searching for them dropped as the vegetation types used by them at different times of the year were recognised, and good vantage points for scanning were found. All but the first few from a total of 16 counts took 11 hours

(± 0.5 h), during which 100 miles (± 5 miles) were driven. On the day before or after the count, the areas of dense, unburnt A. drepanolobium grassland were searched. This vegetation type is used little by hartebeest (p.259). The animals in it rarely totalled more than 50, most of which were single males. Their total was added to the total from the main count. The biases in this method were probably fairly constant between counts, and their results can be confidently compared.

The same method was used in the 7 study areas for counting the hartebeest and the other herbivores in the community study. As the main interest was the distribution of the animals when feeding, the study area sizes were chosen so that counts could be completed in the hours ⁰1630-0930. During this period, the hartebeest have an intense bout of feeding (p.210), which seems common to most herbivores. If the numbers of hartebeest and other animals in an area were low, all were counted in one morning. If the numbers were too high for the count to be finished by 0930, the hartebeest were counted on the first day, and the other species on the next day at the same time. This division was always necessary in the park.

On all counts the hartebeest were classified in to the 5 sex/age groups. Adult male hartebeest were distinguished as territorial or non-territorial, depending on whether they were alone or with other males. The presence or absence of a female herd was recorded. If a female herd contained several males, the behaviour of the males towards each other and towards the females determined whether one was territorial or all were non-territorial. Various other parameters of the hartebeest's distribution, which are described below, were measured at the same time. Information on all other species consisted only of the total number in the group, the vegetation type it was in, and its location on the grid system (above).

Observations were made through 10 x 40 binoculars. When counting the whole park, a recorder wrote down the details of herd size, its composition and location on prepared data sheets. The study area counts were

done single-handed, and any large herds of hartebeest or associations of several species were recorded on tape. These were transcribed as soon as a convenient pause in the count arose. In this way, the rare malfunctioning of the tape recorder was quickly detected and the missing observations could be repeated.

Activity

Hartebeest activity was divided into walking, feeding, lying, standing or running. On counts, the activity recorded was that performed by the majority of adults in the herd.

Vegetation sampling

On the occasion of each count, the vegetation in the 8 most extensive vegetation types in the park study area and 16 vegetation types in the 6 plains blocks was sampled.

The standing crop of herbage was measured by clipping inside 4 quadrats measuring 0.5 x 0.5 m. This was the largest number of quadrats which could be clipped in the time available. To reduce the sampling variance, the same site in each vegetation type was returned to on each sampling occasion. The quadrat was then thrown randomly from the site, landing in any direction up to 30 m away. The site at which this was done was chosen deliberately as typical of the vegetation type in terms of its species content, location, slope, grass volume etc.

All non-woody vegetation was cut to less than 1 cm above ground, collected and weighed immediately. 4 quadrats were clipped in each vegetation type and were treated separately. All were dried in a purpose-built oven at 60°C for a minimum period of 7 days, and reweighed. This allowed calculation of the water content, and the standing crop of dry, non-woody vegetation. The dicotyledonous material was then extracted by hand-sorting, and was weighed. Usually, it formed less than 10% of the total weight. The standing crop of dry grass was then calculated from the

mean weight of dry grass in each quadrat. The 4 replicates were then mixed and divided in to 2 samples for subsequent chemical analysis. This same procedure was followed when quadrats were cut for any other purpose.

At each sampling site the structure of the vegetation was assessed. The herb layer was considered to consist of successive vertical layers, 10 cm deep. With the herb layer mentally stratified in this way, the 10 cm interval in which most of the leaf table occurred was called the dominant height layer of the vegetation. It was recorded as 1 if between 0 and 10 cm above ground, 2 if 10 - 20 cm, 3 if 20 - 30 cm etc. The proportion of the ground surface covered by this layer was assessed using the categories 1-20%, 20-40%, 40-60%, 60-80% and 80-100% coverage. The area over which this assessment was made was approximately that in which a thrown quadrat might land.

The highest and lowest 10 cm layers, irrespective of their areas, were recorded in the same way, and called the maximum and minimum height layers. The density of culms was assessed in terms of 4 arbitrary categories of abundance (none, low, medium, dense) and their height layer recorded, as for the leaf table. Grass flowers were classed as absent, immature, mature or seeding. The proportion of grass leaves and stems which were green rather than brown were recorded on the 20% interval scale above. Culms were recorded as green, brown or grey.

In addition to assessing the proportion of the area covered by the dominant height layer of the vegetation, the proportions covered by bare earth, by surface rock or stones, and by dicotyledonous plants were estimated in the same way. The extent to which the vegetation was trampled was described as none, slight, moderate, severe or, if the sward was very short, as not applicable.

Certain grass species were typical of most or some vegetation types and their abundance assessed as absent, occasional, frequent or abundant. This method is described further in Chapter 5 (p. 53). The species

were Themeda triandra, Pennisetum mezianum, Digitaria macroblephara, Harpachne schimperii, Setaria phleoides, Hyparrhenia lintonii, Ischaemum afrum, P. stramineum, Cymbopogon poschpilii and Panicum sp. The abundance of the woody shrub Aspilia mossambicense was also assessed, but on the proportion of ground which it covered, as for the height layers of grass.

The grass samples were analysed at the National Agricultural Laboratory, Nairobi, for crude protein, crude fibre, ether-extractives, nitrogen-free extract (equivalent to cell carbohydrates) and inorganic ash. Energy determinations were made by bomb calorimetry on the duplicate samples in Oxford. A few samples were also subjected to proximate analyses, including determination of their in vitro digestibility, by the Agricultural Development and Advisory Service, Reading.

The measurement of rainfall and effective rain

To measure local rainfall, a storage rain gauge was set up in or near each of the 6 study areas in the plains. Their location and those of the East Africa Meteorological Department stations around the plains are considered in Chapter 4 (p. 45).

The rain gauges consisted of 18" (46 cm) lengths of cylindrical, tin fall-pipe, with a diameter of 3.5" (9 cm) on to which a bottom was soldered. These were sunk 6" in to the ground and primed with a few centimetres of water and a 1 cm layer of engine oil. The incoming rain sank below the oil and was stored without evaporative loss. The initial level was read to the nearest 0.5 mm with a dipstick, on which the upper oil surface left a clear mark. The monthly total rainfall was then taken as the differences in the level over a period of a month. Levels were measured on the last day of each month. Each gauge was uprooted, emptied and replaced when the accumulated rain was approximately level with the ground surface.

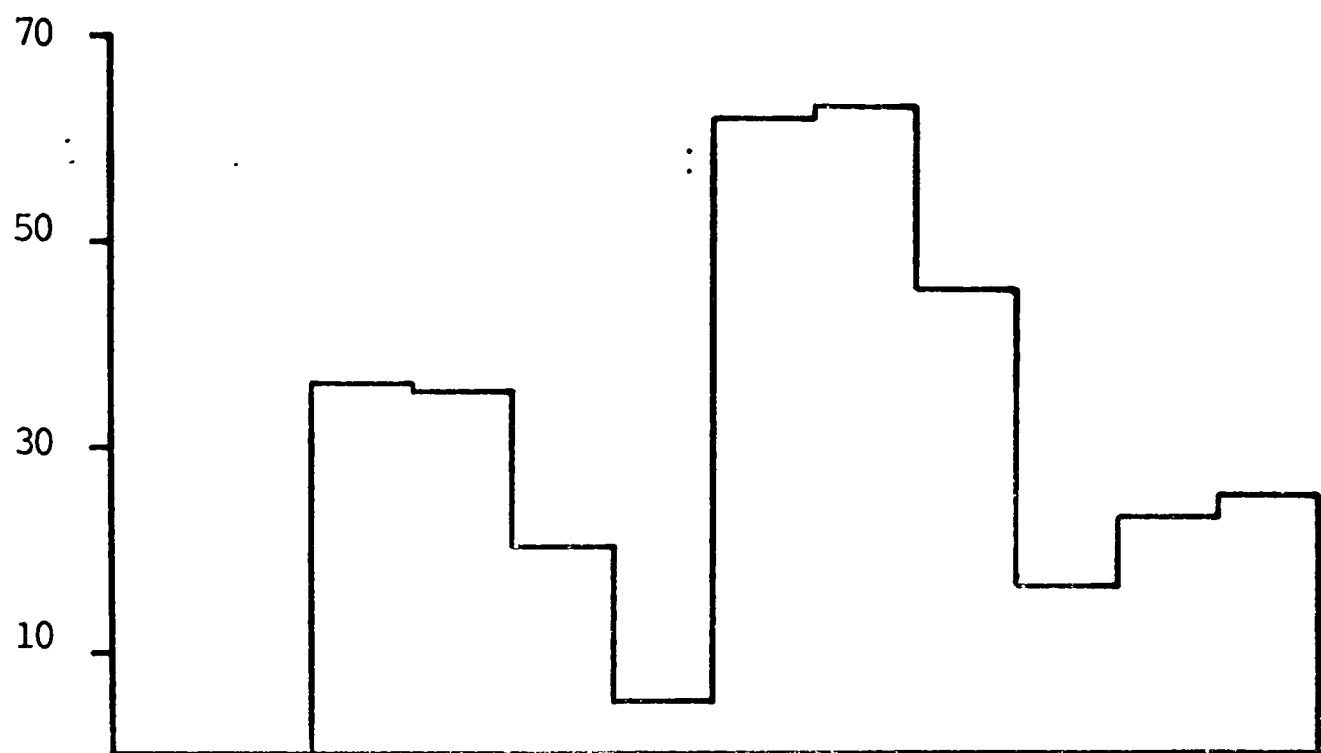
To protect the gauges a square enclosure (1 x 1 m) with 2 rails on each side was constructed of sisal poles around each. Where necessary,

further protection from cattle was afforded by a low ring of thorn branches around the enclosure. The effect of the enclosure on the collection efficiency of the gauges was assessed at Athi River, where identical, fenced and unfenced storage gauges were compared. The amount of rain caught by these gauges was also compared with the summed totals from a daily rain gauge. Over a period of 12 months, the difference in the monthly totals of the 2 storage gauges never exceeded 2 mm, and their recorded rainfall was always within 6% of the sum of the daily measurements. This allowed the results from the storage gauges to be integrated with those of the E.A.M.D. stations.

Although a rain gauge records all the rain falling, it is not all available for plant growth. The proportion lost depends on such factors as the timing and intensity of the rain, the local topography and soil, which affect the infiltration and run-off rates, and the drying power of the atmosphere. The effect of topography and soil is shown qualitatively in the next chapter. The vegetation zones of the plains differ widely in their ability to retain water through rainless months.

On the other hand, the amount of "effective rain" in a period can be estimated by taking account of the evaporative power (E_o) of the atmosphere (Barry 1969). In East Africa, monthly values of E_o fluctuate little between years because of their dependence on solar radiation (Woodhead 1968), and values for near Nairobi have been published (Woodhead loc. cit.). E_o is the potential evaporation from a water surface and therefore exceeds the rate at which plants in saturated soil will lose water by transpiration. Multiplication of E_o by 0.8 produces E_t , known as the potential evapotranspiration (Brown and Cocheme 1969). The ratio of monthly precipitation to monthly evapotranspiration, P/E_t , is a simple and satisfactory way of assessing the effective rainfall (Brown and Cocheme loc. cit.). If P/E_t exceeds 1.0, the water requirements of the vegetation are met and the soil profile is recharged with water. When P/E_t falls below

Grass moisture, %



P/E_t

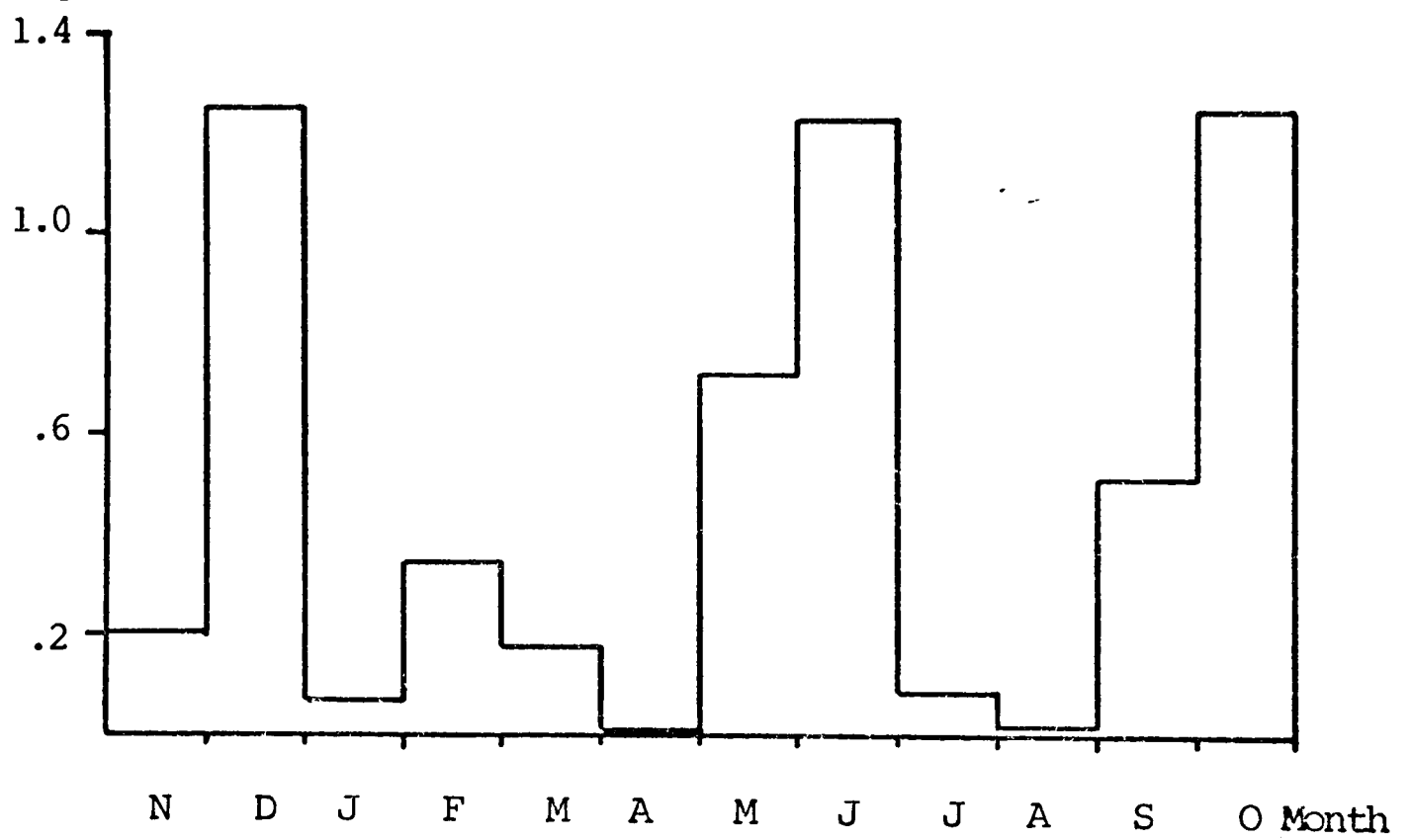


Fig.2.2. The effective rainfall, P/E_t , and the moisture content of the grass (% fresh weight) in the Nairobi Park in each month between November 1971 and October 1972.

1.0, the water stored in earlier wetter periods is used for transpiration.

The effective rainfall over cumulatively longer periods can be calculated by adding up the total precipitation and dividing it by the total evapotranspiration. Thus the effective rainfall over n months, $P/E_t(n)$, is:

$$\frac{P_1 + P_2 + P_3 + \dots + P_n}{E_{t.1} + E_{t.2} + E_{t.3} + \dots + E_{t.n}}$$

Seasonality

Rainy periods tend to start and finish abruptly in the arid parts of East Africa, and it is usually easy to describe months as "wet" or "dry". But rain has residual effects shown, for example, by the water content of grass (Fig. 2.2). The monthly moisture contents are the means of those in 8 vegetation types in the Nairobi Park (Appendix 17).

As rain stimulates grass growth at the end of a dry season, and this *represent the course of the growing season (Braun 1974)*. As the moisture content *includes the synthesis of protein, changes in the moisture content/declines*, the grass flowers and sets seed, and growth gradually ceases. Its nutritive value also declines (Milford 1969, Spahr et al. 1961). Therefore, grass moisture can be used as a simple basis for dividing or combining months in to "seasons". For the park, the months October 1971 - September 1972 have been divided in to the 3 seasons:

Season	Month	% moisture	Season	Month	% moisture	Season	Month	% moisture
Wet	Dec.	-	Medium	Jan.	36.2	Dry	Nov	-
	May	62.0	wet	Feb.	35.9		March	20.1
	June	63.0					April	5.3
	July	45.4					August	16.2
							Sept.	23.0
							Oct.	25.1

Using this criterion, the occurrence of "medium wet" months after rain depends on the rate at which the grass dries out.

This division is used in Chapter 6 in the analysis of the herbivore community.

Locations and distances

On ground counts, the distances between each group of hartebeest and the nearest water and the nearest Acacia drepanolobium were recorded. The water source had to be one at which the hartebeest would drink (see below). Both distances were recorded on the scale < 500 m, 500 - 1000 m, 1 - 2 km, 2 - 3 km, etc. A range finder showed whether the distance was less than 500 m. If greater than this, the map distance was used.

The position of the hartebeest on the valley slopes was of interest in view of the marked succession of vegetation types down the slopes of some areas (p. 37). The slopes were divided into 4 equal, horizontal bands called the ridge quarter, the upper and lower middle quarters, and the sump. These were coded as 1 - 4 respectively.

Water

After the ground counts of animals in each study area, an approximate assessment of the volume of water in the area was made by estimating the surface area of all water sources. The size of this task varied greatly between seasons. Each water source was classed as either flowing, artificial (i.e. dam), river pool, well, spring or rain pool (away from any river course). The methods used to estimate the area varied with their size and shape. Flowing rivers were usually treated as rectangles, pools as squares or rectangles, and dams as triangles. The appropriate dimensions of these shapes were measured by eye for small areas, by pacing alongside for larger areas, or with a range-finder for the largest expanses of water. The lengths of flowing rivers were taken from the map.

Not all the water in an area was available to the hartebeest for drinking. The sites and situations in which hartebeest were seen to drink in the Nairobi Park were used as a basis for a fairly intuitive

judgement as to whether a water source in the plains would be used by them. The types of site which were considered to be used, subsequently turned out to be similar to those described by Jarman and Mmari (1971). River pools lying in deep gorges were considered unavailable. In the plains I had no evidence of hartebeest drinking from concrete troughs at man-made bore-holes, but they drink from mud-troughs, built by the Maasai in the dry season to hold water lifted from wells in river beds. The hartebeest are claimed to damage these troughs when drinking from them and they are emptied when the cattle have finished. The surface area of all these sources was estimated and recorded as "unavailable". In the relatively well-watered park, the surface area of only the available water was measured.

The collection of hartebeest

Hartebeest were collected periodically to examine their rumen contents, physical condition etc. The size and composition of the samples and their frequency are described on p.151. Within a sample the animals were not selected randomly. The first choice depended on whether an adult male, female or an immature animal was required. Within any of these groups except the adult females, no particular choice was made, but the sample may be biased towards containing relatively approachable animals. No adult female with a calf which was not at least partly weaned (more than 3 - 4 months old), was taken, unless the calf was also taken. The under-representation of females with young calves in the sample might lead to biased estimates of the proportions of females in various reproductive states in the population. But as a total of only 25 females was collected, this bias is likely to be small compared with the sampling error associated with small sample sizes.

A Winchester rifle with a $2\frac{1}{4}$ x telescopic sight was used to shoot the animals. A neck shot, advocated by Hofmann and Scholz (1968), from a distance up to 120 m resulted in instantaneous death without damaging

the internal organs. The carcass was weighed intact (dead weight) using a tripod and pulley, and scales with a 2 lb (0.9 kg) interval. External measurements of the body were made over the curve with a steel tape measure, and recorded to the nearest 1 mm. The hind foot length was taken from the outside of the leg from the tip of the hock (tuber calcis) to the tip of the hoof with the lower part of the leg fully extended. The head was taken from the field for subsequent ageing of the animal from the dentition.

Internal organs, foetuses, muscles etc. were weighed on a triple-beam balance with an accuracy of 0.1 g. The procedures for sampling the rumen contents and fat reserves of the body are described later in the appropriate places. Material from these animals was also used by a variety of other research workers with the following interests: external and internal parasites, tissue culture, serology, virology (Reid and Rowe 1973), the histology of the female reproductive tract (Kayanja and Stanley Price 1973), and the structure and secretions of the interdigital and antorbital glands.

For the analysis of the results, the animals were divided into 7 groups according to their social or physiological status. Single males with or without females were called territorial, and a male shot from a group was non-territorial. Four female groups were defined on whether each animal was either pregnant or non-pregnant, and either lactating or dry. The immature animals formed a seventh group.

Miscellaneous

To determine the areas of the park, the plains, the study areas and their vegetation types, the shape of each on a map of known scale was cut out of heavy typing paper. As the surface area is proportional to the weight of each cut-out, values for their absolute areas were determined from comparison of their weights with those of paper squares of known areas.

Table 2.1. The information collected, with its variable names, at each hartebeest sighting.

<u>Variable</u>	<u>SPSS name</u>	<u>information</u>
1	MONTH	sample month
2	BLOCK	study area identification
3	SIGHTING	sighting number
4	HOUR	hour of day
5	KONGDENS	total hartebeest in herd
6	MALES	no. of males in herd
7	FEMALES	no. of females in herd
8	SUBADS	no. of subadults in herd
9	JUVS	no. of juveniles in herd
10	NEWBORN	no. of newly-born calves in herd
11	SOLITERR	presence/absence of territorial male without females
12	ACCTERR	presence/absence of territorial male with females
13	BACHELOR	no. of non-territorial males
14	VEGTYPE	vegetation type
15	CATPOS	position on the catena
16	WATER	distance to nearest water
17	ACTIVITY	the herd's activity
18	DREPDIST	distance to nearest <u>Acacia drepanolobium</u>
19	LOC	grid square location

Table 2.2. The information collected, with its variable names, for each vegetation type in the community study.

<u>Variable</u>	<u>SPSS name</u>	<u>information</u>
1	MONTH	sample month
2	YEAR	1971. or 1972
3	BLOCK	study area identification
4	VEGTYPE	vegetation type to which following data refers
5	CATPOS	catena position of sampling site
6	WATER	distance from the nearest water
7	DREPDIST	distance from the nearest <u>A. drep-anolobium</u>
8	DOMHTVEG	dominant height layer of herb layer
9	MAXHTVEG	maximum height layer of herb layer
10	MINHTVEG	minimum height layer of herb layer
11	DOMCOV	ground coverage by DOMHTVEG
12	BARECOV	extent of bare earth
13	ROCKCOV	ground coverage by rock, stones
14	VEGGREEN	vegetation greenness
15	DICOTCOV	coverage by dicotyledonous plants
16	FLOWER	grass flower stage
17	CULMHT	maximum height layer of culmes
18	CULMDENS	culm density
19	CULMCOLOUR	culm colour
20	TRAMPLE	degree of trampling
21	THEMLDA	abundance of <u>Themeda triandra</u>
22	PENNIS	abundance of <u>Pennisetum mezianum</u>
23	DIGIT	abundance of <u>Digitaria macroblephara</u>
24	HARP	abundance of <u>Harpachne schimperii</u>
25	SETAR	abundance of <u>Setaria phleoides</u>

Table 2.2 continued.

<u>Variable</u>	<u>SPSS name</u>	<u>information</u>
26	HYPAR	abundance of <u>Hyparrhenia lintonii</u>
27	ISCHAF	abundance of <u>Ischaemum afrum</u>
28	STRAM	abundance of <u>P. stramineum</u>
29	CYMB	abundance of <u>Cymbopogon poschipilii</u>
30	PANIC	abundance of <u>Panicum</u> sp.
31	ASPILIA	ground coverage of <u>Aspilia mossambicense</u>
32	CROP	grass dry standing crop, kg/ha
33	MOISTURE	moisture content of grass
34	AREA	area, km ² , of vegetation type
35	LOC	grid squares location
36	CATTLE	cattle numbers in vegetation type
37	WILD	wildebeest numbers in vegetation type
38	ZEBRA	zebra numbers in vegetation type
39	THOMMY	Thomson's gazelle numbers in vegetation type
40	GRANT	Grant's gazelle numbers in vegetation type
41	IMPALA	impala numbers in vegetation type
42	HOG	warthog numbers in vegetation type
43	WATBUCK	waterbuck numbers in vegetation type
44	OSTRICH	ostrich numbers in vegetation type
45	ELAND	eland numbers in vegetation type
46	GIRAFFE	giraffe numbers in vegetation type
47	SHOAT	sheep and goats number in vegetation type
48	KONGONI	hartebeest numbers in vegetation type

Table 2.2 continued

<u>Variable</u>	<u>SPSS name</u>	<u>information</u>
49	ALLWAT	total surface area of water, m ² .
50	FLOWING	area of flowing water, m ² .
51	DAM	area of water in dams, m ² .
52	POOL	area of river pools, m ² .
53	WELL	area of water in wells, m ² .
54	SPRING	area of spring water, m ² .
55	TEMP	area of rain pools, m ² .
for the plains only		
56	AVAIL	total area of water available to hartebeest, m ²
57	UNAVAIL	total area of water not available, m ² .

The taxonomic names and authorities of the animal species mentioned in the text are presented in Appendix 1 . The mean adult weights used to calculate biomasses^{are}/shown in Appendix 2 , with their sources.

2.3 Data analysis

Ground-work in the 7 study areas of the park and plains resulted in a large mass of data on the numbers, distribution and habitat utilization of the hartebeest and 12 other species. Anything but the simplest analysis required the storage of this mass of information in the computer, from which it could be accessed and manipulated.

The information was divided in to 2 parts. The first concerned the hartebeest alone, the second all the herbivore species. For the first, the size and composition of all hartebeest herds were recorded in the field on to computer coding sheets. As "herd" here includes a single male, the term "sighting" is preferable. Table 2.1 shows the information collected for each sighting as 19 variables. This information was punched on to computer cards with one sighting as the basic unit, or case.

Information on the community was contained in a total of 57 variables (Table 2.2). Many of the variable values, such as the total amount of surface water were the result of adding up all the component values. This was done at the end of field-work. Each case in this file is one vegetation type, identified as variable 4. The number of each herbivore species, the amount of water, the vegetation parameters and the area all refer to one vegetation type.

To analyse this data the Statistical Package for the Social Sciences (Nie, Bent and Hull 1970) was used. Known as SPSS, this package is available as a library programme for the Oxford University ICL 1906A computer. The mixture of variables (Tables 2.1, 2.2) with either continuous values (e.g. CROP), or with an interval scale (e.g. DOMHTVEG) or with arbitrary categories (e.g. TRAMPLE) are similar to those encountered in social science research. Therefore, SPSS seemed suitable for this

data. Its repertoire of analytical techniques includes the following:

- one-way frequency distributions
 - table displays of the relationships between two or more variables.
- Both of these facilities have a range of descriptive statistics.
- bivariate correlation analysis.
 - multivariate correlation and regression.
 - factor analysis techniques including principal components analysis.

The most characteristic feature of SPSS is its flexibility. This applies to the format of the data, the extent to which the files can be manipulated, and new variables added or others deleted. It can also give variables new values, select specified cases for calculations, handle missing data and provide optional statistical tests with each run. This flexibility is demonstrated after describing the file structures.

Information on the hartebeest herd size and structure and their distribution (Table 2.1) was stored as file AKHART (Athi-Kapiti hartebeest) for the plains and as file NNPHART (Nairobi National Park hartebeest) for the park. Within each, the data cases of individual sightings were divided by giving the SPSS file a subfile structure, based on the month in which the data were collected. Because 12 counts were made in the park and only 3 in the plains (p.11), NNPHART had 12 subfiles, while AKHART had 3. As a safety measure and as an aid to data selection, the month was also coded as a variable (variable 1 in Table 2.1). Within each subfile further division was possible so that data from each of the 6 blocks could be identified and accessed separately. This was done by variable 2 (BLOCK) which specified whether the data referred to block 15, 22, 30, 35, 39 or 62. In the Nairobi Park data this variable was assigned the value of 00 throughout.

The data on the animal community and environment were held in 2 files called AKCOM and NNPCOM for the Athi Plains and Nairobi Park respectively. Both also contained the subfile structures of 3 and 12 months,

and the block identification variable (BLOCK). Within each block, variable 4 (VEGTYPE) identified the vegetation type to which the data referred. The identification number of each vegetation type was that used later when describing them (Ch. 5). Also included in the data of each block was a vegetation type, numbered 99, which contained the sum of all the animals of each species and of water recorded in each of the block's component vegetation types. The vegetation parameters in this case were assigned values which had been defined as missing for computational purposes. The inclusion of vegetation type 99 imposed a hierarchical structure on the file: the data referring to either the whole block or separate vegetation types could be analysed, and the steps required to specify which was required are described below.

Most of the analytical methods of SPSS mentioned above were employed at some stage of the analysis. Almost continuous use was made of the capacity of SPSS to extract data and present them broken down by time or place. This capacity illustrates the programme's flexibility, referred to above. Within a file, the subfile structure allows a computation to be performed on the data from all the months together or any combination of them, by using the PROCESS SBFILES instruction. If one is interested in the changes in one vegetation type (e.g. 02) between months, the instruction:

```
SELECT IF          (VEGTYPE EQ 02)
```

causes the subsequent task to be performed on cases referring to vegetation type 02 only. The SELECT IF instruction is used on each run with the community files. "SELECT IF (VEGTYPE EQ 99)" causes the summary data for the whole block to be used (above). If "SELECT IF (VEGTYPE NE 99)" is used with NE (not equal to) replacing EQ (equals), the task is run on the information on each vegetation type.

Obviously, more complicated data-selection procedures are possible. For example:

LE NNPCOM2 (CREATION DATE = 31/07/73) NAIROBI PARK COMMUNITY FILE 2
BFILE DEC MAY JUNE JULY

ITERION VARIABLE GRANT
BROKEN DOWN BY CROP
DESCRPTION OF SUBPOPULATION
GRANT NOS
STANDING CROP KG/HA

VARIABLE	CODE	VALUE LABEL	MEAN	STD DEV	VARIANCE	N
FOR ENTIRE POPULATION			16.613	16.885	285.112	31
CROP	2.00	400-800	34.000	10.100	102.000	4
CROP	3.00	800-1200	16.125	17.545	307.839	8
CROP	4.00	1200-1600	16.600	14.381	206.800	5
CROP	5.00	1600-2000	21.000	22.379	500.800	6
CROP	6.00	2000-2400	10.000	14.142	200.000	2
CROP	7.00	2400-2800	4.750	5.620	31.583	4
CROP	8.00	2800-3200	0.000	0.000	0.000	1
CROP	9.00	GT 3200	2.000	0.000	0.000	1

TOTAL CASES = 31

Fig.2.3. A specimen output from SPSS.

PROCESS SBFILES (APRIL, NOVEMBER)

SELECT IF (VEGTYPE EQ 02 OR VEGTYPE EQ 05)

This would cause only those cases referring to vegetation types 02 and 05 in April and November to be used.

New variables are created by the instruction COMPUTE. Using the area of each vegetation type (variable 34, Table 2.2), the densities of animal species, surface water etc. can be calculated in the following way:

COMPUTE (ZEBRA / AREA) = ZEBDENS

ZEBDENS, the density of zebra, is a new variable, and can be stored in an up-dated version of the file.

SPSS has been used in this way to create many variables including those of the density, biomass and biomass density of animals. With the data selection facility, the values of these variables can be broken down in innumerable ways. Fig. 2.3 shows, for example, the distribution of Grant's gazelle in December, May, June and July combined, in areas of different standing crops of grass. These crop categories have been created from the range of continuous values for this variable (p.122) by the RECODE instruction.

Extraction of such results by hand would be extremely time-consuming. The main use of SPSS has been to output such results to be used as input for smaller programmes, written for specific purposes. Calculation of the diversity and overlap indices in Chapter 7 was only practical with this capability.

Chapter 3.

THE TOPOGRAPHY, GEOLOGY AND SOILS OF THE ATHI PLAINS

3.1 The Athi Plains as a unit

The Athi Plains cover 4100 sq. km., lying immediately south, but extending to the north-east, of Nairobi in central southern Kenya. The township of Athi River, at $37^{\circ}00' E$, $1^{\circ}25' S$ and an altitude of 1540 m. (5000 feet) a.s.l. is approximately at the centre of the plains, and is situated on the Athi River which is the main drainage system of the area (Fig. 3.1).

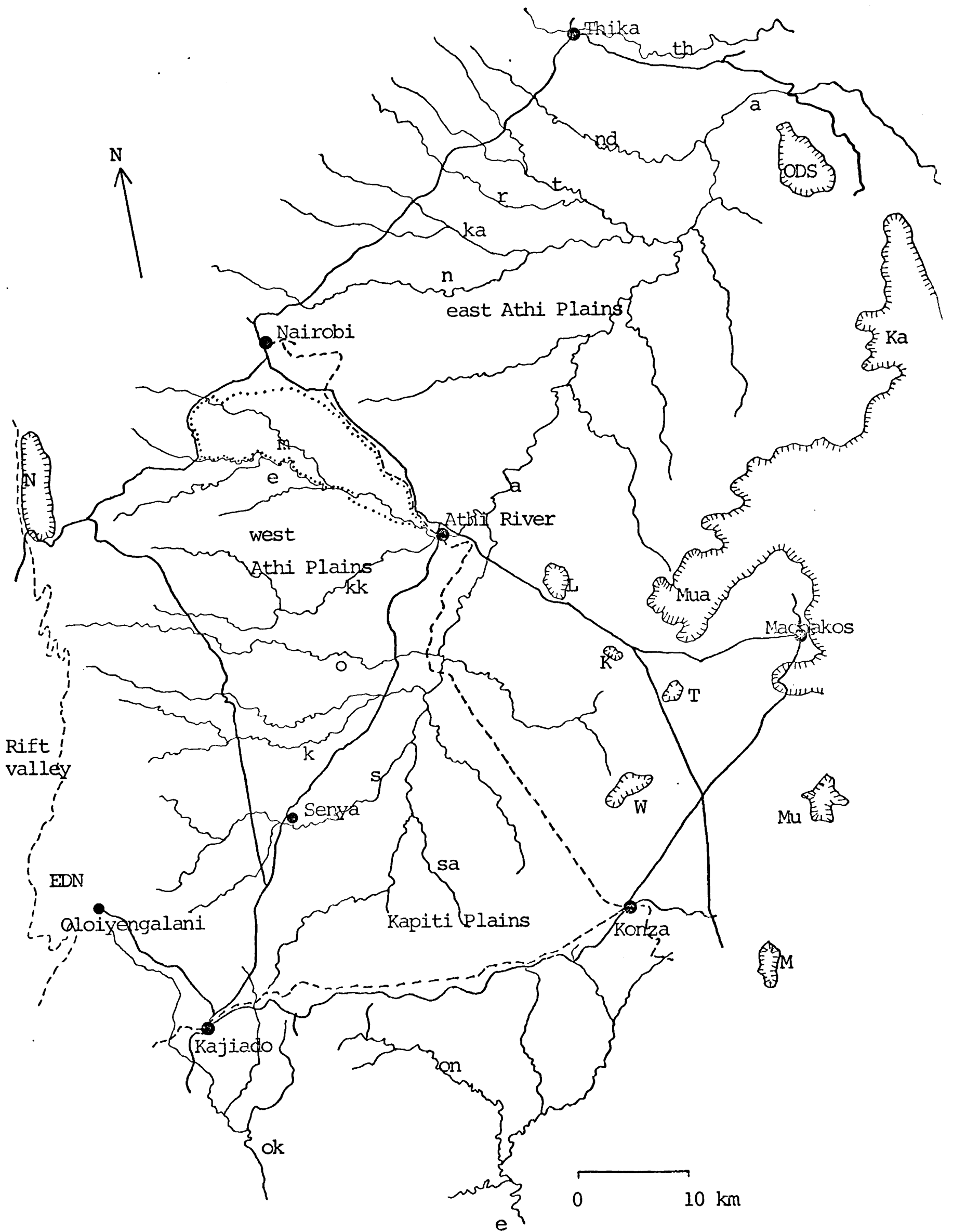
The boundaries of the plains are naturally distinct on the basis of abrupt changes in the topography. In the west, the plains rise to approximately 1900 m., ending as the escarpment of the east side of the Rift Valley. The escarpment which runs due north-south joins the Ngong Hills at its northern end, and with its almost vertical drop of 1000 feet it marks a drastic change in topography, climate and vegetation and is a major watershed. Surface water from this side of the plains is collected mainly by the Kitengela, Loitigoshi, Kesajui and Senya rivers and their tributaries, all of which join the Athi River.

The higher land to the north, with its indigenous forest vegetation (Ch. 5) forms the north-western boundary of the plains, with Nairobi at the junction of these two major zones. This area has a considerably higher rainfall than the plains (p. 43) and is drained by a number of rivers, notably the Nairobi, Ruiru, Thiririka, Ndaruga and Komu, all of which flow south-east in to the plains to join the Athi River. The Thika river also runs off these highlands and marks the extreme north-east extent of the plains.

The plains are limited along their eastern edge by their junction with the hill ranges of the Wakamba Reserve. The main hill ranges, rising sharply from the plains to approximately 6400 feet, run in a general

Fig.3.1. The geography of the Athi Plains.

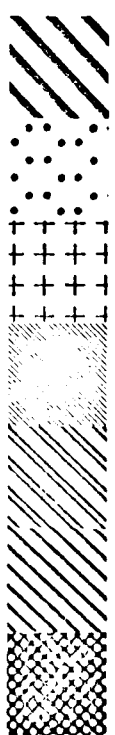
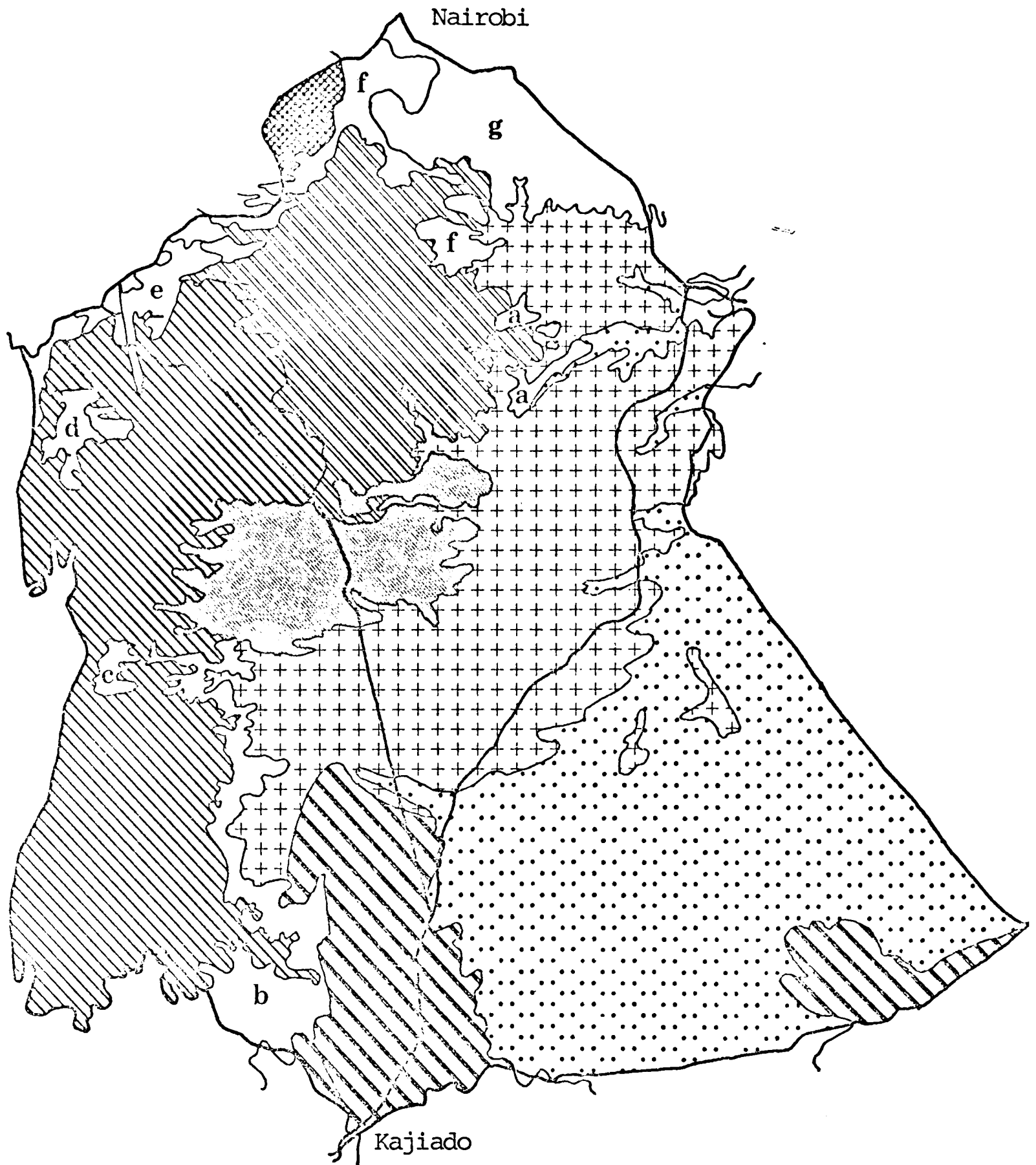




north-south direction and consist of Ol Doinyo Sabuk, the Kanzalu range, Kangundo Hill, the Iveti and Mua hills, Mumandu and Mulumini. The drainage system of these hills is more developed on their east-facing sides, with the result that most of their surface water does not flow across the Athi plains to join the Athi River.

The southern boundary of the plains between Konza and Kajiado is marked by a change in topography and vegetation from open, undulating country to an area of thick bush which drops in altitude southwards. This junction with the plains is a watershed and the area to their south is drained by a south-draining system, including the Olkejuado and Eselenkei rivers. The most southern plains are drained by the Olturoto river and its tributaries which run north-wards to join the Stony Athi river and then the Athi River.

The Athi Plains are, therefore, a natural physiographic unit, contained by higher ground on their north and east, and by lower ground to their south and west. Until the beginning of this century the plains were also an ecological unit, supporting the most spectacular concentrations of wildlife in East Africa (Simon 1962). Subsequently, the plains to the west of the Konza-Athi River - Nairobi railway line were settled for European ranching, leaving only the area to the east of this line for the original Maasai inhabitants to continue their traditional pastoralism. The cumulative effects of these two forms of land use over 60-70 years have been considerable, and today the remaining wildlife populations especially of the migratory species, are almost confined to the Maasai portion of the plains. The hartebeest was studied only in the latter, which is distinguished as the "west" plains, with an area of approximately 1850 sq. km., as opposed to the slightly larger "east" plains extending to Thika (Fig.3.1). The west plains include the Nairobi National Park, and the significance of this different form of land use in the ecology of the west Athi Plains has been mentioned (p. 7).



Basement system

Kapiti phonolite

Upper Athi tuffs

Olorgesailie phonolitic nephelinite

Mbagathi trachyte

Ol Doinyo Narok agglomerate

Nairobi trachyte

a Basement rocks

b Olorgesailie biotite phonolite

c Phonolite in Ol Doinyo Narok agglomerate

d Ol Esayeiti phonolite

e Ngong mixed volcanics

f Kerichwa Valley tuffs

g Nairobi phonolite

Fig.3.2. The geology of the Athi Plains.

3.2 Geology and topography

East Africa lies in a volcanic zone stretching from Ethiopia to Malawi, and although relatively quiescent now, its earlier activity is largely responsible for the contemporary physiography of much of Kenya. The Athi Plains were formed by volcanic activity, and the following description shows how the underlying rock formations have determined the present topography and drainage systems. This leads to a discussion of the soils of the area, and their combined influence is reflected later (Ch. 5) in the patterns of vegetation cover over the Athi Plains.

Description of the geology relies on the publications of Baker (1954), Saggerson (1971), Matheson (1966) and Fairburn (1963). Scott, Webster and Lawrance (1971) have described the land surfaces of the Athi Plains, and their names are used for the land systems. These are areas composed of recurring land facets, and can be mapped at scales of 1:250,000 to 1:1,000,000 (Scott, Webster and Lawrance loc. cit.).

The Athi-Kapiti Plains are composed, essentially, of successive layers of lava extruded from the nearby volcanos of the Rift Valley and overlying the Basement System rocks (Fig. 3.2). These rocks were laid down in the Archaean Period of the Precambrian as sediments, which have been metamorphosed and locally granitized to a variable extent. The end product is generally a crystalline, granitoid gneiss, and a sample from the area is dated at 505 ± 2 million years.

The post-Archaean and Early Tertiary period was one of repeated uplift and erosion, and by the late Cretaceous (70 million years ago), a peneplain covered the whole area. The existence of the peneplain is inferred from the roughly equal heights of the Wakamba mountains which rise to 6400 feet and are composed of the harder rocks of the Basement Series. Further erosion in the Early Tertiary produced a new base level 2300 feet lower, only leaving as relics these hills and the inselbergs of Kyumvi, Theki and Wami, with the newly-formed sub-Miocene peneplain

on either side. Even then, the watershed formed by these mountains must have been of some importance because of the north-eastern course across the Athi Plains of the Athi River, which runs round the northern end of the range before turning southwards to collect the drainage from its eastern face.

This long period of volcanic inactivity ended 13 million years ago, at the beginning of the Miocene, with the eruption of volcanos to the west of the peneplain, associated with the formation of the Rift Valley. Much of the surface of the peneplain was covered by Kapiti Phonolite lava which extended as far as Ol Doinyo Sabuk, and now forms the Kapiti Plains. As part of the Athi land system, these are extensive, undulating plains of low interfluves and gently convex slopes.

South of the Kapiti Plains, the Basement System rocks have no capping of lava with the result that they have eroded to a new base level 800 feet lower, now forming the Maiyani Variant land system. As the drainage area of the Olkejuado and Eselenkei rivers, this is characterised by extensive ridges of steep or moderately steep slopes and valleys with a dendritic pattern. The junction of this land system with the Athi system of the Kapiti plains marks the southern boundary of the Athi Plains.

Overlying the Kapiti Phonolite on its west side is a thick deposit of lava, called the Upper Athi Tuffs. The occurrence of fossil molluscs in stratified rock indicates that these sediments were laid down in a shallow lake which extended from Nairobi to the Athi River and as far as Thika. Such tuffs are friable and therefore only form a capping over the Phonolite, rather than building any pronounced features. The plains above this rock are also part of the Athi land system, but have a higher and steeper relief with broader flood plains than the Kapiti Plains.

The rocks of the Basement System also outcrop in the plains in an area of 7 x 14 kms. north of Kajiado and in a smaller area west of Konza. These outcrops form the Ndolo land system and are limestone erosion

surfaces developed only in Pleistocene and Recent times. Reaching 5800 feet the area is one of low ridges and plains with river courses at the edges, and is therefore higher and less dissected than the Maiyani land system.

The rest of the west plains belongs almost entirely to the Embakasi land system, which consists again of plains of low gradient with few small drainage lines but many parallel river courses developing in to deep gorges as they approach the plains of the Athi system. Because the rocks of this system are younger and harder, this system forms a ridge of land about 200 feet higher than the Athi Tuffs and the Kapiti Phonolite, and ends in an escarpment at its eastern limit.

This ridge of high land is formed by the rock of three groups of lava flows. The first and oldest is the Mbagathi Trachyte whose flow over the Upper Athi Tuffs produces very gentle undulating plains and ends in an escarpment on the Kitengela river. Above this rock, lies the second group of the lavas of the Olorgesailie series, which also originated from the Rift Valley between 5 and 10 million years ago. The oldest of these, the Olorgesailie Biotite Phonolite, now only outcrops in a thin band around the southern edge of En Doinyo Narok. To the north of this, a flow of Olorgesailie Phonolitic Nephelinite forms the ridge of Loitigoshi which ends again as a prominent escarpment over the Upper Athi Tuffs, but abuts the Mbagathi Trachyte on its north side without any major discontinuity.

The youngest rock of this series is the En Doinyo Narok Agglomerates which forms the high crest of the Rift Valley escarpment at about 1970 m. The Agglomerate is coarse and hard, producing the scarps of En Doinyo Narok; passing north the rock becomes more tuffaceous and has been eroded more severely, producing a more even topography. Consequently, the northern areas of this lava are more rounded in appearance and they merge without any unconformity with the Olorgesailie Phonolitic Nephelinite and the Mbagathi Trachyte.

The third major rock type in the Embakasi system is the Nairobi Phonolite which only just extends in to the west plains as a flat area in the east end of the Nairobi Park. Again, this rock forms an escarpment of 100 feet where it terminates over the Upper Athi Tuffs. Locally, a surface breccia of this rock is found.

During the Pliocene there was also a slight eastward flow of lava from the Rift Valley volcanos of Ol Esayeti and the Ngong Hills. Rock from the Ol Esayeti Series is seen only locally in the north-west of the plains as Oligoclase Tephrite and Ol Esayeti Phonolite. The Ngong volcanic rocks do just intrude in to the plains and are represented by Tephrite Basanites and mixed rocks. These rocks have no significant effect on the physiography of the area.

The northern boundary of the plains is marked by an escarpment which forms the beginnings of the Kikuyu Highlands. This discontinuity is formed by a flow of Nairobi Trachyte which extends in to the Nairobi Park as the Karen land system, represented here by low hills and small plains with river beds in steep-sided valleys. Following the deposition of this lava there was a period of quiescence and erosion, and deep valleys were cut. In the vicinity of Nairobi these were subsequently filled in by flows of Kerichwa Valley Tuff lava, dated at 1.7 million years. Further towards Thika, the edge of the plains is delimited by the southernmost extent of this rock. The accumulated thickness of the Nairobi Trachyte and the Kerichwa Valley Tuffs is responsible for the major differences in climate and vegetation which naturally distinguish these highlands from the plains.

3.3 Soils of the Athi Plains

Although the soils of the Athi Kapiti Plains are mostly residual weathering deposits (Fairburn 1963), their composition is controlled more by their situation and conditions of formation than by the present rock. Thus, Gethin-Jones and Scott (1970) show the soil of almost the whole

west plains as their type 22, "Black clays (grumosolic soils). Consist of a range of "Black Cotton" soils and include the calcareous and non-calcareous variants. They are mainly derived from colluvium and occur on plains varying from sea-level to 2000 m. Rainfall 400-1100 mm."

The other main type of soil found is over the Upper Athi Tuffs lava. Although its development has been influenced by the topography, it is distinguished by its derivation from lacustrine deposits, and is a dark grey-brown calcareous clay loam.

The influence of the topography in the formation of the soils has been mediated through its effect on water movement. This is seen best in the northern part of the Athi Plains where the land relief of the Embakasi system is more pronounced. On these slopes, a succession or catenary sequence of soils occurs.

The term "catena" was proposed by Milne (1935) as a unit of convenience when mapping soil at an intermediate level of detail in East Africa. Although the soils of a catena might be structurally diverse and might have been derived from different parent materials, he stressed that the characteristic features of these soils were due to topographic conditions, and these would be repeated wherever the same conditions were found. Although it was recognised that each soil zone would carry a characteristic-plant cover, this was not central to the definition or recognition of a catena.

This association was more important to Morison, Hoyle and Hope-Simpson (1948) who defined a catena as a grouping of soil/vegetation types. Their thesis was, basically, that in the seasonally dry tropics, the development of the soil of a site is mainly determined by the local topography through its effect on water movement. Thus, three soil phases are recognisable.

1. The eluvial soils are found on the ridges and suffer the downward washing of their particles or surface erosion. They are, consequently, shallow and coarse.

2. Colluvial soils are found on the slopes. They both receive material from above and lose it towards the sumps, while acting as a filter mechanism. They are deeper than the eluvial soils, becoming progressively finer down the slope.

3. The illuvial soils of the sumps receive this suspended material while losing little. They are therefore, deep and heavy.

The actual pattern of these zones depends on the micro-relief and the nature of the drainage. If water flows away freely, the phases will be zoned; if the drainage is impeded, a mosaic pattern is produced because of minor differences in relief.

Like the Sudan where this catenary sequence was recognised, the Athi Plains lie in the seasonally dry tropics, and the same basic sequence can be observed. Therefore, this association of soil and vegetation due to position on the slope is used as the basis for the definition and classification of vegetation types (Ch. 4). Typically (e.g. Morison, Hoyle and Hope-Simpson 1948, Bell 1970), a catenary sequence develops on slopes which level out towards their sumps, producing a concave cross-section. However, in the Athi Plains, there are areas where the ridges between adjacent valleys are broad and flat, and the gradient increases towards the sumps. Such slopes are convex in section, and the development of the soils has been slightly different. The ridges are the areas of shallow slope and impeded drainage with the typical illuvial soils and vegetation of these conditions, although little material can be washed in to them from elsewhere. The middle and lower slopes are more freely drained and on these are found the more leached soils. These are generally red or strong brown friable clays with a lateritic horizon, and may be derived from transported material (Gethin-Jones and Scott 1970). The sumps occupy only a small area because adjacent slopes usually meet in a narrow, steep-sided river bed, often lying in a gorge. Under these conditions their soil is well-drained, shallow and stony.

The plains contain areas with both the normal and reverse catenary sequences of soils and vegetation although the development of the sequence has not been uniform throughout the area. Locally, there are also variants of these basic types, such as the shallow soil on the Basement rock in the plains which contains large numbers of limestone fragments, which affect its plant cover. This close association between the soil and the vegetation it supports forms the basis for the detailed classification of the latter (Ch. 5).

Chapter 4.

THE CLIMATE OF THE ATHI PLAINS AREA

4.1 Introduction

The dominant influence on the weather of Africa is the low pressure zone known as the inter-tropical convergence zone (ITCZ) (Brown and Cocheme 1969). Because of the annual north and south oscillation of this zone, areas near the equator are affected by its associated weather twice a year. Thus, Nairobi, at 1°17' South, has a distinct bimodal or equatorial pattern of rainfall, compared with the tropical regime of one rainy season in areas further north and south.

On the east side of Africa, the prevailing winds blow from the Indian Ocean, with an effect on the weather which gradually decreases inland. Similarly, winds from the Atlantic Ocean affect the climate of the West Coast of the continent. This latter influence does extend as far as the East African highlands, but its influence on the weather of the Nairobi area is negligible (Brown and Cocheme loc. cit.). The large inland water mass of Lake Victoria (area 83,000 sq. km.) also has a considerable effect on rainfall locally (Norton-Griffiths, pers. comm. 1974) but is only of importance west of the Rift Valley. Thus the weather systems of the Nairobi area and Athi Plains have a predominantly eastern origin.

Rainfall distribution in East Africa is highly irregular in time and space, and water resources are usually the limiting factor in the assessment of site potential or in any land development scheme (Kenworthy 1964). Thus rainfall is the most important meteorological element and is considered in greater detail in subsequent sections.

The effects of the climate on the large mammal populations are many. The advent of rain at the end of a dry season signals the beginning of a period of vegetative growth, with its accompanying effects on herbivore

Table 4.1

Mean monthly and annual rainfall at Nairobi, 1931-1960 (m.m.)

Jan	Feb	March	April	May	June	July	Aug	Sept	Oct	Nov	Dec	Year
35	48	119	201	128	41	15	24	24	53	98	69	855

distribution (Ch. 6) and their diet (Ch. 8), food intake (Ch. 9) and water requirements (Ch. 14). Seasonal changes in the other main parameters of climate probably have less impact on the herbivores, but, instead, their diurnal variation may be of greater consequence and importance in affecting the activity of animals within a 24 hour time-span (Ch. 11).

4.2 Annual rainfall cycle

Although rain has been recorded in Nairobi at least once in every month of the year between 1931 and 1960, giving a mean annual rainfall of 855 m.m. (Thompson and Sansom 1967), the monthly distribution of rainfall is most uneven (Table 4.1).

During the North-East Monsoon period from December to mid-March there is a persistent north-east wind and a low rainfall. This period is known as the 'short' dry season. In late March the winds become lighter and more variable and move to the south east as the high pressure zone over southern Africa intensifies. This is associated with the breaking of the 'long' rains which may continue until the end of May, with April as the wettest month with an average rainfall of 201 m.m. As the long rains end, the South East Monsoon blows strongly, producing a long dry season from June to October. Although this dry season is the longer of the two, its mean air temperatures are lower, so that its effect on the vegetation and water resources may not be as severe as that of the short dry season. During October the winds again drop and in November move north-east again because of the development of a high pressure ridge over North Africa and Arabia, which heralds the arrival of the 'short' rains. November is the wettest month of these rains with an average of 98 m.m. of rain at Nairobi.

The annual rainfall at Nairobi is highly variable (Thompson and Sansom 1967), which is characteristic of tropical regimes. Over the years 1931-1960, the total has ranged between a minimum of 487 m.m. and

a maximum of 1526 m.m. The upper and lower quartiles which represent the range of rainfall in which half the actual rainfall totals have occurred (so that any total has a 50% probability of falling inside or outside these limits), are 1033 and 667 m.m. respectively. Variability of the same order is found at Kajiado at the southern edge of the plains, although it has a considerably lower mean annual rainfall (485 m.m.).

This variation in annual rainfall shows a periodicity over a short time scale (Lumb 1972). Analysis of the rainfall records for Machakos, where the rainy seasons are the same as those of the Athi Plains, shows that in each decade, since 1896 when records began, there have been two consecutive years of greater than average rainfall at 10 or 11 year intervals. Such wet years are usually those of maximum sunspot activity, although there is a nearly perfect coincidence of the first wet year occurring three years after the year of minimum activity in that decade.

This relationship obviously has predictive value, even if the relationship between sunspot activity and rainfall maxima is only one of association rather than causation. From the point of view of the present study it is significant that 1970-1972 were years of less than average rainfall. Furthermore, in the decade of 1960-1970 the wettest years in this cycle were 1967 and 1968 (Table 4.2), which, with late 1966, was the period of study of Gosling. Such large differences in rainfall might result most obviously in differences in the primary production and its subsequent utilisation by the herbivore species. Therefore, the different climatic conditions must be considered in any comparison of the animal populations in the two periods.

Table 4.2 Annual rainfall totals at Wilson Aerodrome, Embakasi and Machakos, mm

	1964	1965	1966	1967	1968	1969	1970	1971	1972
Wilson	818.0	889.7	889.8	1234.4	1099.8	848.0	908.9	936.1	831.7
Embakasi	572.4	408.1	571.3	940.1	984.8	603.5	786.7	738.4	644.0
Machakos	753.2	701.7	739.2	1039.2	1474.1	776.0	-	-	-

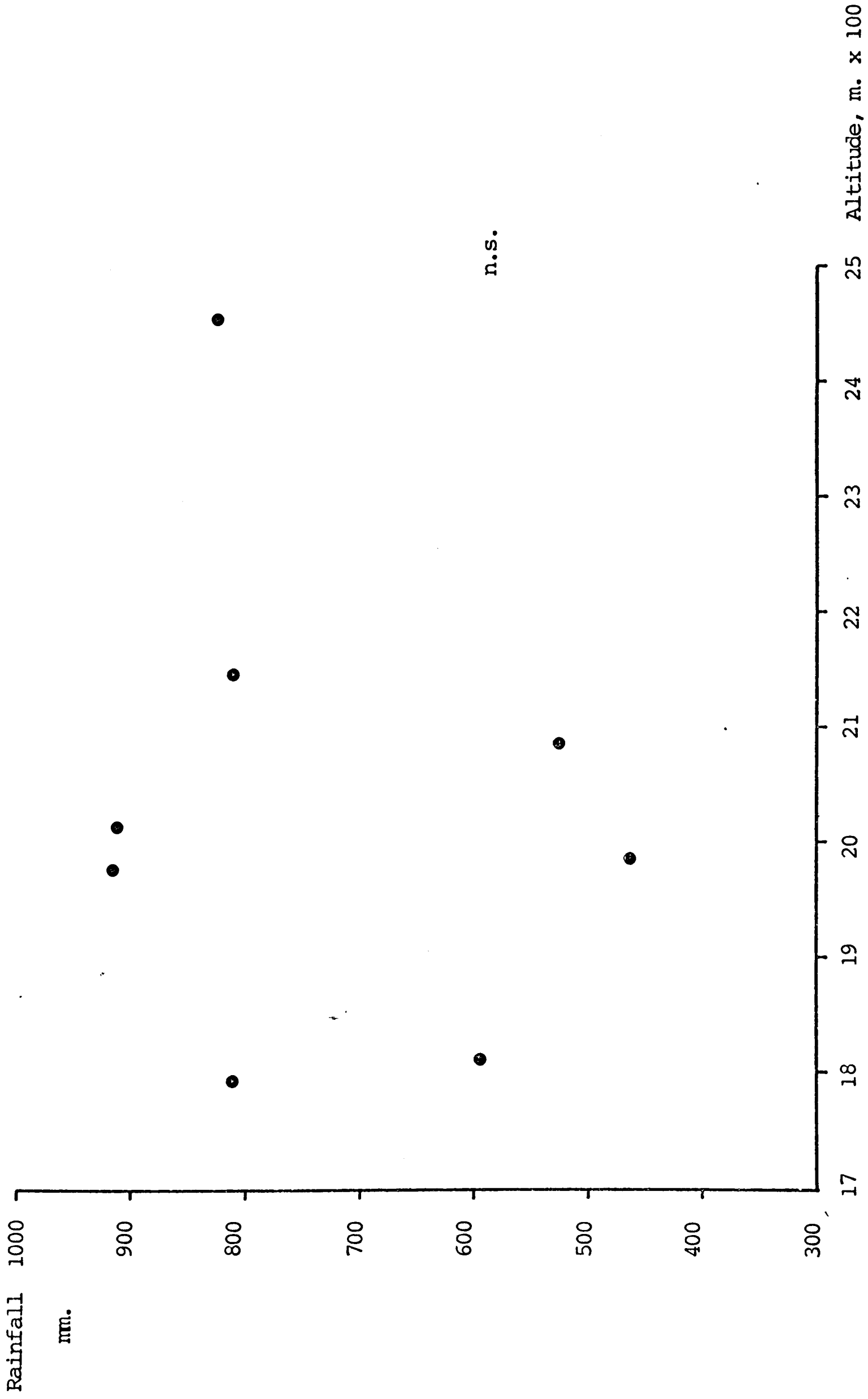


Fig.4.1.1. The altitude and mean annual rainfall at 8 stations around the Athi Plains.

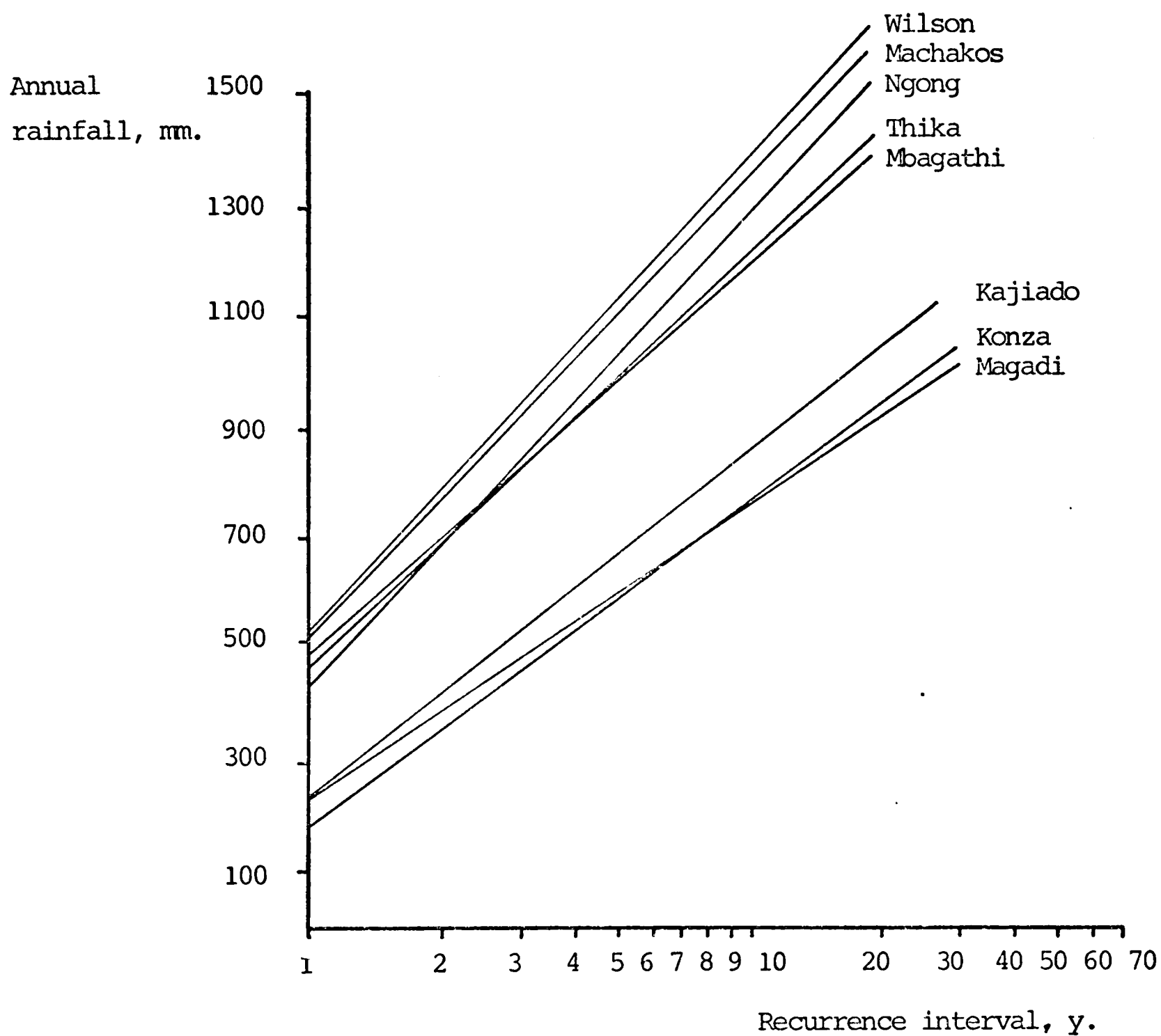


Fig.4.2. The rainfall recurrence interval at 8 stations
around the Athi Plains.

4.3 Rainfall totals around the Athi Plains

The Athi Plains might be expected to have a lower rainfall than the Kikuyu or Wakamba highlands because of the general, positive relationship between altitude and rainfall (Brown and Cocheme 1969). On a scale of 1:4,000,000 Griffiths (1967) shows that these highlands will experience more than 30-50 ins. (76-127 m.m.) of rain in four years out of five, while the area of Nairobi and the east Athi Plains will receive more than 20-30 ins. (51-76 m.m.) with the same frequency. By contrast, the rainfall of the west Athi Plains will exceed only 20 ins. (51 m.m.) in four years out of five, although their altitude is slightly greater than those of the east.

The position of the mean annual rainfall isohyets of Thompson and Sansom (1967) confirm the greater rainfall of the east plains, and there is thus no relationship between the altitude and annual rainfall for eight stations (Ngong, Mbagathi, Wilson, Thika, Athi River, Machakos, Konza and Kajiado), around the plains which range in altitude from 1756 to 2269 m a.s.l. (Fig. 4.1). The higher rainfall of the eastern plains is probably due to their being flanked by two high land masses (Fig. 3.1).

The recurrence interval (Dury 1968) predicts the repeatability of any particular rainfall total. This has been calculated and plotted for 8 stations in or around the Athi Plains (Fig. 4.2). The interval is calculated by:

1. Ranking the annual totals from 1 to n, with the highest total assigned to the rank of 1.
2. The recurrence interval, r_i , = $\frac{n+1}{r}$, where n = no. of observations, r = rank of particular total.
3. Each recorded total is plotted against its calculated r_i on a semi-logarithmic scale.

The lines plotted use data varying from 17 years (Wilson) to 22 years (Machakos), and because the points obtained for each station will lie

nearly on a straight line, these have been fitted by eye in Fig. 4.2. One important consequence of this straight line relationship is that the calculated recurrence intervals are independent of the length of period for which records are available.

Fig. 4.2 shows that the rainfall recurrence intervals of Ngong, Mbagathi and Wilson at the northern edge of the west plains, and Machakos on the southern side of the east plains are almost the same. The rainfall patterns of Kajiado and Konza at the southern limit of the west plains appear to be closely related, but are also similar to that of Magadi, even though the latter lies 1300 m. lower in the Rift Valley.

Apart from the distinct differences in expected rainfall between the two groups, the gradients of the lines of the low rainfall group are much flatter. While, for example, Wilson will receive at least 700 m.m. of rain every two years and 1400 m.m. every 10 years, Kajiado will enjoy 700 m.m. of rain every 6 years, but a total of 1400 m.m. will fall only once every 60 years.

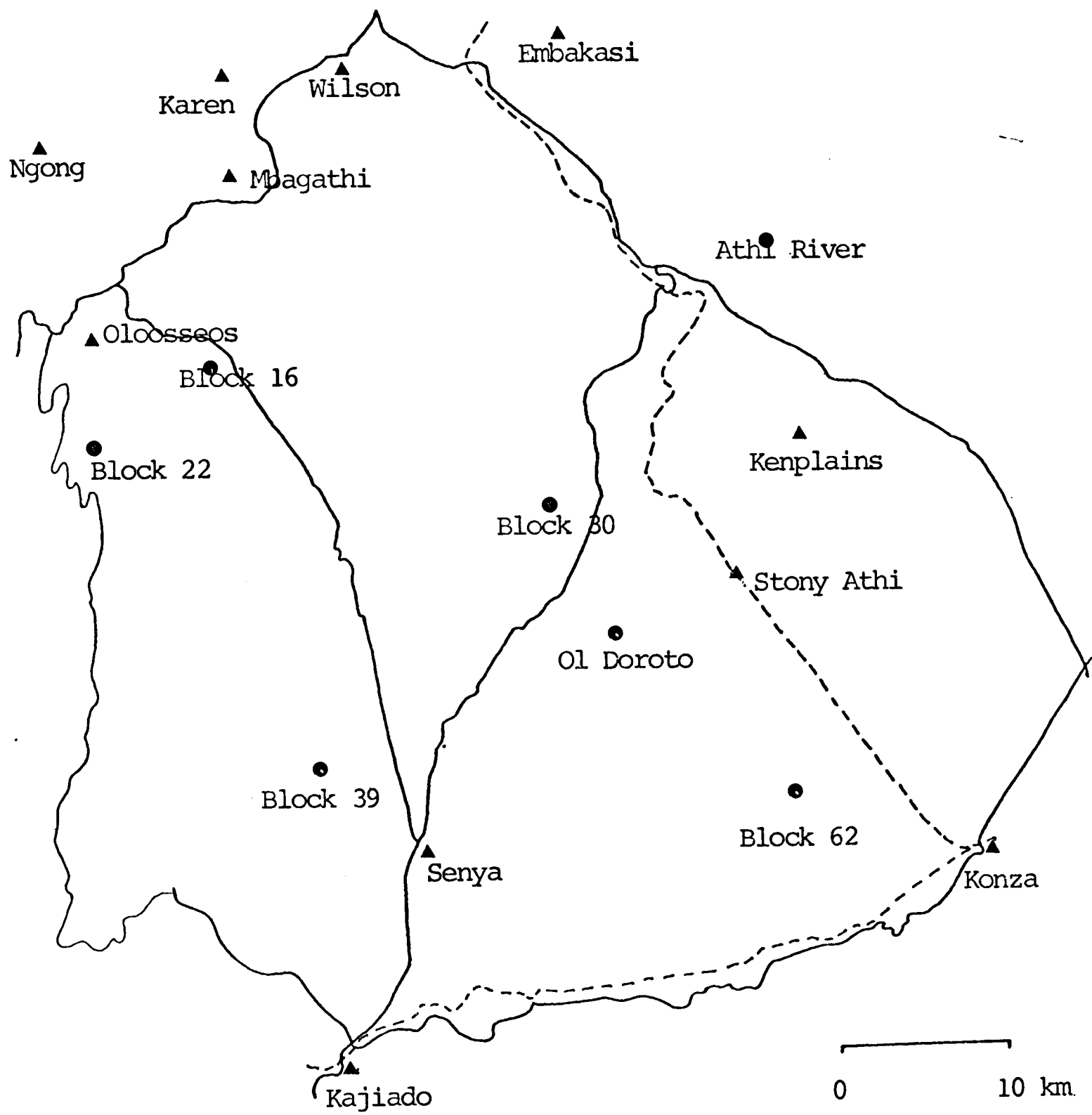
Thus, the stations which lie round the edge of the plains and are near high ground have a considerably higher rainfall than the stations at the southern edge of the plains. In addition, for a unit increase in the annual rainfall, the recurrence interval of stations of the latter group increases more than that of the high rainfall areas, indicating a lower probability of experiencing higher rainfall totals.

4.4 Rainfall within the west Athi Plains

The locations of the rainfall stations discussed above show that there are virtually none in the west plains and adjacent Rift Valley.

After the first year of this study a more accurate picture of the rainfall patterns within the west plains was required than a series of stations around the plains could provide. This was necessary for the following reasons:

1. Rainfall maps prepared from existing rainfall stations would fail to



▲ E.A.M.D. daily rain gauge

● Monthly storage gauge

Fig.4.3. The location of 18 rainfall stations in and around the Athi Plains.

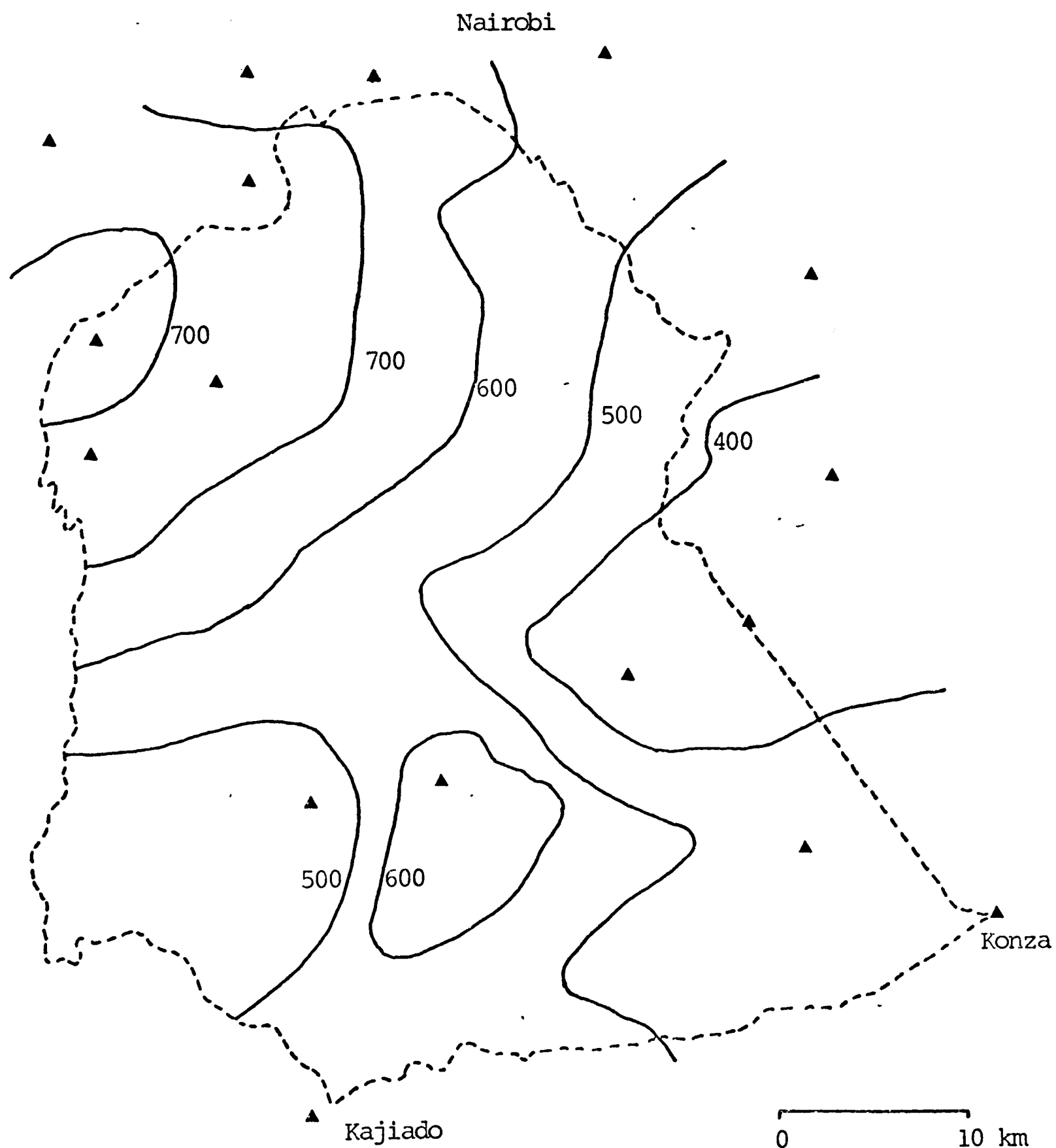


Fig.4.4. Rainfall isohyets over the west Athi Plains between September 1971 and October 1972, with the stations (▲) from which data were used.

take into account the internal topography of the plains and its local effect on the rainfall.

2. The existence of a predominantly north-south gradient of decreasing rainfall across the plains is obvious from the rainfall recurrence intervals. More rainfall stations in this area might enable the isohyets of this gradient to be more accurately located.
3. Highly local outbursts of rain are common in semi-arid Africa, and such local storms can have an immediate and dramatic effect on the distribution of the large mammal populations (Pennycuick 1974).

As one aim of this study was to see what factors might determine the distributions of the herbivores, a rainfall map from data recorded around the plains might be too 'coarse-grained' to show such local effects, or indeed might produce spurious relationships. Thus, the establishment of more rainfall stations would enable a more detailed map to be made.

To do this, six storage rain gauges were set up in the plains in September 1971, and one further gauge was installed in February 1972. The design of these gauges, their accuracy and criteria for siting are described in Ch. 2. Fig. 4.3 shows their location and those of the 11 East Africa Meteorological Department stations which were of immediate use for this study.

The monthly rainfall totals between October 1971 and September 1972 and altitudes of these 18 stations are given in Appendix 3.

Fig. 4.4 shows the isohyets plotted at 100 m.m. intervals, for the period October 1971 to September 1972. As a complete set of data for the gauge in Block 30 was not available, this station has not been used in the construction of this map.

The predominant trend is of rainfall decreasing across the plains along a north-west to south-east axis, so that the Ngong Hills and their environs receive the highest rainfall and the low-lying ground near Stony

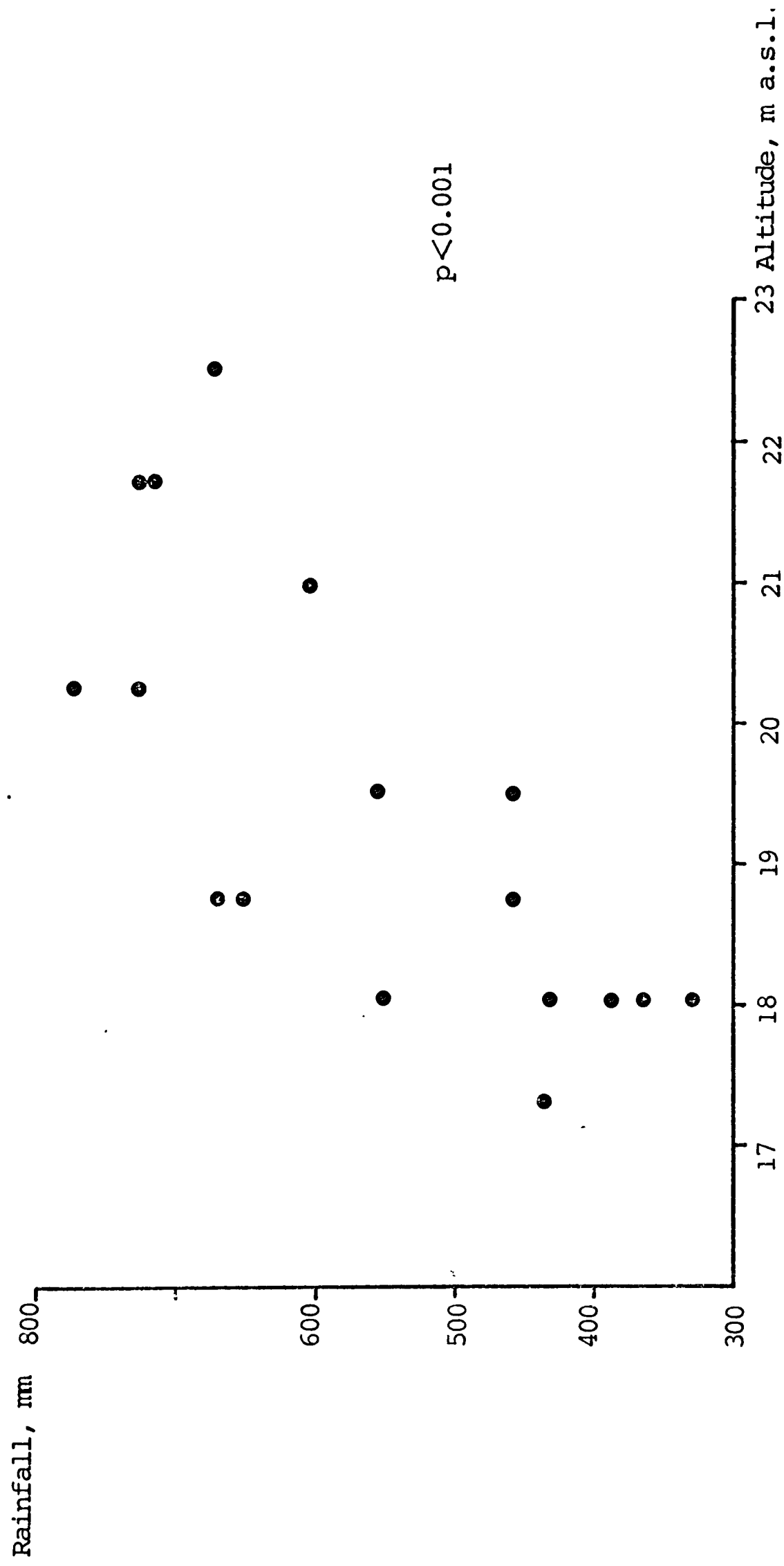
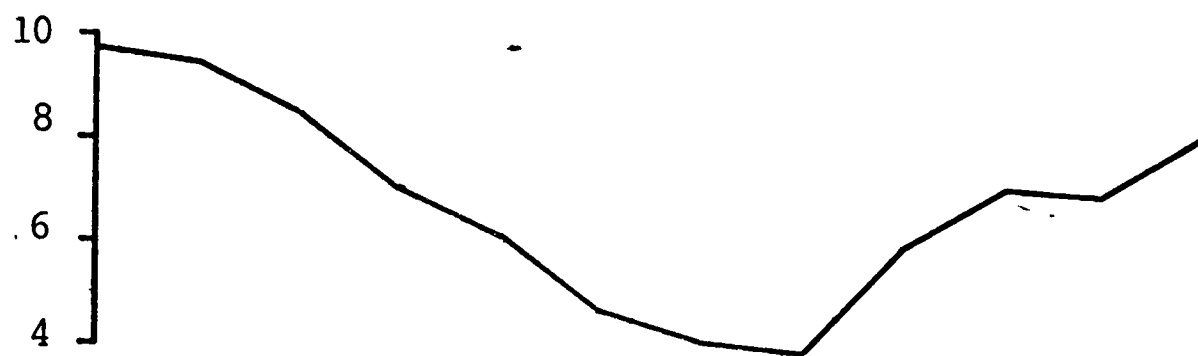
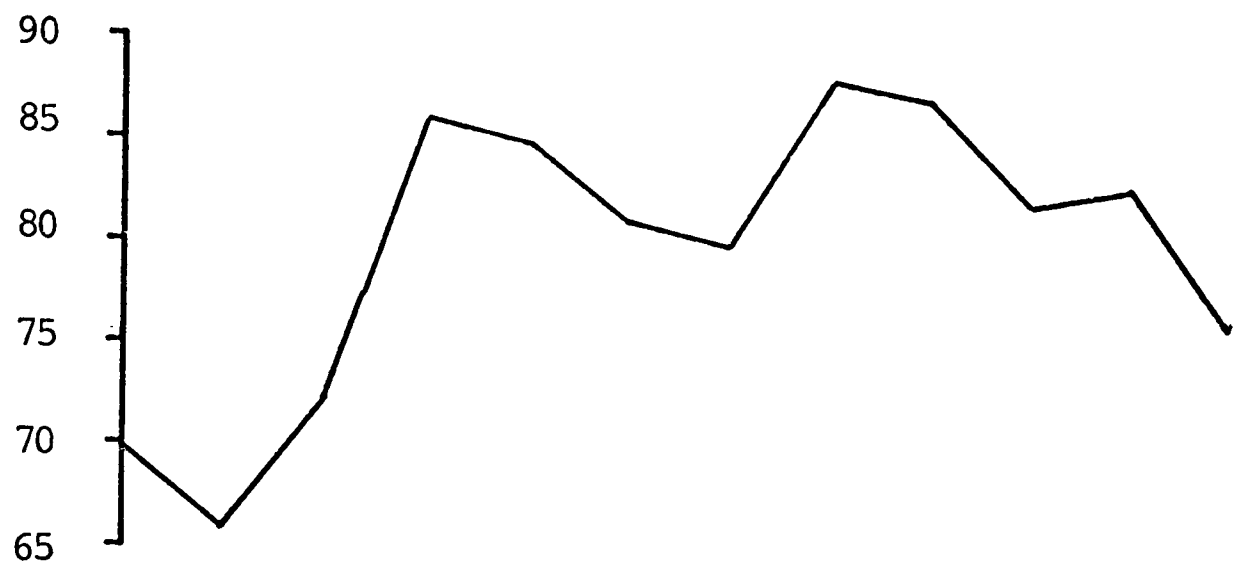


Fig.4.5. The altitude and total rainfall between October 1971 and September 1972 at 17 rainfall stations in and around the west Athi Plains.

hours of sunshine



Relative humidity, %



Air temperature, °C

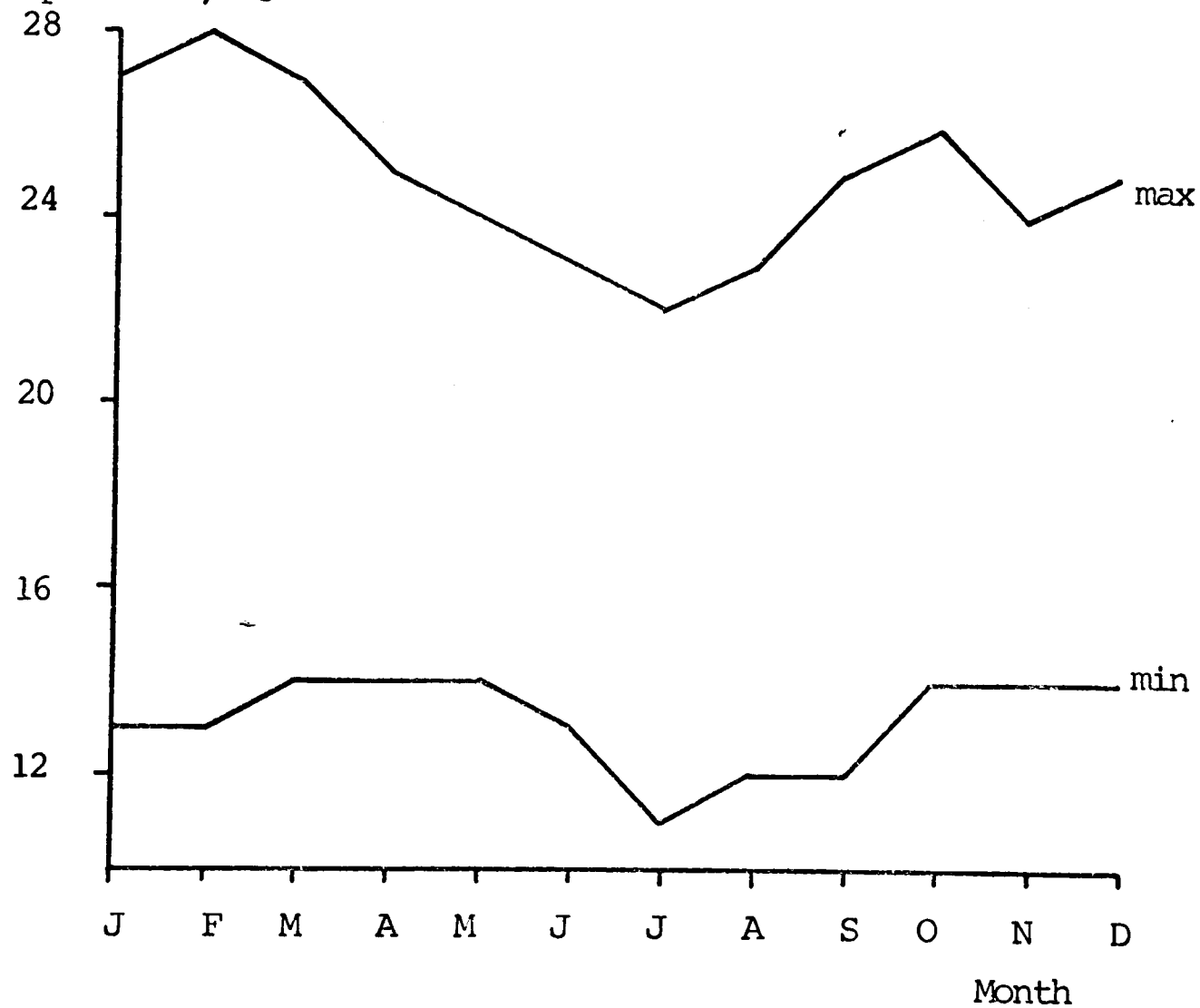


Fig.4.6. The monthly mean maximum and minimum air temperatures, the relative humidity at 0900 h, and the daily hours of sunshine at Nairobi.

Athi the least. The rather high rainfall around Senya appears rather anomalous, and is difficult to explain in view of the lack of any marked topographic irregularity in the area. Although there is some evidence that Senya does lie in a local rain-belt (R. Slade, pers. comm.), a longer run of data might produce a different picture.

In Fig. 4.5 the total rainfall in the same period has been plotted against the altitude of each station. These two factors are significantly correlated ($c = .739$, $p < .001$), showing that in the west Athi Plains the amount of rain received by an area in the year was related to its altitude.

4.5

Other meteorological elements

Although rain is the most important component of the climate of the dry tropics, the sunshine, temperature and humidity regimes are characteristic of the Nairobi area and may influence the animal populations.

Sunshine and cloud cover

Although the sun shines for an average of 6.9 hours / day through the year at Nairobi, the distribution through the months is far from uniform (Thompson and Sansom 1967). Fig. 4.6 shows how sunshine is at a maximum 9.7 hours / day during the North East Monsoon, but decreases as the short rains proceed. During the long dry South East Monsoon the area is often covered by dense stratocumulus cloud so that the sun shines for only 4.0 hours / day in August. It increases again from September until January, although the short rains cause a slight check in November. Because Nairobi is situated near the equator, the length of day varies only very slightly from month to month, so that the simple comparison of the total sunshine hours / day reflects genuine trends.

Temperature

The average temperature at Nairobi is more equable than its latitude might indicate, and this is a result of its altitude (1675 m.). On the

whole, the annual range of air temperature is narrow (Fig.4.6) with the mean monthly maximum reaching 28°C in February and declining through subsequent months to 23°C in July. This maximum then increases again, but the short rains cause a drop of 2°C from the October mean of 26°C .

The mean minimum temperature shows less variation through the year, and has two broad maxima of 14°C roughly co-inciding with the periods of rain (Fig. 4.6). This suggests that the greater amounts of moisture in the earth, vegetation and atmosphere due to rain maintains the minimum, and hence night, temperatures.

Although such mean figures are useful for the long-term picture, more extreme values than these are frequently recorded. Thus an absolute maximum of 33°C has been recorded at Nairobi in February, March and September between 1904 and 1956. Similarly, absolutely lower temperatures are experienced and as a random observation, on July 9th 1971 the night temperature in the Athi Plains fell to a minimum of 4°C . Because of this variation, simple meteorological data were always collected simultaneously with any observations on the activity of animals (Ch. 11).

Humidity

The level of relative humidity behaves similarly to the mean temperature in that very extreme values are not recorded in any season. In general, as Fig. 4.6 shows for readings at 0900 hours, the lowest humidity occurs during the hot dry months of the North East Monsoon, when it drops to 66%, and it reaches a maximum of over 80% during the cold dry season of June to September. The arrival of the rains causes the humidity to rise.

One important aspect of relative humidity is that the diurnal range of values is almost as great as the seasonal variation, and for this reason, again, humidity was always measured at intervals during any observational work on the activity of hartebeest.

4.6 Discussion

The relationship between altitude and rainfall at first appears inconsistent for, as shown above, there is no relationship between these variables when the long-term means of 8 rainfall stations around the edge of the plains are used, but there is a highly significant positive relationship for the rainfall of one year for 17 stations in the west Athi Plains, a smaller area. Brown and Cocheme (1969) found that over the whole East African highlands any general relationship between these two variables was masked by the effects of geographical position and exposure. The area of the Athi Plains is extremely small by comparison to that of the East African highlands, so that a significant effect of geographical position can almost certainly be discounted. However, the effect of exposure over the whole Athi Plains is probably considerable because of the varying width of the plains and differing proximity of higher land masses, which causes the east plains to have a slightly greater rainfall than the higher west plains. But, because the topography of the west plains rises in a generally north-west direction towards the Ngong Hills (Fig.3.1, p.32), the plains are uniformly exposed to the rain-bearing, south-east winds. Under these circumstances a positive relationship between altitude and precipitation might be expected, and an analogous situation is described for the south-east face of Mt. Kenya (Thompson 1966).

The rainfall map (Fig. 4.4) refers only to one 12 month period and in view of the year to year variation in precipitation the picture from a longer series of records might differ in one of two ways. Either the pattern of isohyets of Fig. 4.4 over the area might be erroneous, or the pattern might be substantially correct but the relative positions of the isohyets might be wrong. The validity of this map can be checked by comparison with that of Thompson and Sansom (1967). These authors show a decrease in average rainfall in a south-easterly direction across the

plains with Nairobi and Kajiado on the 900 and 500 m.m. isohyets respectively. A tongue of higher rainfall is shown to extend along the ridge above the Rift Valley, but "there is no observational evidence for this" because of the lack of rainfall stations there. Although there was no rain gauge in the present study south of that of Block 22, the isohyet pattern in Fig. 4.4 does not confirm this prolonged southward extension of the tongue of higher rainfall, and incidental evidence from two sources confirms this. Although the Maasai are not intensive cultivators, some maize is grown in areas of adequate rainfall; the site of the Block 22 rain gauge marks the observed southward limit of any cultivation in the area. In addition, if the plateau of En Doinyo Narok had an annual rainfall of a size proportional to its altitude alone (2300 m.), it might be used by the large mammal populations in the dry season. The evidence from aerial counts (Ch. 6), though, indicates that this is not the case. For these reasons, I conclude that the isohyet pattern in Fig. 4.4 is a better representation of the natural situation.

Even if the pattern of isohyets is substantially correct, their positions on the map may be incorrect. Comparison with the rainfall map of Thompson and Sansom (1967) reveals the 1971-1972 period as drier than the long term average over the north of the area and about average in the south. Thus, in a more typical year the gradient between north and south would be more exaggerated and most isohyets would be displaced further south. Despite this difference, it is assumed that the qualitative picture of rainfall gradients described above would still be valid. Moreover, for the present purposes of considering the effects of rain on the animal populations, the picture obtained from long-term records is obviously less relevant than the contemporary one.

Chapter 5.

THE VEGETATION OF THE ATHI PLAINS

5.1 Introduction

The dependence of herbivores on the primary production of a given habitat demands that an understanding of the vegetation must precede a study of herbivore ecology. This will usually involve describing the vegetation and mapping it to show its variation through the area and its relation to the land form and physiography.

For the purposes of the study (Ch.1) a vegetation map of the west plains was necessary. With the exception of Heriz-Smith's (1962) description of the vegetation of the Nairobi Park, the plains have only been described as part of much larger areas. Descriptions at this scale are said to refer to the Athi Plains ecological unit, a distinction which may be justified in view of the natural boundaries of the plains (p.32).

In order to investigate phenomena such as the distribution of animals within the plains, some subdivision was necessary, with the result that the west plains are divided into eight vegetation zones, two of which are subdivided. These zones are sufficiently uniform to allow recognition of their boundaries with other zones, and each of them exhibits a characteristic pattern of soil-vegetation associations which may form a catenary sequence (Morison, Hoyle and Hope-Simpson 1948). The vegetation of each association is identified as a vegetation type, which is the most detailed level of description used here.

5.2 Criteria for mapping

The contemporary vegetation of the Athi Plains at all these levels is due to the interaction of many factors, both abiotic and biotic, and this is recognised in the classification and description of the vegetation. The most important of the former are geology, topography, soil

and climate, and their effect can usually be assessed by observation or measurement. In the case of climate, the requisite short-term records may exist. On the other hand, the biotic factors such as the modifying effects of man and his livestock and the wildlife species can rarely be quantified, so that past records are almost invariably anecdotal and, therefore, of qualitative value only.

At the level of the vegetation zone, the map produced is extensive because the 8 zones cover the whole western plains. Coverage of this area at the scale of the vegetation type would have been impossible in the time available; therefore, only representative areas have been mapped at this intensive, detailed scale. The areas chosen were the 7 study areas in the Athi Plains and the Nairobi Park (p.17), and although these areas were not located randomly in their vegetation zones, the vegetation types are considered to be typical of their zone. In a few places there were vegetation associations which did not conform to the typical arrangement, and these are classified and described as local variants.

Different criteria were used for the definition of the ecological unit, vegetation zones and types because of the hierarchical organization and great differences in size of these categories. The following methods were used:

1. The ecological unit is described in the terminology of several authors from the literature, but is also described in terms of the physiognomy of its vegetation according to the classification of Pratt, Greenway and Gwynne (1966).
2. The physiognomy of the vegetation varies little throughout the plains, and the definition of the zones had to include other criteria. Each zone is characterised by the rock upon which it predominantly lies, taken from the maps of Baker (1954), Matheson (1966) and Saggerson (1971), and by the associated land system (Beckett, Webster and Lawrance 1971), as described and used in Ch. 3.

Precipitation varies across the plains (Fig. 4.4). This variation in rainfall is used to put the vegetation zones in to ecological zones (Pratt, Greenway and Gwynne 1966) and to calculate their indices of available water (Woodhead 1970). The latter is defined as:

$$\frac{\text{Water available for evaporation or transpiration}}{\text{Total annual potential evaporation}}$$

which is measured as

$$\frac{(\text{Total annual rainfall}) - (\text{Total water surplus})}{\text{Total annual potential evaporation}}$$

The ecological zone and available water index of each vegetation zone are taken from the 1:3,000,000 maps of these authors.

In the general description of each zone, various other factors are used. These include the predominant type of soil, any plant species that appear especially characteristic, and the nature of the river beds from the point of view of their water-retaining capacity.

3. The areas of the individual vegetation types are too small to be distinguished on the basis of geology, site potential or available water index, so that their identification and classification uses other approaches. The first is their position on the slope or in the catenary sequence, if the latter exists. The second approach is the use of their component plant species, and two groups of plants are recognised:
 - (i) Those that are peculiar to one particular vegetation type, and are therefore highly characteristic of that type. Such species probably tolerate only a narrow range of environmental conditions, and include the grasses Hyparrhenia lintonii, Cymbopogon pospichilii, Eragrostis tenuifolia, Sporobolus pyramidalis and Harpachne schimperi.

(ii) Those species that are found in a number of types, but their abundance is highly variable. When a number of such species are considered, their different patterns of abundance can indicate a catenary sequence of vegetation types. This group contains such species as Acacia drepanolobium, the shrub Aspilia mossambicense and the grasses Themeda triandra, Setaria phleoides and Ischaemum afrum.

Species abundance was gauged by recording each species as abundant, frequent, occasional or absent. Species recorded as absent from a vegetation type are usually those which are indicator species of contrasting types. Thus, the absence of a species can be a diagnostic feature of a vegetation type. Abundance is measured by the frequency of individuals of a species rather than their contribution to the total above ground biomass.

Soils were crudely distinguished on the basis of colour and consistency, but other edaphic factors were considered. The abundance of Acacia drepanolobium is related to the height of the water table and possibly also to the depth of the soil (Birch 1952), and these relationships are assumed to hold over the Athi Plains. Thus differences in the density and height of individuals of this and other species are cautiously ascribed to topographic and edaphic differences rather than fire which occurs only rarely and locally (p. 75). Similarly the presence of stony ground and either a patchy plant cover or low growth form of species known to be taller elsewhere are assumed to be causally related, and may diagnose a vegetation type.

5.3 Mapping methods

The existence of the vegetation zones was obvious in the field because of the gross differences in topography, soil and plant cover which distinguish them. Similarly, the catenary sequence of soil types with their associated vegetation types was apparent because of the characteristic species of the latter.

Specimens of the most common and dominant plants of the Athi Plains were collected and identified by the staff of the herbarium of the Department of Botany, University of Nairobi. The authorities of the specific names of all plants mentioned are given in Appendix 4.

The boundaries of the vegetation zones were recognized on the ground primarily by topographic irregularities which varied from escarpments to gentle changes in gradient, but the precise position of the boundary was always determined by the change of vegetation. The position of these boundaries was drawn in the field on 1:50,000 maps (Survey of Kenya), which were then refined with the aid of a complete photo-mosaic at a scale of approximately 1:50,000.

The boundaries of the vegetation types were drawn straight on to the aerial photographs because the 1:50,000 maps showed insufficient detail. Difficulties sometimes arose over the location of boundaries because the abundance of the dominant plant species varied continuously through a catenary succession of vegetation types. This problem could usually be resolved by using other species with discontinuous distributions to define the vegetation types.

After the field work, the boundaries of the vegetation zones were fitted together to form a composite map. Slight differences in scale between aerial photographs were adjusted to a uniform 1:50,000 scale with a Grant projector. This map was then reduced to a scale of 1:250,000. The scales of the vegetation type maps of the seven study areas were also adjusted to 1:50,000 without any further reduction.

5.4 The ecological unit

Although the vegetation of the Athi Plains has not been described specifically, the ecological unit is included in a number of descriptions and maps varying in their detail and coverage. Thus Shantz and Marbut (1923) map the plains as "Acacia-tall grass savannah", while Edwards and Bogdan (1951) describe them as "Scattered Tree Grassland (Acacia-Themeda)",

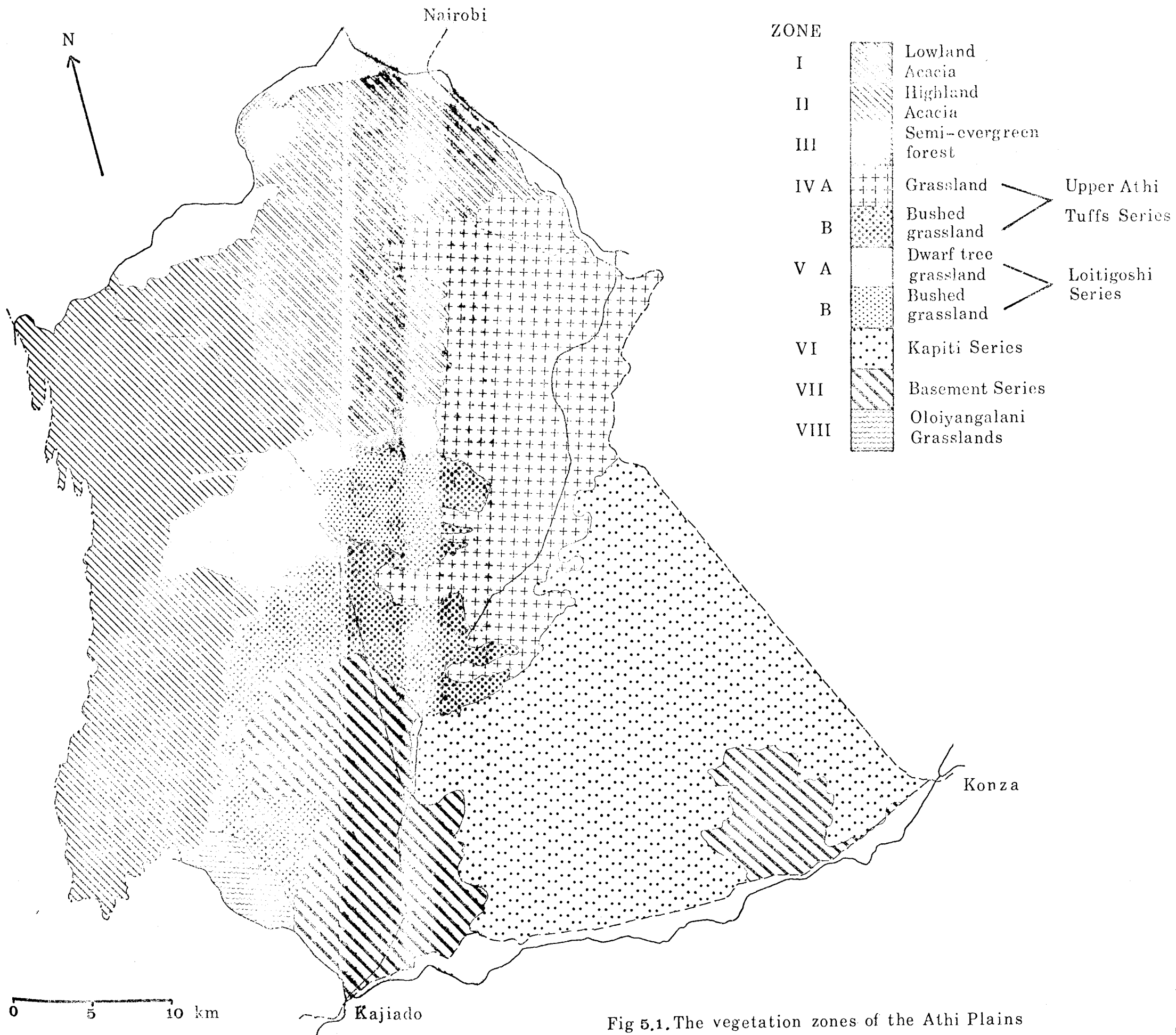


Fig 5.1. The vegetation zones of the Athi Plains

although this category includes areas whose vegetation is physiognomically very distinct from that of the open plains.

Aubreville et. al. (1958) map the plains at a scale of 1:10,000,000 as "Wooded Steppe with abundant Acacia and Commiphora". In view of the confusion surrounding the meaning of "steppe" in the context of East Africa and the fact that Commiphora spp are absent from the plains, this classification is considered inappropriate for the present purposes. Rattray (1960) classified the vegetation of Africa at a scale of 1:10,000,000 on the basis of its grasslands, and described the Athi Plains as the Kenyan form of "Themeda grassland ... of open savannah, treeless or with scattered Acacia drepanolobium at 1100 - 2000 m. with a rainfall of 640 - 900 mm.". Because only grass species are considered in this classification, areas of very different plant cover, such as parts of the Kenya Rift Valley, are also covered by this description and greater precision is therefore desirable.

This is possible with the methods of Pratt, Greenway and Gwynne (1966), and in this scheme the Athi Plains consist of medium-height Themeda-Pennisetum seasonally waterlogged grassland and of medium height Themeda-Setaria-A.drepanolobium seasonally waterlogged dwarf tree grassland. This physiognomic approach is also inherent in the construction of the AEFTAT-UNESCO map (in press) at 1:5,000,000 which shows the Athi Plains as edaphic grasslands of Evergreen bushland and Acacia grassland. This last description assumes that the grasslands are the natural vegetation cover of the area and are not secondarily derived.

To summarise, the most important features of the vegetation of the Athi Plains are included in their description as seasonally water-logged, medium length, natural Themeda grasslands which are either treeless or carry scattered A. drepanolobium trees.

5.5. The vegetation zones and vegetation types

The eight vegetation zones are shown in Fig. 5.1. Fig.2.1 shows

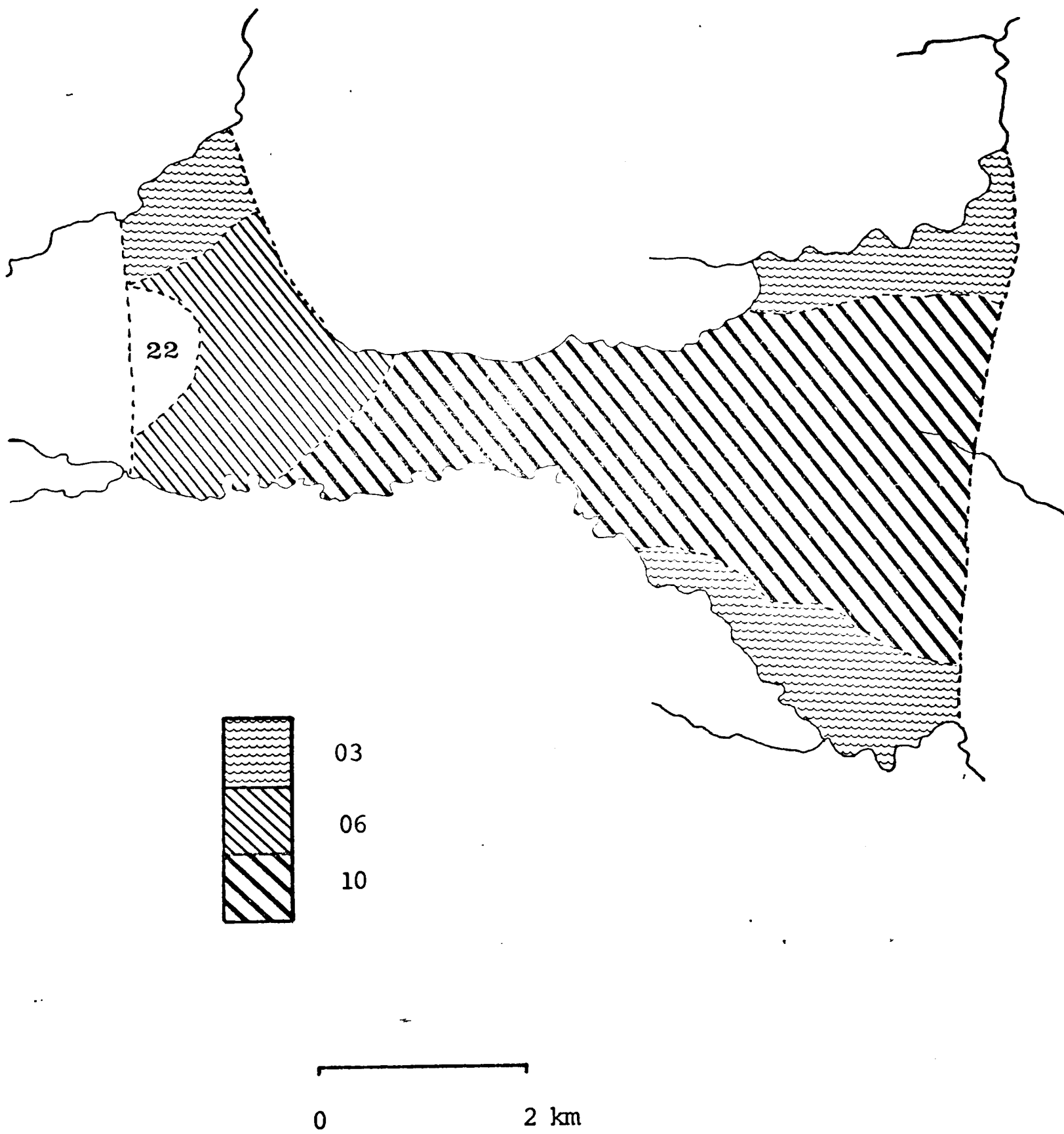


Fig.5.2. The vegetation types of Block 15.

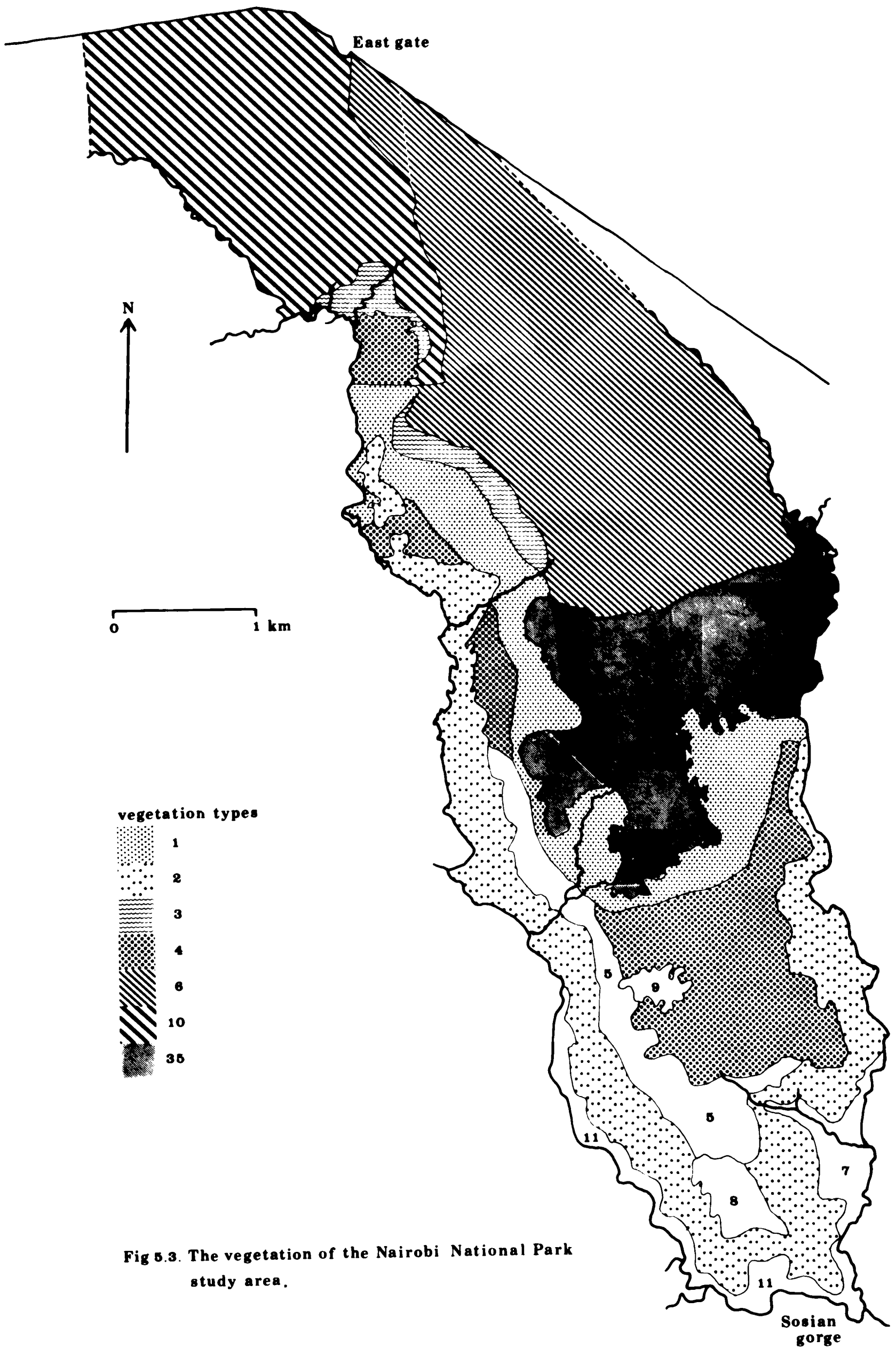


Fig 5.3. The vegetation of the Nairobi National Park study area.

the location within the zones of the seven study areas (Blocks) whose vegetation was mapped in detail.

Vegetation Zone I; Lowland *Acacia drepanolobium*

(including Nairobi National Park study area and Block 15)

Although the flows of Mbagathi Trachyte and Nairobi Phonolite underlie this zone, the topography of the Embakasi land system is uniform throughout. Ecologically, the zone lies in the semi-arid zone, but its annual index of available water of 40 - 50% is the highest of the plains because of the influence of the nearby highlands. In section this land form is highly convex giving rise to extensive flat ridges of impeded drainage which support *Acacia drepanolobium*. The vegetation of the zone is, accordingly, described as Dwarf Tree Grassland.

The rivers invariably run through rock beds, and may be flanked by gorges. Because of these factors and the high index of available water, these river beds retain water better than those of any other zone. In the Nairobi Phonolite portion, the gorges cause large height differences between the ridges and sumps, enabling the unambiguous separation of the vegetation types in to a reverse catenary sequence (p.38). The Mbagathi Trachyte is less deeply dissected by river courses, and because this area is flatter, the catenary sequence is less marked (p.38). Fig. 5.2 shows the vegetation of Block 15, while Fig. 5.3 shows the vegetation of the Nairobi Park study area at a larger scale.

Vegetation type 10

This is the extensive *A. drepanolobium* grassland of the flat ridges and very gentle upper slopes, lying on deep cracking Black Cotton soils. The *A.drepanolobium* is locally dense and up to 2m high. In the Nairobi Park the dominant grasses are *Ischaemum afrum* and *Setaria phleoides* which are abundant, and *Themeda triandra* which is frequent. *Aspilia mossambicense* is short (up to 40 cms) and occasional to frequent. The biomass of grass in such areas is high, at approximately 3000 kg/ha.

In the areas of this grassland in the Nairobi Park there are frequent termitaria and occasional clearings with no Acacia. Both these features support almost pure stands of T. triandra, and their mosaic distribution is characteristic of an area of impeded drainage (Morison, Hoyle and Hope-Simpson 1948). Where this grassland occurs outside the Park on the Mbagathi Trachyte, the sward contains less I. afrum and more T. triandra, indicating that the drainage of these slopes is marginally less impeded.

Vegetation type 06

Edaphically and topographically, this type is the same as vegetation type 10, but differs in consisting of areas which were burnt in November 1970. This includes a small area in Block 15 and a large proportion of the Nairobi Park study area, but in both cases the effects of the fire were still apparent at the end of the study two years later. Although the vegetation composition was not recorded before the fire, all subsequent differences are assumed to be due to the fire and the associated patterns of animal use. In both areas the A. drepanolobium is now less dense but the T. triandra has suffered a more serious reduction. S. phleoides is now dominant and abundant.

Vegetation type 04

This is open grassland lying on red soils which develop either on the middle slopes below vegetation type 10 or on ridges whose slope is sufficiently great to allow the free drainage of water. In the latter case in Nairobi Park, the slope of the ridge is $2-3^{\circ}$ from the horizontal, whereas the slope under type 10 is a maximum of only 1° from the horizontal.

Within this type, the shortest grass occurs on the ridge and its height increases downhill, which may reflect a gradient of increasing soil depth. T. triandra increases from occasional to abundant down the slope. On the ridges Nesaea lythroides and Becium obovatum are

both frequent, but as the height of the grass increases, individuals of the former species become taller, while the frequency of the latter decreases. On the short grass ridges, Sporobolus pyramidalis, Microchloa kunthii and Aristida adoensis are frequent, with Digitaria macroblephara abundant and Panicum poaeoides locally abundant.

Vegetation type 01

This consists of areas of open plains which were burnt in November 1970, and were probably the same as type 04 before the fire. The effects of the fire were again long-lasting in that two years after the fire the grass biomass was only half that of type 04. The dominant species are D. macroblephara and M. kunthii, both of which are abundant. Plant cover in this area is sparse in the dry season.

Vegetation type 05

This scrub grassland type lies below vegetation type 04, and is variable in its development, occurring only on comparatively shallow slopes. In its species composition it is highly heterogeneous with some patches with grass species characteristic of higher catena levels, and others from lower.

In the open patches D. macroblephara is frequent, and Panicum sp. and H. schimperi occasional. N. lythroides grows to 1 m in height. The scrub patches are due to Hibiscus flavifolius, which reaches 1.5 m, Grewia similis, Sericocomopsis hildebrandtii, Lippia javanica and Omocarpum trichocarpum. Within these bush areas, T. triandra, Rhynchelytrum repens, A. adoensis and Pennisetum stramineum are occasional, with Hyparrhenia lintonii and Cymbopogon poschippilii frequent.

Vegetation type 02

In this vegetation zone the lowest slopes of the catena are the steepest. Where opposite slopes of up to 15° from the horizontal meet, forming a rocky river bed, this vegetation type covers both slopes. Their red

lateritic soil is naturally shallow and stony with frequent outcrops (Heriz-Smith 1962).

This is the tallest grassland on the catena because of the preponderance of species with tall culms. The grass biomass is, in fact, less than that of type 10. The dominant grasses are C. poschipilii and H. lintonii, both of which are abundant. D. macroblephara and T. triandra are frequent, and Pennisetum stramineum is the dominant grass of the infrequent termitaria of this type. The coverage of shrubs is less than in type 05, but the common species are the same.

Vegetation type 35

Although its drainage is as impeded as that of vegetation type 06, which it adjoins, this type lies on Black Cotton soils which contain large amounts of surface breccia (Saggerson, 1971). This difference in soil has produced a distinct vegetation type. The presence of the breccia results in a patchy plant cover, while the A. drepanolobium is more scattered and shorter than on the deeper soils of type 06. Low-growing individuals of T. triandra, Pennisetum mezianum and D. macroblephara are all frequent. This soil dries out and cracks in the dry season and is waterlogged after heavy rain. In the rainy season Orthosiphon parvifolium is abundant and Senecio discifolius is frequent.

Vegetation type 03

This type is found at the junction of the areas of Black Cotton soil with those of lateritic soil. Its soil is dark brown which suggests that it is an intermediate form, which enjoys less impeded drainage because of a slight increase in slope. Although variable in its development and occurrence, this vegetation type is an important ecotone between the areas of A. drepanolobium and the open grasslands. The ecotone is striking for its scattered A. drepanolobium bushes and the predominance of T. triandra, which is abundant. P. mezianum and A. mossambicense are frequent, although

the latter occurs only as a low bush, probably because soil conditions here are less than optimum compared to the true clays of vegetation type 10. P. poaeoides is frequent after the rains.

Vegetation type 07

This is a minor type on Black Cotton soil, although it lies on hillsides of 15° from the horizontal. A small escarpment at the top of these hillsides is probably responsible for the necessary conditions for the development of this soil. The ground is stony, supporting a coarse sward. T. triandra is abundant, and P. megianum is frequent. Eustachys paspaloides, S. pyramidalis, I. afrum and P. stramineum are all occasional.

Vegetation type 08

This type consists of a mosaic of small areas of Black Cotton and lateritic soils, but the associated vegetation communities occur at too small a scale to map separately. The plant species found are characteristic of vegetation types 04 and 10.

Vegetation type 09

Locally in the Nairobi Park, there are small depressions on high ground. These are, in effect, isolated sumps with deep Black Cotton clays, bearing characteristic vegetation. The grass species are the same as those of vegetation type 10, but the type is distinguished by the total absence of A. drepanolobium and the scarcity of S. phleoides. I. afrum is abundant and A. mossambicense may form dense patches of medium height. Locally, Balanites aegyptiaca occurs.

Vegetation type 11

When the lower slopes of the valleys exceed 15° from the horizontal, rocky gorges are found with a characteristic vegetation, composed predominantly of trees and bushes on a thin soil.

Vegetation type 12

This vegetation type is only important in the Nairobi Park, where it consists of all graded roads and quarries where road metal is excavated. The essential feature of this type is that it represents a considerable area of bare earth. Although it is not shown on the vegetation map (Fig. 5.3), it is a significant feature of the hartebeest habitat.

Vegetation type 13

This includes all river beds whether dry or not. As with type 12, recognition of this type became necessary when recording hartebeest habitat utilisation.

Vegetation type 29

This type is composed of three small areas at the foot of the forest escarpment, where there is a seepage of ground water. A lush, short grass sward forms, containing a coarse Setaria sp .

Vegetation type 32

This is the vegetation of a small area at the edge of the Nairobi Park. The dense stands of regenerating Acacia spp, indicate the recovery of this area from human disturbance.

Vegetation type 36

This type occupies an area of level topography, with a deep Black Cotton soil, which becomes highly waterlogged. Although this type mostly overlies the Kerichwa Valley Tuffs rather than the Nairobi Phonolite of type 10, differences in their plant covers are probably due to differences in relief. The A. drepanolobium of vegetation type 36 is scattered or even absent, an indication of a higher water table (Birch 1952). This allows the growth of almost pure stands of T. afrum, while P. mezianum and T. triandra are almost absent.

Vegetation type 37

Although it is an area of Black Cotton soil, the vegetation of this type is very heterogeneous, which may be a result of past human activity, of which the most obvious sign now is the stand of Eucalyptus sp. At the bottom of the slopes, A. mossambicense is dense with S. phleoides and T. triandra frequent. Slightly higher up, the soil is browner and B. insculpta and Conyza aegyptiaca frequent. The gradient of the area of this type is too slight for these catenary differences to be mapped as separate associations.

Vegetation type 33

This is the riverine forest dominated by the Fever Tree, Acacia xanthophloea.

Vegetation Zone II: Highland Acacia drepanolobium (including Block 22).

This large area lies on the ridge above the Rift Valley and is mostly above 1780 m . These plains are of fairly low gradient with highly convex sections because of the marked shoulders above the deep river courses. The latter are typical of the Embakasi land system, as in vegetation zone I. The slope of the interfluves may reach 15° from the horizontal where the Ol Doinyo Agglomerates of this zone run against the low-lying Mbagathi Trachyte of Zone I.

Although the northern end of this zone has the highest rainfall of the plains (Fig. 4.4), it is classified as semi-arid with an available water index of 30 - 40%. Physiognomically, the vegetation is a Dwarf Tree Grassland, and, despite the sloping topography, no catenary sequence is apparent. Black Cotton grumosols are uniformly present.

In the very steepest places there are rock exposures in the river beds but these are usually earth-lined. Water retention is, therefore, poor, but the sub-surface water is presumably sufficient to support the Acacia kirkii which usually line the river course of this zone. There

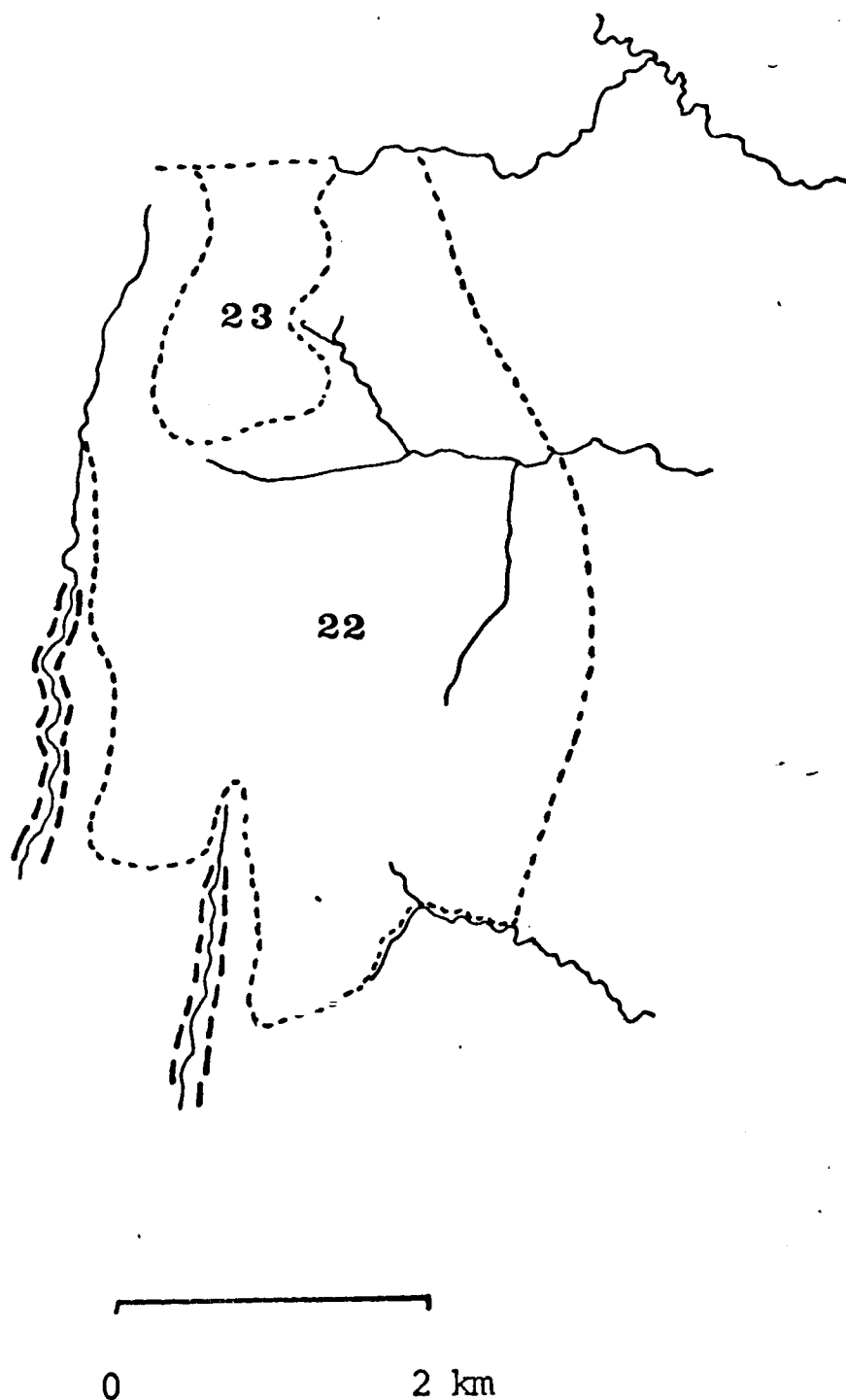


Fig.5.4. The vegetation types of Block 22.

are a number of springs around Ol Doinyo Narok hill and in Block 22.

Fig. 5.4 shows the vegetation of Block 22.

Vegetation type 22

This is an area with much loose surface rock, causing a low grass coverage. The grass sward and the A. drepanolobium are shorter than in vegetation zone I. T. triandra is frequent, though locally abundant while S. phleoides is abundant. A. mossambicense has a low growth form and is scattered; I. afrum is not found.

Vegetation type 23

Small areas of lava from the Ol Esayeiti volcanos underlie the northern end of Block 22, producing a short grass sward on red, lateritic soil. A. drepanolobium and S. phleoides are absent, but T. triandra is abundant. Solanum incanum and various herb species are also abundant.

Local variants

1. On the ridges in the north-east corner of this zone, adjacent to zone I, there are scattered trees of Akocanthera friesiorum and Acacia gerrardii, producing patches of Tall Wooded Grassland. The conditions which cause this particular development are unknown. Although A. drepanolobium is absent, T. triandra and S. phleoides are both abundant, and A. mossambicense is low but dense. Because of the occurrence of these species and the small size of the area, it is not distinguished from vegetation type 22.

Vegetation Zone III: Semi-evergreen Forest

This small zone (Fig. 5.1) is physiognomically Upland Forest and part of the Karen land form. On both these criteria it is not part of the plains but is included here because of its occurrence in the Nairobi National Park. As the southern limit of the Nairobi Trachyte flow, it is at the edge of the Kikuyu Highlands which have a higher rainfall (p.43). Accordingly, this zone lies in the dry sub-humid/semi-arid ecological zone with an available water index of 50 - 60%.

The density of rivers is greater in this area than in the plains. The rivers are rock-lined and flow for a greater proportion of the year than those of the lower rainfall plains.

Vegetation type 38

This is dry semi-deciduous forest, lying on deep humic soils. The dominant species are Croton megalocarpus, Brachylaena hutchinsii, Calodendron capense, Teclea spp., and Diospyros abyssinica.

Vegetation type 39

This consists of the clearings of open grassland in the forest. On red soil, almost pure stands of T. triandra are found, with Becium obovatum common. Locally patches of short grass with Eragrostis sp. and Sporobolus pyramidalis are found. S. phleoides is only occasional.

Vegetation Zone IV: Upper Athi Tuffs Series (including Blocks 30, 35).

The northern end of this zone (Fig. 5.1) extends into the Nairobi Park as the Athi River Basin. It overlies the Upper Athi Tuffs which are lacustrine deposits. Thus although the zone is part of the Athi land form, it is one of gently rolling plains without marked features, but with hill and valley systems which are highly concave in section. The zone lies in the Semi-arid ecological zone with an index of available water of 30 - 40%. The vegetation occurs as two physiognomically distinct halves of Grassland and Medium Height Bushed Grassland, and the Zone is divided on this basis.

The sumps of both parts are Black Cotton plains with deep and heavy soil. The river beds are lined with earth, and surface water retention is consequently poor in the dry season. There are rock pools in this zone along the Kesajui River and these have been excavated further by the Maasai to form wells.

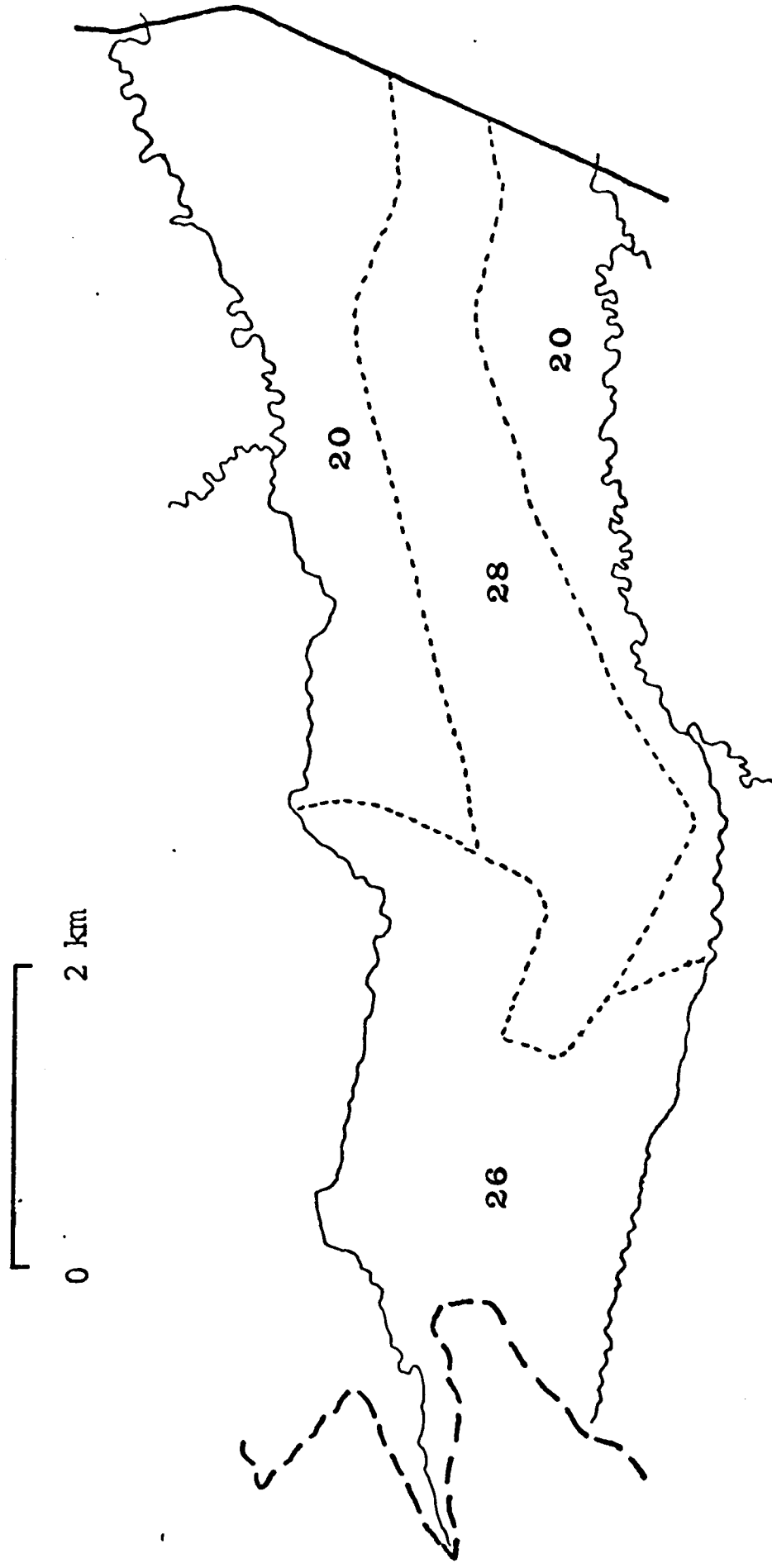


Fig.5.5. The vegetation types of Block 35.

Zone IVA, including Block 30.

Vegetation Type 20

Open treeless plains of gentle slope (Fig 5.5). The ridges and upper slopes carry a grey-black calcareous clay (Scott, in Heriz-Smith, 1962). P. mezianum is abundant, with P. stramineum locally abundant, producing a very coarse sward. T. triandra and D. macroblephara are frequent, with Cynodon dactylon, H. schimperi, B. obovatum and Abutilon sp. occasional.

Vegetation type 28

This covers the lower slopes and the flood plains of deep Black Cotton soils. There is much bare earth and a low coverage of grass species. P. mezianum is abundant, while T. triandra is frequent. Differing from type 20 further up the catena, S. phleoides is frequent and I. afrum is occasional. A. mossambicense is low but frequent, and A. drepanolobium is found on the lower slopes and along the river courses.

Local variants

1. Ridges of very short grass are found at the east of the zone near its junction with the Kapiti series (Fig. 5.1). The short grass seems due to the shallow soil and many surface pebbles. The slope of these areas is only $2 - 3^{\circ}$ from the horizontal, which is similar to the Basement Series (Zone VII). Aerial photographs and the nearby rock pools along the Kesajui river suggest that the rocks of the Basement series, which are not overlaid by Upper Athi Tuffs deposits here, are near the surface.

On these ridges the soil is grey. D. macroblephara is abundant with T. triandra frequent and P. mezianum, H. schimperi and P. stramineum all occasional. Eustachys paspaloides and Bothriochloa insculpta are frequent and occasional respectively; both species are found on the short grass areas of the Basement Series.

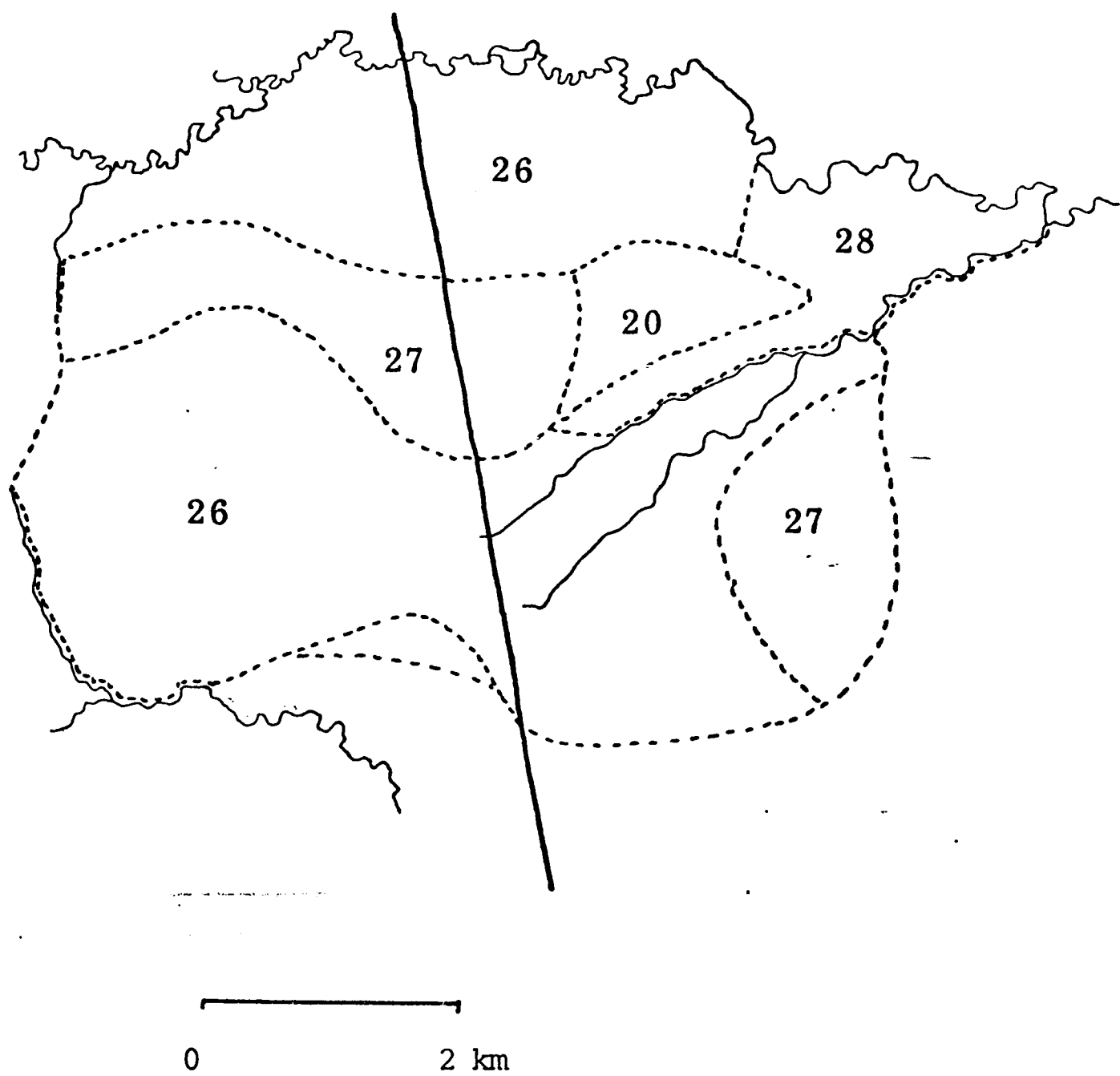


Fig.5.6. The vegetation types of Block 35.

Zone IVB, including Block 35

This part of Zone IV is a medium height Bushed Grassland. As it is an area of low hills and gentle slopes, there is little development of any catenary sequence, with the result that large areas are covered by a typical sump-like vegetation (Fig. 5.6).

Vegetation type 26

The predominant species is A. mossambicense which may cover up to 60% of the ground, growing up to 1.5 m. S. phleoides and I. afrum are both abundant, while T. triandra and P. mezianum are frequent. The first two species often occur in a mosaic of patches amongst the A. mossambicense, which is a characteristic pattern in areas of highly impeded drainage (Morison, Hoyle and Hope-Simpson 1948). The grass biomass of this type is the highest of the plains, exceeding 4000 kg/ha. It also suffers from prolonged water-logging after rain, which probably accounts for the total absence of A. drepanolobium.

Vegetation type 27

This type occupies the only hill in Block 35 that is sufficiently steep for the improved drainage to have allowed the development of a different vegetation. It covers slopes that are more than 3° from the horizontal.

The density of A. mossambicense is variable but is always less than 20% of the ground cover. This is in marked contrast to type 26, and confirms the presence of comparatively shallow, well-drained soils on the steeper slopes. P. mezianum and P. stramineum are abundant, while T. triandra and D. macroblephara are frequent. H. lintonii and B. insculpta, which are characteristic species of the nearby Basement Series grassland (Zone VII) are locally abundant and occasional respectively.

Vegetation Zone V: Ololoitigoshi Series

Although the series (Fig. 5.1) overlies the Olorgesailie phonolitic

nephelinite, it is subdivided into two parts. Both parts, though, are in the Semi-arid ecological zone with 30 - 40% of their annual water available for transpiration or evaporation. No vegetation types are described in detail for either part.

Zone VA

This is Dwarf Tree Grassland, and part of the Embakasi land form as is Zone II.

Although only a small area, a clear reverse catenary sequence exists. The Black Cotton soils cover about 50% of this part of the zone. On these A. drepanolobium is of medium height and density. S. phleoides is abundant, while A. mossambicense, D. macroblephara, P. mezianum and T. triandra are all occasional.

The red soils support a typical short-grass community. T. triandra is abundant, with P. mezianum frequent and D. macroblephara occasional. Solanum incanum is frequent but A. mossambicense is absent. Rhamphicarpa montana flowers profusely after the rains.

The river beds are entirely lined with rock and shallow gorges may be present. Surface water retention is, therefore, good throughout the dry season.

Although the land form and vegetation physiognomy are the same as those of Zone II, there are important differences between the two:

1. The vegetation of Zone VA is more heterogeneous because it has patches of both grumosols and lateritic soils. It also has rock outcrops along the rivers, an important feature for the hartebeest.
2. The slopes of the hills of Zone II are usually $4 - 5^{\circ}$ from the horizontal. Those of Zone VA are considerably more shallow at 3° .
3. Zone II has earth-lined river courses usually associated with A. kirkii.

These three differences were the main criteria used in the field to locate the common boundary of these zones.

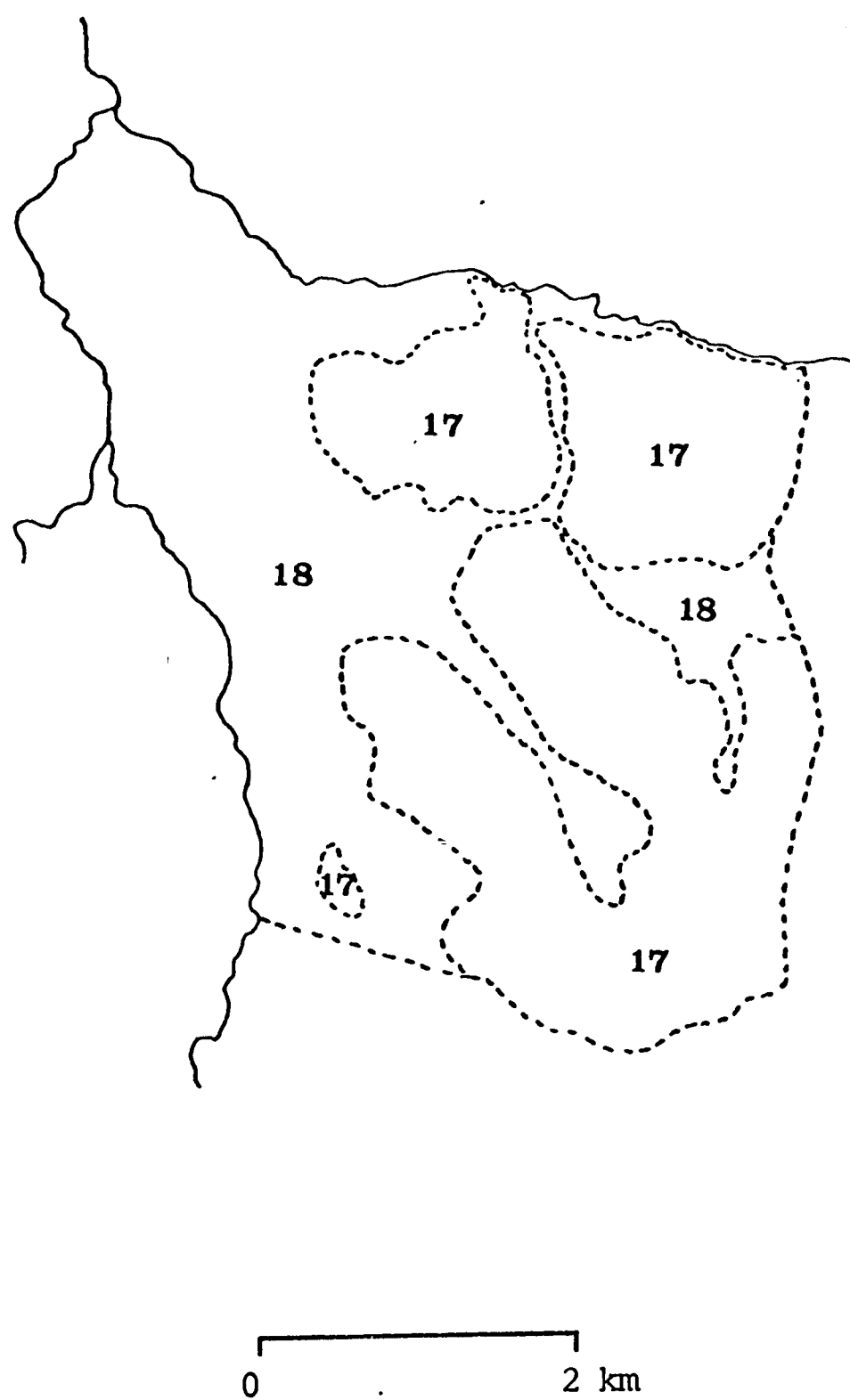


Fig.5.7. The vegetation types of Block 62.

Zone VB

This area comprises one small plateau. The vegetation is a Medium Height Bushed Grassland of great uniformity. The plateau is flat with a heavy Black clay soil, supporting dense clumps of A. mossambicense of medium height (up to 70 cms). Loose surface stones are common, resulting in a large proportion of the ground being devoid of any vegetation. A. drepanolobium is occasional and local. I. afrum and S. phleoides are frequent, but T. triandra and P. mezianum only occasional. There are no river courses on the plateau.

Vegetation Zone: Kapiti Series (including Block 62)

The whole Kapiti Plains comprise this zone (Fig. 5.1). The underlying rock is the Kapiti Phonolite which outcrops at the surface as extensive lava beds. The plains are included in the Athi land form as plains with large interfluvial distances and gentle slopes. They are almost straight in section, producing a normal catenary succession, although the soil changes are not very marked. The river beds are mostly lined with boulders, although stretches with Black Cotton sumps are found.

The Kapiti plains have the lowest rainfall of the west plains (Fig. 4.4), classing them as being in the arid zone, with an available water index of only 20 - 30%. Physiognomically, the vegetation is a mixture of Grassland and Dwarf Tree Grassland (Fig. 5.7).

Vegetation type 17

This contains the hill-top areas of low grass biomass on fine, grey soil. P. mezianum and Brachiaria serrata are both abundant. D. macroblephara and Microchloa kunthii are frequent. T. triandra is only occasional, as are also E. paspaloides and H. schimperi. Both A. drepanolobium and A. mossambicense are absent, although Abutilon sp. and S. incanum are occasional.

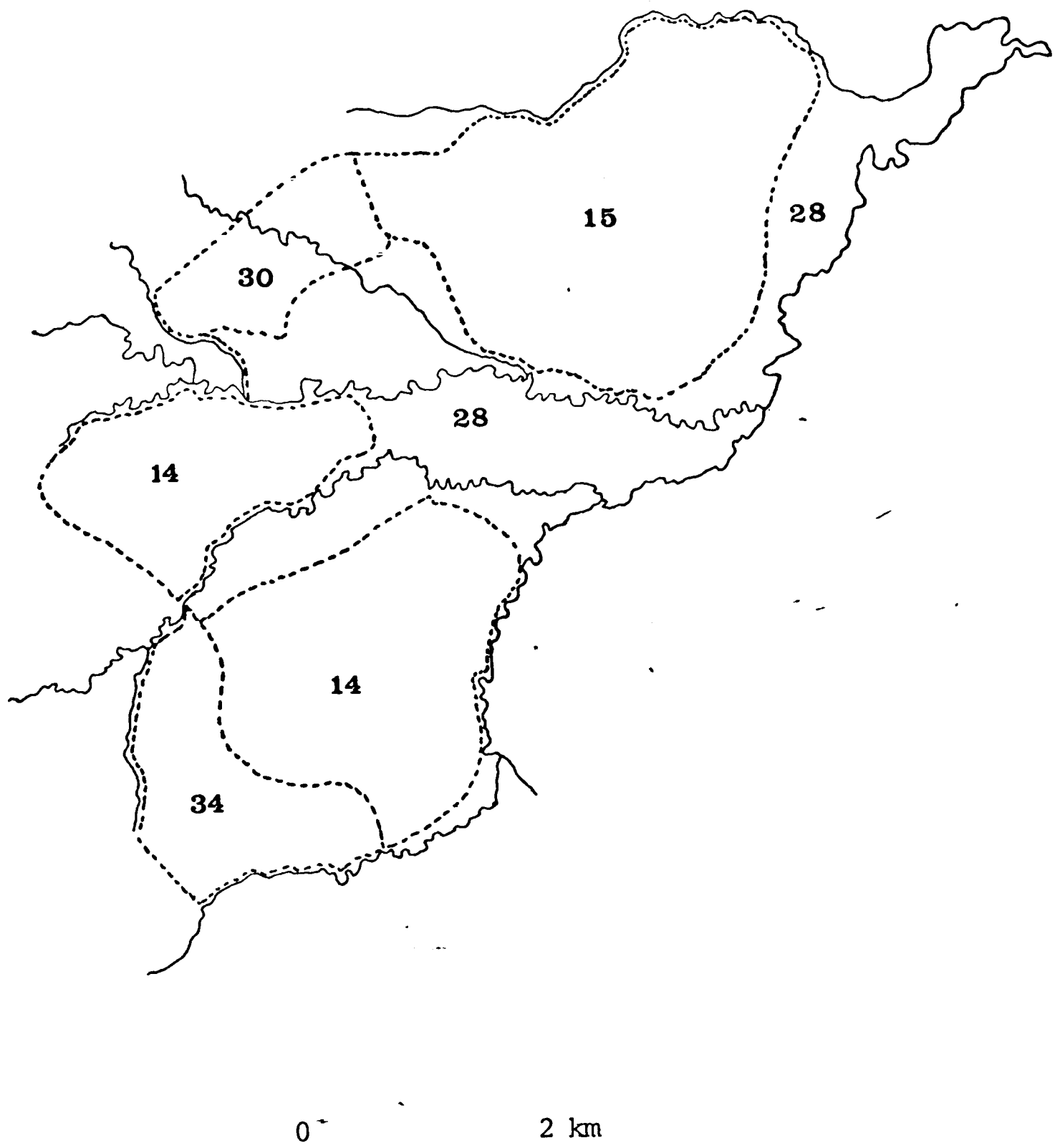


Fig.5.8. The vegetation types of Block 39.

Vegetation type 18

This type covers the slopes and small drainage lines. Medium height A. drepanolobium is dense, and is frequently found amongst the lava boulders. Consequently the grass growth on the grey-black soil is low and patchy. A. mossambicense is abundant. The most common grass is P. stramineum, while P. mezianum and D. macroblephara are frequent. I. afrum is locally abundant while T. triandra is occasional to frequent. After the rains, Senecio discifolius is common.

Vegetation type 19

This is the vegetation of the clay sumps, and is therefore of occasional occurrence only. The deep Black Cotton soil supports dense and nearly impenetrable stands of Acacia stuhlmannii, with P. mezianum and Cynodon dactylon abundant in between. P. stramineum is frequent.

Vegetation Zone VII: Basement Series (including Block 39)

This vegetation zone of Grassland with occasional Dwarf Tree Grassland covers the recent erosion surface of the Basement limestone (Fig. 5.1). It lies in the Arid zone with an available water index of only 20 - 30%. These plains of the Ndolo land form are concave in section, producing marked catenary differences in the soil and vegetation where the gradient is sufficient. Soil depth also appears to be an important modifying factor locally.

The concave section has resulted in the development of deep earth-lined river beds, with meandering courses and ox-bows. Locally there are rock pools with a better water-retaining capacity. Block 39 contains a series of large springs which collect the underground run-off from the Ol Doinyo Narok massif. The hills are also lined with small water courses which are now permanently dry. Fig. 5.8 shows the vegetation of Block 39.

Vegetation type 14

This is an open grassland type of ridges and slopes whose sward is short probably due to shallow soil and large numbers of surface pebbles. The soil is grey, but locally sandy. T. triandra and B. insculpta are abundant, with P. mezianum, D. macroblephara and E. paspaloides frequent. A. drepanolobium is absent, and the occasional A. mossambicense is stunted.

Vegetation type 15

This appears very similar to type 14 but their differences are probably due to the deeper soil of the former. It is also found on ridges and upper slopes. T. triandra and B. insculpta are still both abundant but P. mezianum is frequent. P. stramineum and H. lintonii occur occasionally. H. schimperi occurs locally in areas of low plant cover.

This grassland is typical of most of the zone, and is found across complete dry valley systems whose relief is too slight to show any significant catenary effect. Under these conditions, A. drepanolobium is found but is scattered and stunted, again suggesting sub-optimum soil conditions.

Vegetation type 28

This type, which is more typical of Zone IVA and is described with that zone, covers the narrow sumps of this zone. The major water-courses dissect this deep clay area.

Vegetation type 30

This type occupies the broader flood plains of Black Cotton soil. A. mossambicense occurs at medium density and reaches 75 cms in height. There is no A. drepanolobium, and the proportion of bare earth is high. I. afrum and S. phleoides are abundant, with T. triandra and D. macroblephara only occasional.

Vegetation type 34

This small type is found very locally on the steeper bottom slopes

below type 14. The soil is stony and the A. mossambicense appears highly stunted, reaching only 30 cms. E. paspaloides is abundant amongst this shrub, while S. phleoides is frequent. There is no A. drepanolobium.

Vegetation type 31

This is a small flood plain grassland type found only along river banks which are seasonally inundated. I. afrum and a coarse Setaria sp. are the only species found. Because of its distribution this type remains green for more of the dry season than any other vegetation type. Type 28 is found slightly higher up the slope.

Vegetation Zone VIII: Oloiengalani Series

This is a small zone of undulating plains in the Athi land form (Fig. 5.1), overlying rock of the Olorgesailie series. It is included in the semi-arid zone with an available water index of 30 - 40%. Physiognomically, it is an area of Grassland with gentle slopes and occasional inselbergs, with earth-lined river beds often supporting A. kirkii.

The soil of the area is uniformly brown and no catenary sequence is recognisable. The dominant grass species in the short sward are P. mezianum and P. stramineum, both of which are abundant. D. macoblephera and E. paspaloides are both frequent, but T. triandra only occasional. A. drepanolobium is absent.

5.6 The Vegetation of the Nairobi National Park

Although the Nairobi Park study area was mapped accurately (Fig. 5.3), a more extensive map was needed at this detailed level for the following reasons:

1. A knowledge of the dynamics of the Park vegetation is essential for its management, and although the vegetation had been described (Heriz-Smith 1962), no map existed. Therefore, an extensive but detailed map would form a base-line against which gross changes in the vegetation could be detected.

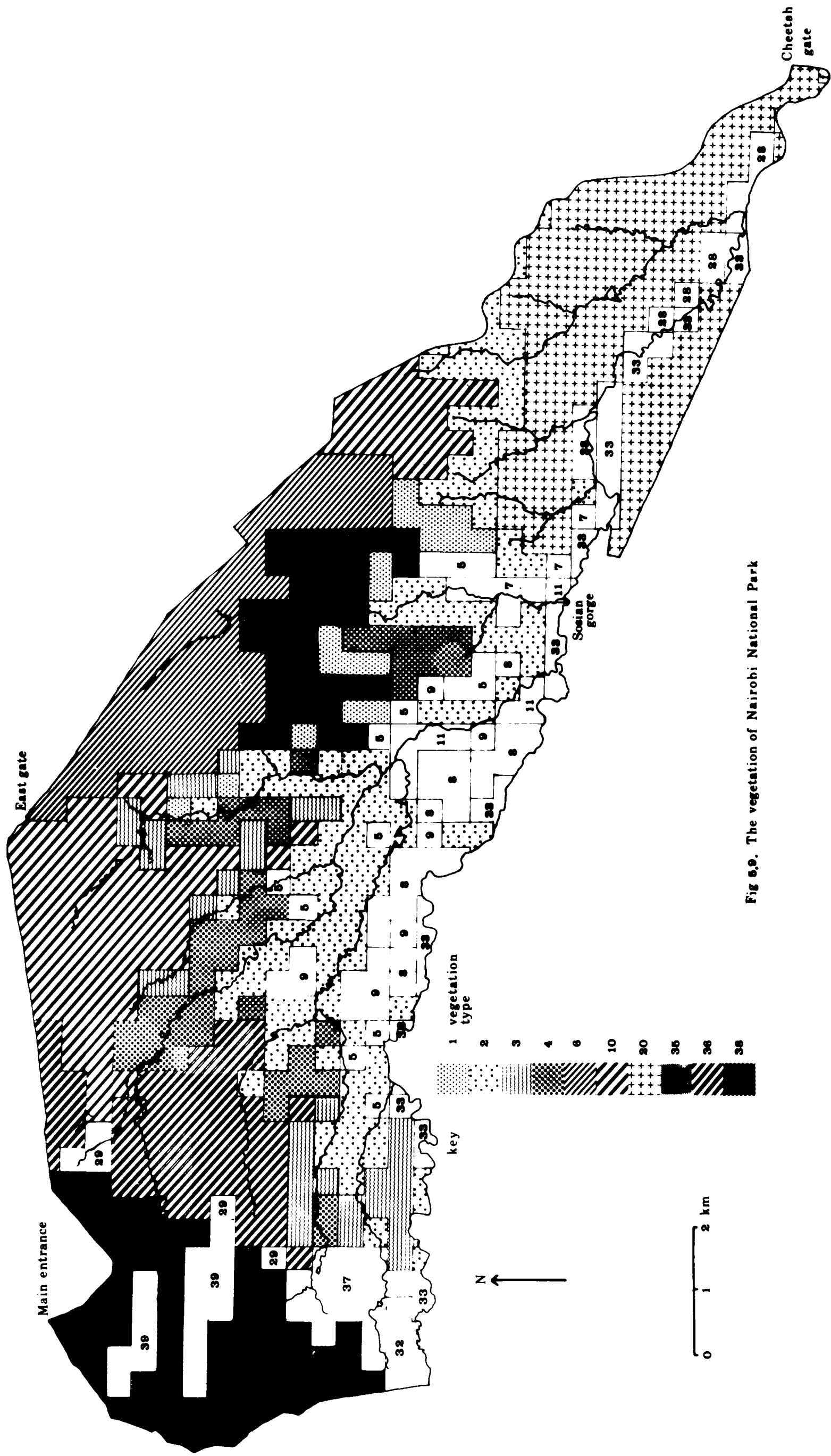


Fig 5.9. The vegetation of Nairobi National Park

Table 5.1. A summary of information defining the Vegetation Zones.

Vegetation Zone	Ecological Zone	% Annual index of available water	Land System	Geology	Vegetation Physiognomy
I Lowland <u>Acacia drepanolobium</u>	IV Semi-arid	40 - 50	Embakasi	Mbagathi Trachyte & Nairobi Phonolite	Dwarf Tree Grassland
II Highland <u>Acacia drepanolobium</u>	IV Semi-arid	30 - 40	Embakasi	Ol Doinyo Narok Agglomerates	Dwarf Tree Grassland
III Semi-Evergreen Forest	III Dry sub-humid - semi-arid	50 - 60	Karen	Nairobi Trachytes	Upland Forest
IV Upper Athi Tuffs Series	IV Semi-arid	30 - 40	A. Athi	Upper Athi Tuffs	A. Grassland
			B. Athi		B. Medium height bushed grassland
V Olooloitigoshi Series	IV Semi-arid	30 - 40	A. Embakasi	Olorgesailie phonolitic nephelinite	A. Dwarf Tree Grassland
			B. Athi		B. Medium height bushed grassland
VI Kapiti Series	V Arid	20 - 30	Athi	Kapiti Phonolite	Grassland & dwarf tree grassland
VII Basement Series	V Arid	20 - 30	Ndolo	Basement gneisses	Grassland & dwarf tree grassland
VIII Oloiyaangalani Grasslands	IV Semi-arid	30 - 40	Athi	Olorgesailie phonolitic nephelinite	Grassland

2. Even to a casual observer, the vegetation of the Park is highly heterogeneous, partly because three vegetation zones are represented in this small area. This meant that the vegetation of the study area, which was part of the predominant zone, could not be typical of the whole park. Consequently, the patterns of utilisation of the grasslands might not be the same throughout the park.

For this map the grid system of 400 x 400 m squares, described in Ch. 2 (p. 17) was used. The boundaries of each square were marked on a 1:25,000 map and could be located in the field with an accuracy of about ± 50 m, by reference to prominent trees, river courses, roads etc. which were shown on the map. Each square was visited and its dominant vegetation type and all others present were recorded. Dominant is used here in the sense of covering the largest fraction of the total square. Fig. 5.9 is the composite map of the dominant vegetation types of each square.

The map obtained from imposing a regular grid on to a mosaic of vegetation types depends largely on the size of the grid squares. The true pattern will be observed if the squares are small compared to the areas of the vegetation types. However any reduction in grid size greatly increases the necessary field-work. A compromise must, therefore, be made between the scale required to obtain a satisfactory representation of the vegetation and the effort expended to obtain it.

To test whether a grid size of 400 x 400 m was satisfactory in the Nairobi Park, the vegetation of the study area, for which the precise boundaries of the types had been established (Fig. 5.3) was remapped using the grid system. A comparison of Fig. 5.3 and the relevant portion of Fig. 5.9 shows that the grid map is, for the most part, extremely similar to that of the more detailed version. The 400 x 400 m grid was therefore considered sufficiently precise.

5.7 Discussion

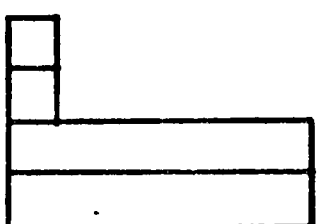
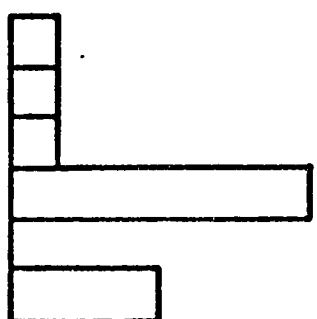
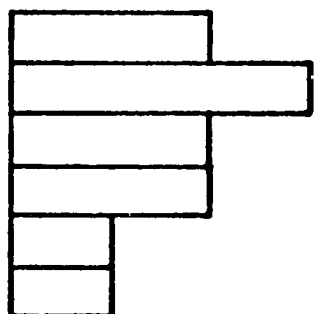
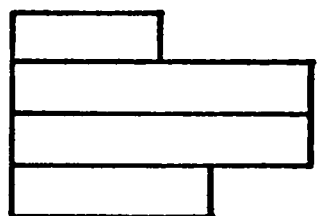
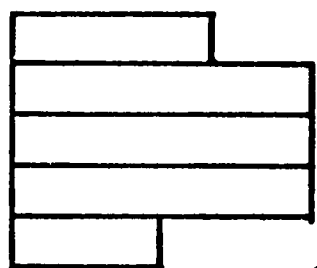
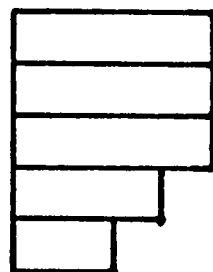
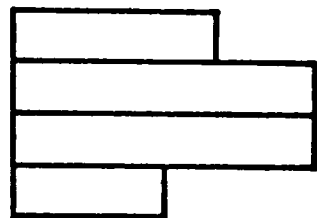
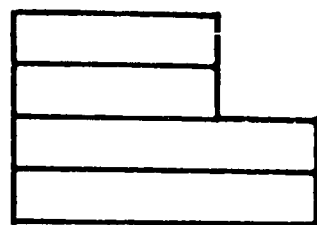
Table 5.1 summarises the information on the geology, topography,

free drainage

lateritic soils

Black soils
Cotton

highly
impeded
drainage



Themeda
Sporobolus
Aristida
Digitaria

Themeda
Cymbopogon
Hyparrhenia
Digitaria

Themeda
A.drepanolobium
Setaria
Aspilia
Ischaemum

Themeda
A.drepanolobium
Setaria
Ischaemum
Aspilia

Themeda
A.drepanolobium
Aspilia
Ischaemum

Themeda
Pennisetum
Setaria
Aspilia
A.drepanolobium
Ischaemum

Themeda
A.drepanolobium
Pennisetum
Ischaemum
Setaria
Aspilia

Themeda
Setaria
Ischaemum
Aspilia

absent
occasional
locally frequent
frequent
abundant

Fig.5.10.Plant species abundance in a catenary sequence of vegetation types,

climate and site potential as measured by the amount of available water and vegetation physiognomy of the eight vegetation zones of the west plains. Although two or more zones may be identical with respect to one or more of these parameters, the combination of values is unique for each zone. This suggests that if the Semi-Evergreen Forest is excluded, these zones are genuine, fundamental divisions of what appear at first to be uniform "open plains".

Of these parameters, the most important single one in defining the zones is the underlying geological formations. This is shown by the similarity of the geological map (Fig. 3.2) to that of the vegetation zones (Fig. 5.1). This coincidence is not surprising because, in an area of recent volcanic activity, the rock formations are the main determinants of the contemporary physiography and the related factors of drainage patterns, soil depth and quality, and vegetation.

Two features of the soils and vegetation of the Athi Plains are particularly notable. The first is the prevalence of soils of the Black Cotton type, and the second is the widespread abundance of Themeda triandra, which is reflected in many of the descriptions of this type of grassland (e.g. Rattray 1960).

The gradient of the plains is usually too slight to cause the formation of marked catenary differences in the soil except in the Lowland A. drepanolobium zone and, to a lesser extent, in the Kapiti Plains. Thus large areas of black clay soils are found, which are characterised by severe water-logging in the rains followed by progressive drying out and cracking. These soils must be largely responsible for the composition of the current vegetation.

The prevalence of Themeda seems due to its tolerance of a wide range of environmental conditions. Fig. 5.10 shows a series of vegetation types, drawn from some of those described, which are arranged in order of increasingly impeded drainage, irrespective of their actual position on

the slope. Starting with the two well-drained vegetation types of O2 and O4 on lateritic soil, T. triandra occurs frequently in each case, but in the company of two predominantly different sets of species: Sporobolus pyramidalis and Aristida adoensis in O4, and Cymbopogon poschpilii and Hyparrhenia lintonii in O2.

T. triandra is also abundant on the best drained of the Black Cotton soil vegetation types (type 10 in Block 15), but is associated with A. drepanolobium, Setaria phleoides and Ischaemum afrum. As the drainage becomes more impeded (type 10 in Nairobi Park through types 18, 28, 36 and 09) the A. drepanolobium and S. phleoides gradually decrease in abundance as I. afrum and Aspilia mossambicense increase. Although T. triandra is scarce in highly water-logged areas, it is the only grass species of any significance to be found on lateritic and moderately impeded clay soils. Heady (1966) found that T. triandra was the dominant component of grasslands over a variety of soils and its abundance was not related to any detectable soil characteristics.

The extensive Themeda grasslands of Africa are often regarded as sub-climaxes, held there by grazing and fire (Ndwala-Senyimba 1972). The effect of the latter on the species has been investigated experimentally. When a Themeda seed falls from the parent plant to the ground, the arrow-like awn penetrates the soil with its hygroscopic movements (Edwards 1942). The depth of burial is probably sufficient to protect the seed from the high temperatures experienced by the surface soil when the vegetation burns (Lock and Milburn 1971). Although Themeda seedlings appear in profusion following rain on a burnt area, the same effect can be obtained by clipping and removing the plant cover, and experiments suggest that light may be important in stimulating germination (Lock and Milburn loc. cit.). Coupled with the observation that the Themeda regrowth after a burn has a large number of flowering culms (McKay 1971), it is obvious that this species is well-adapted to the occurrence of periodic

fires or defoliation by other agencies, and this adaptation is undoubtedly important in the maintenance and continued existence of the grasslands dominated by it.

However, fires in the Athi Plains are now rare and there is no indication that the Maasai deliberately start fires as a management technique to stimulate the growth of fresh grass. This is in marked contrast to other areas of Maasailand which are almost totally burnt each year.

During the study period from October 1970 to December 1972, there was only one fire in the plains, and this affected an area of only a few square kilometres. It proved impossible to find out whether the fire was accidental or not. Although Blixen (1937) records the Maasai as burning the plains in the late dry season, it seems that burning on a large scale ended about twenty years ago (Lamprey, pers. comm. 1974). Trump (1967) says that over the past few years the coverage of A. drepanolobium has increased which he infers is a result of the respite from being burnt. A photograph of the Kapiti Plains taken in 1956 (Anon 1956) shows an area of open grassland which can be located precisely; today, slightly less than half of it is occupied by A. drepanolobium.

Although fire has not been an important influence on the vegetation for this period of time, T. triandra is still widespread and abundant, and this abundance is probably due to its tolerance of soil conditions and the effect of large herbivores. In four areas of "Themeda triandra grassland" in East Africa, Heady (1966) found that the proportion of T. triandra in the sward decreased as the number of grazing animals increased. Experiments in the Rift Valley (McKay 1971) and in western Kenya (Bogden and Kidner 1967) showed that with high stocking rates of cattle and continuous grazing, the proportion of T. triandra remained constant, although in the latter study it decreased under conditions of heavy stocking and rotational grazing. The significance of light utilisation to the species was apparent at Athi River where T. triandra increased from 40% to 53% of the sward under conditions of hay cutting at the end of the dry season

(Ndwala - Senyimba 1972). Complete protection had no effect on its status, while intensive mowing eliminated the species.

The maximum stocking rate of 4.4 acres/steer used by McKay (loc. cit.) is equivalent to a biomass of about $27,300 \text{ kg/km}^2$, which is at the upper end of the range of values for the biomass of domestic stock and wild herbivores in the Athi Plains (p.140). It is, therefore, unlikely that the grazing pressure of these animals is sufficient to reduce the T. triandra, and may indeed be stimulating its growth.

Although Themeda is equally ubiquitous in the Nairobi Park, this area presents a slightly different case because a policy of rotational burning has been in operation for the last few years so that most of it has been burnt at least since 1963. These fires should allow the Themeda to re-establish itself by seeding (Lock and Milburn 1971), but it is certainly not abundant in the most recently burnt areas (vegetation type 06, p. 57), although there may have been overriding, adverse edaphic conditions. The absence of cattle from the Park is associated with a lower biomass of grazers, but their grazing pressure may be more continuous through the year. Again, these conditions would appear to favour Themeda.

Although part of the west plains, the area of the Nairobi Park can be further distinguished. The three vegetation zones represented in this small area, are due to the heterogeneous nature of the underlying rock (Fig. 3.2) and the variety of land relief, drainage patterns and vegetation that this produces. Fig. 5.9 shows the concomitant variety of vegetation types in the park, and there are clearly three groups of types: an eastern group in the Semi-Evergreen Series, the large central one of the Lowland A. drepanolobium Series which is far from homogeneous, and the western one of the Upper Athi Tuffs Series.

The comparison between the Park and the plains can be taken further with the park study area and Block 15, both of which are located in vegetation zone II. Although the drainage of the Black Cotton areas of Block

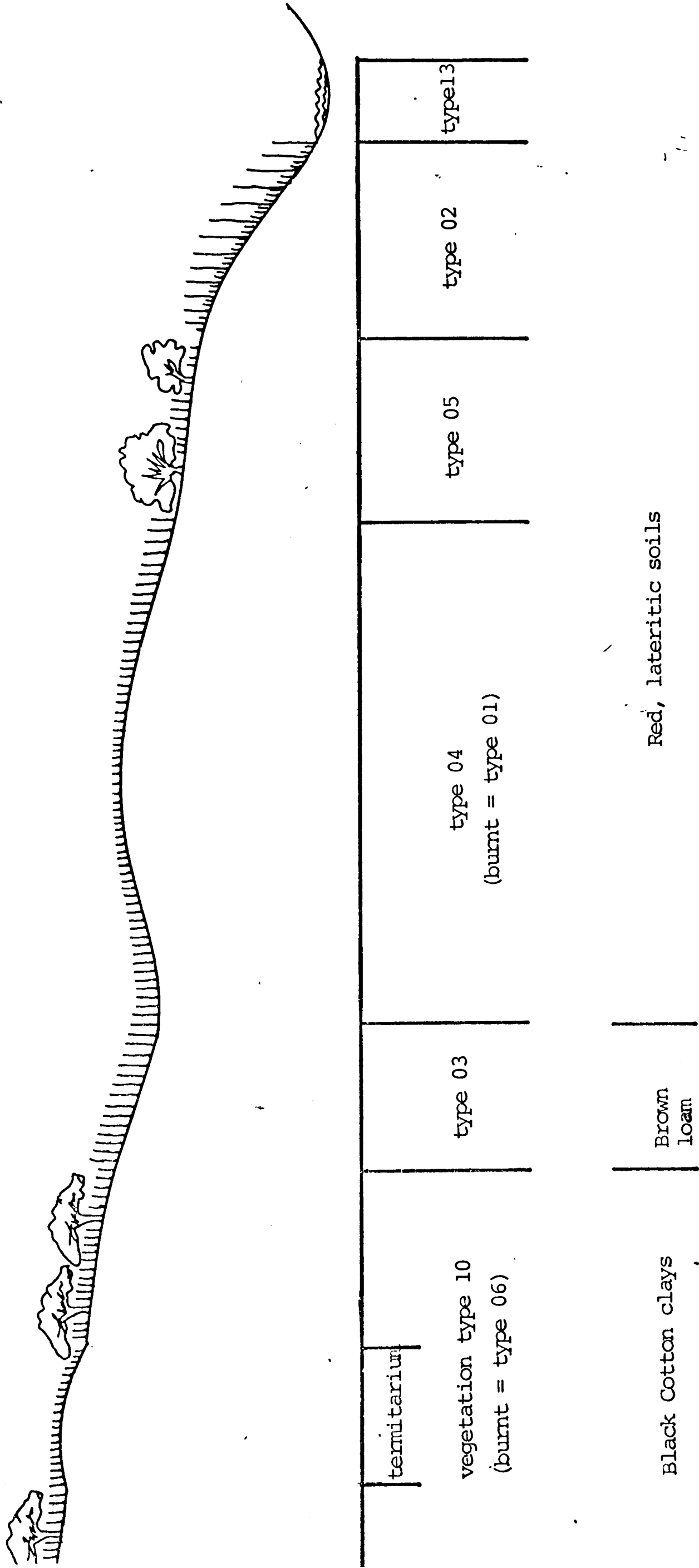


Fig.5.11. Diagrammatic profile of the vegetation and soils of the Nairobi Park (Lowland *A.drepanolobium* grassland)

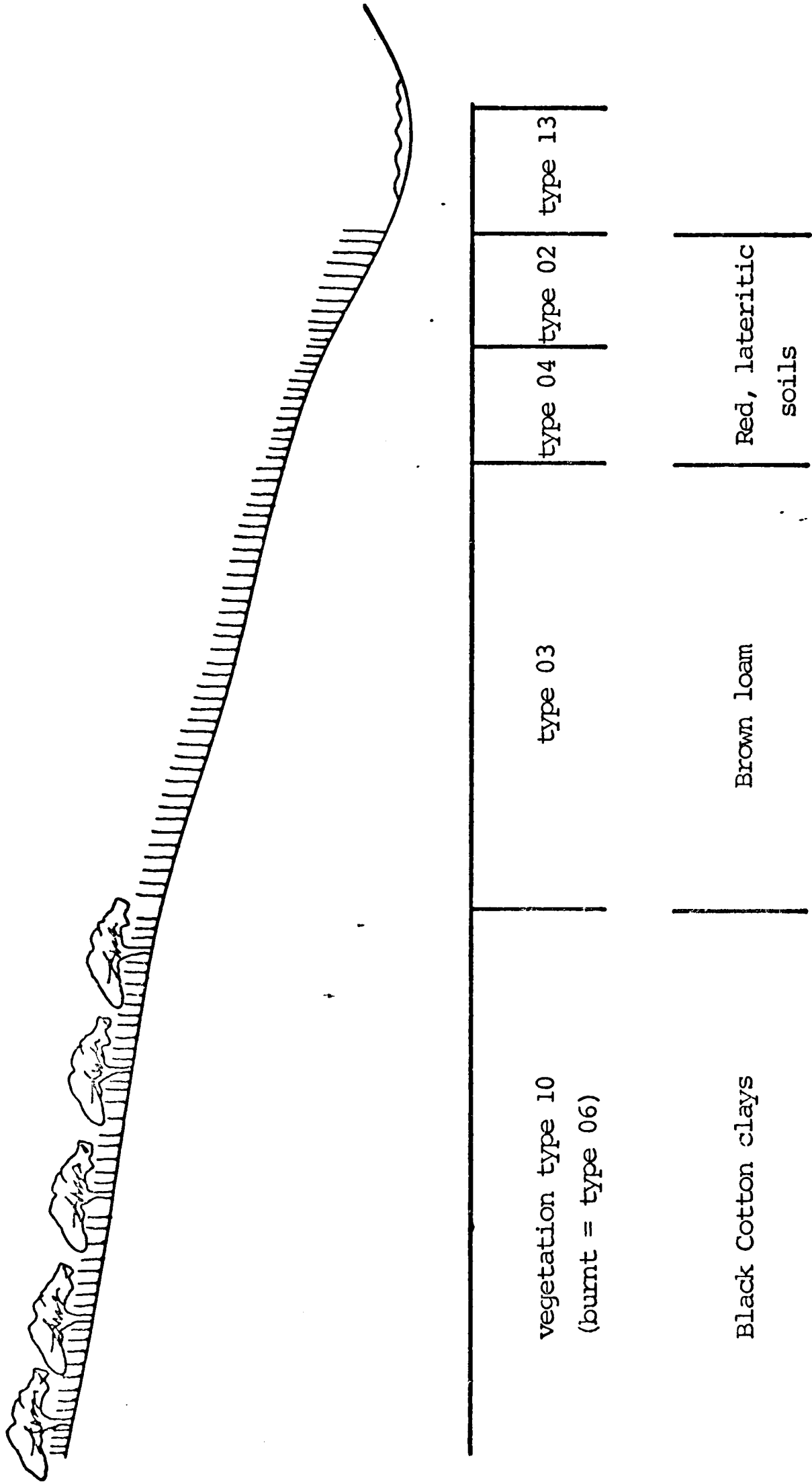


Fig.5.12. Diagrammatic profile of the vegetation and soils of Block 15 (Lowland A.drepanolobium grassland).

15 is less impeded than in the equivalent areas in the park (producing a greater density of T. triandra), the lower slopes of the catena are not as steep. This is a result of the less frequent development of riverine gorges and their lesser depth in Block 15 than in the park. Because of this lower gradient, the well-drained lateritic soils have developed only patchily, and their associated vegetation types are too small in area to show on the map (Fig. 5.2). On the other hand, the brown soil which appears as an intermediate between the black clays and the lateritic soils is comparatively extensive and supports its usual vegetation (type 03). Figs. 5.11 and 5.12 show typical sections through the catena in the Nairobi Park study area and Block 15 respectively. The scarcity of the lateritic soils and the preponderance of vegetation types 10 and 03 in the latter is striking. As type 03 is largely composed of Themeda and it is abundant in type 10, Block 15 has more Themeda than the Park study area. However, its diversity of vegetation types is lower.

Thus, within the ecological unit of "Acacia-Themeda" plains, the Nairobi Park has a great variety of geological structure and land relief, with a comparable variety in its vegetation at the levels of the whole park and the study area. The composition of the large mammal community and the ecology of the hartebeest in the park are strikingly influenced by this diversity and this is emphasized in subsequent chapters.

Chapter 6.

THE POPULATION OF THE HARTEBEEST AND OTHER HERBIVORES

6.1 Introduction

The difference between the Nairobi Park and the Athi Plains in the density of hartebeest was immediately obvious on the ground. To compare the areas (p. 7), measurement of the actual densities was required. The methods employed stemmed partly from the size and nature of the two areas, and partly from the need to answer the following questions:

1. Did hartebeest move in to and out of the park in significant numbers through the year?
2. Despite the possibility of these movements, was the size of the park population changing?
3. Were hartebeest moving in to and out of the plains, apart from any possible exchange with the park?
4. How and where were the hartebeest distributed in the plains?

To answer the first two questions, a method yielding a precise estimate, in the sense of having a low standard error (Watt 1968), was necessary. If this were achieved, a biological explanation could be given to any observed variation in the population estimate. But although a highly repeatable sampling method with constant biases may fulfil this objective, the estimate may not be accurate in the sense of being close to the true population figure (Watt loc. cit.). Although an accurate estimate of the size of the hartebeest population was also desirable, precision was considered more important for the following reasons:

1. The small size and good network of roads in the park (p. 17) made conditions ideal for total counts. No error can be attached to total counts, but as their cost in time and money was relatively low, they could be repeated frequently. As the sampling procedure could be highly standardised, their precision should have been high, although incalculable.

2. The results of independent total counts of the park, organized in a different way, were available for comparison. If the results, of the two methods, with their own biases, were in close agreement, they could be assumed to be fairly accurate.

The Athi Plains, excluding the park, cover 1800 km². As a total count over such an area would be impractical as well as inaccurate, the censusing of sample areas was necessary. Although open plains reduce the problems associated with the differential visibility of species (Lamprey 1963, Harris 1972), and are therefore suitable for ground transect counts, this approach was abandoned because much of the plains was too rough or precipitous to keep to a transect accurately. Under these circumstances, counts were made from the air. A high precision was again the objective, and it could be assessed from the sample counts. The biases were reduced as far as possible, but without notable success (below). The results of other aerial censuses over the area also enabled some check on the accuracy of the results.

For all but two of the counts, all parts of the plains were covered systematically and equally. The variances of the population estimates from these counts were high. In an attempt to reduce these, thereby improving their precision, the sampling effort was stratified. The object of stratification is to increase sampling efficiency by dividing the population into internally homogeneous and non-overlapping sub-populations (Watt loc. cit.). In the present circumstances, the plains were divided to produce strata with different, but internally uniform, densities of hartebeest. This procedure is described fully in the next section.

The number and frequency of aerial counts of hartebeest were determined by financial considerations. However, once an aircraft is in the air, the added cost of counting more species is small. Therefore, after the first counts on which hartebeest only were counted, and the observers gained

experience, wildebeest, zebra and cattle were progressively included in the censuses. Admittedly, this introduced new errors and biases in to the accuracy of the hartebeest estimates, but this disadvantage was outweighed by the value of the new information obtained.

In this chapter, the results of the counts of hartebeest, wildebeest and zebra in the park and the plains, and of cattle in the latter are presented. Comparison of the densities of hartebeest in the two areas is followed by a comparison of their age class structure. Finally, the seasonal variation in distribution of the 3 wild species is described and compared. This points to a fundamental difference between the behaviour of the hartebeest and of the others.

6.2 Methods

Ground counts

16 total counts were made in the Nairobi Park at monthly intervals between January 1971 and April 1972, using the methods described earlier (p. 17). All individuals were classified in to the sex/age groups of adult males, adult females, subadults, juveniles and newly-born calves (p. 15).

Since 1960, the National Parks authorities have organised total counts of all the animals in the park. These have been carried out nominally on the last Sunday of each month by pairs of observers in vehicles. Each pair covers one of the 14 zones in to which the park is divided for this purpose. The results of these counts provide a check on the accuracy of my total counts, and give population totals for other species.

Aerial censuses

Aerial censuses were made by traversing a series of systematically arranged transects across the Athi Plains. On all but the last two counts, the transects were the east-west lines of the 10 x 10 km grid on the appropriate 1:250,000 map. Another transect was added between each

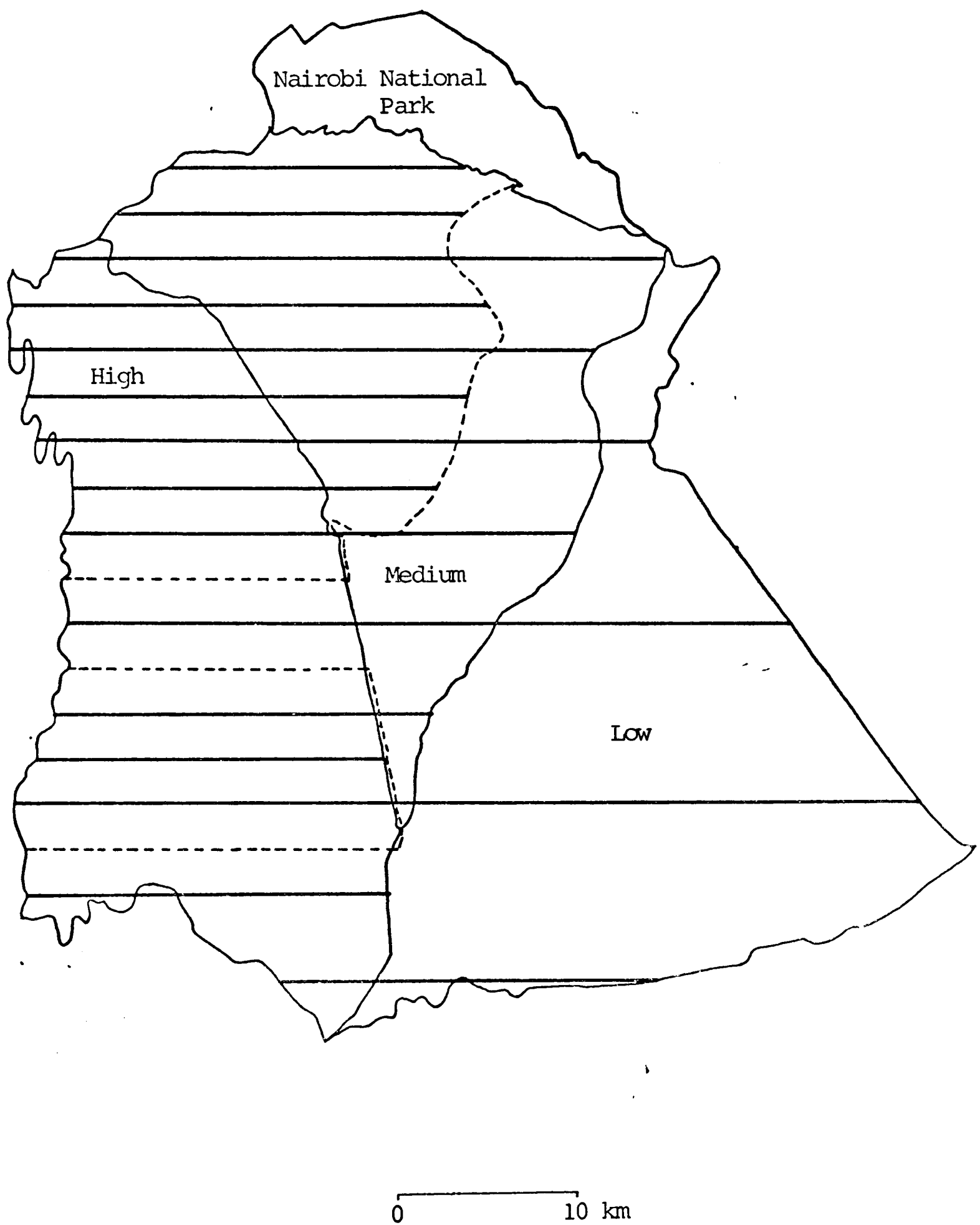


Fig.6.1. The location of aerial transects flown over the Athi Plains in the 3 strata with high, medium and low densities of hartebeest.

grid line, producing a total of 10 transects with 5 km between each.

Counts were made at a flying height of 400 ft (123 m) with 2 observers counting the animals in a strip 400 m wide on either side of the aircraft. Two streamers taped on to the wing strut defined the strip on each side. These were located with the aircraft on the ground in a horizontal flying attitude, using the method of Pennycuick and Western (1972) to obtain the desired strip width at an altitude of 400 ft. The pilot navigated during the count and attempted to keep the airspeed at about 60 mph. The transects were divided in to numbered 5 km lengths on the same grid system, and the pilot informed the observers as each 5 km length started and finished. Because the animals in a 400 m strip on either side were enumerated, and the transects were 5 km apart, the percentage of the area of the plains which was censused was $(800/5000) \times 100 = 16.0\%$. This is known as the sampling fraction.

8 such counts were made at 2-month intervals between January 1971 and March 1972. Two more counts were made in which the sampling intensity was stratified on the basis of the picture of hartebeest density distribution already obtained. Three areas (Fig. 6.1) were defined as high, medium and low density strata. Sampling effort between these strata was allocated optimally (Siniff and Skoog 1964). In populations of large mammals which may have very clumped distributions, the variance of a high density stratum tends to be greater than that of a low density stratum (Siniff and Skoog loc. cit.). The precision of the population estimate will then be improved most by allocating the sampling effort in proportion to the densities in the strata, rather than in proportion to their areas. For this reason, the distances between the transects in the high, medium and low density strata were adjusted to produce sampling fractions of 32, 16 and 8% respectively, when transects of the same width as before were censused.

Table 6.1. Details of 10 aerial censuses, and the animal species counted, over the Athi Plains, 1971-72.

Date	type of census	aircraft type	pilot	number of observers	species censused	observations recorded by
26.1.71	unstratified	P/Cruiser	CJP	2	H	writing
6.3.71	unstratified	P/Cruiser	CJP	2	H	writing
5.5.71	unstratified	P/Cruiser	CJP	2	H	tape recorder
7.7.71	unstratified	P/Colt	DE	1	H	tape recorder
1.9.71	unstratified	C/150	DE	1	H	tape recorder
9.11.71	unstratified	P/Cruiser	WH	2	H, W, Z	tape recorder
13.1.72	unstratified	P/Cruiser	AH	2	H, W, Z	tape recorder
6.3.72	unstratified	C/172	AP	2	H, W, Z, C	tape recorder and C . photographed
27.3.72	stratified	P/Cruiser	WH	2	H, W, Z, C	tape recorder and all species photographed
26.9.72	stratified	P/Cruiser	CJP	2	H, W, Z, C	tape recorder and all species photographed

H = Hartebeest; W = Wildebeest; Z = Zebra; C = Cattle.

The first four and last counts were made with the same combination of pilot, aircraft type and observers. On the middle censuses 3 other aircraft types and 4 other pilots were employed. Two of these counts could only be done with one observer, thereby halving the sampling fraction. This variety introduced new factors affecting the accuracy and precision of the counts, and their comparison, but was unavoidable if the counts were to be made.

Table 6.1 gives details of the counts. On the first 5 only hartebeest were counted, and on all counts but the first two each observer had a tape recorder for recording the number of animals seen, thereby avoiding moving the eyes from the transect to write. On the next two counts, wildebeest and zebra were included, and cattle were also added for the last three counts. All but small herds of cattle were photographed on High-speed Ektachrome film by each observer who had an Asahi Pentax camera and 55 mm lens. Large aggregations of one species or associations of several species were all photographed on the final 2 counts. Photographs were later scored under a 5 x binocular microscope by pricking a clear plastic overlay above each animal as it was enumerated. These totals were then integrated with the transcribed, tape-recorded data of the appropriate transect and 5 km unit.

The flight data were analysed by the method of Jolly (1969) for unequal-sized units. Strictly this is designed for the situation in which all possible sampling units have the same chance of being selected for counting, rather than the present one with systematically spaced units. In practice, use of this method for systematic samples results only in a slight overestimate of the variance (Pennycuik, Sale, Stanley Price and Jolly in prep.) and is acceptable in view of the other advantages of this sampling method. These are, most notably, easier navigation and a distribution map of the animals based on a more even coverage of the area.

The numbers of each species in each transect were totalled and this constituted a sampling unit. The area of each transect was calculated as the product of the strip width and the transect length taken from the flight map. A north-south base-line was drawn across the widest part of the plains. This line was crossed at 90° by the transects. The number of possible transects was calculated as the length of the base-line divided by the strip width. The total area of the plains under survey was measured (p.26) as 1776 km^2 .

The population estimates and their confidence limits for either the whole area or for each density stratum are given by (Jolly loc. cit.):

$$YZ = \frac{Y1 \cdot Z}{Z1}$$

where Z is the total area under survey,

$$\text{and } Y1 = \sum_i N_i \cdot y_i$$

where N_i is the total number of possible sampling units in the i-th stratum, y_i is the average number of animals over the n_i units sampled.

$\sum$ denotes summation over all strata.

$$\text{and } z_i = \sum_i N \cdot y_i$$

where z_i is the average area of the transects over the n_i transects sampled. Therefore, the ratio $\frac{Y1}{Z1}$ is an estimate of the average density per unit area. Multiplication by Z, the total area, gives an estimate of the total numbers, Y2.

The variance of the estimates, $\text{Var}(Y2)$, is found by

$$\text{Var}(Y2) = \sum_i \frac{N_i (N_i - n_i)}{n_i} (s_{y_i}^2 - 2R s_{zy_i} + R^2 s_{z_i}^2)$$

$$\text{where } R = \frac{Y1}{Z1}$$

$$s_{y_i}^2 = \frac{1}{n_i - 1} \left(\sum y_i^2 - \frac{(\sum y_i)^2}{n_i} \right)$$

$$sz^2_i = \frac{1}{ni-1} \left(\sum zi^2 - \frac{(\sum zi)^2}{ni} \right)$$

$$szyi = \frac{1}{ni-1} \left(\sum ziyi - \frac{(\sum zi)(\sum yi)}{ni} \right)$$

The population standard error, $SE(Y2) = \sqrt{Var(Y2)}$, and the 95% confidence limits of $Y2 = Y2 \pm 1.96 \cdot SE(Y2)$.

The distribution and movements of the species censused on the unstratified counts have been related to the vegetation of the plains. By super-imposing the transects on to the vegetation map (Fig. 5.1) each 5 km length has been allotted to a vegetation zone, and the numbers of each species in the units covered by each zone have been summed. By dividing the percentage of the observed animals in each zone by the percentage of the 78 5 km lengths which lie in that zone, an index of selection is obtained (Hunter 1954). This is independent of the absolute number of each species which were counted. An index value of more than 1.0 indicates that more of the population is in that zone than would be expected on a random distribution, and it is therefore being selected. Values less than 1.0 indicate avoidance.

Rainfall

As an estimate of the rainfall over the whole plains during the period covered by the aerial counts, the mean monthly rainfall from Wilson, Embakasi, Stony Athi, Senya, Konza and Kajiado (Appendix 3) is used as the effective rainfall, P/E_t .

6.3 Results

The Nairobi Park

The following figures are the results of the 16 hartebeest counts in the Nairobi Park. The figures in brackets are the results of the count at the end of the previous month, organised by National Parks staff.

month	population size	month	population size
January 1971	1953 (2007)	September	2015
February	2007	October	2067
March	1812	November	2060
April	2114 (1990)	December	2195
May	1865	January 1972	2275
June	1468	February	1988
July	1500	March	2073 (2330)
August	1836	April	2103 (2200)

As the agreement between the two figures in each pair is generally close, the long series of hartebeest totals are considered fairly accurate. In June and July, the areas of Black Cotton soil were so waterlogged after heavy rain (Appendix 3) that a complete survey was not possible, and this is reflected in the lower population estimates. These 2 counts are excluded in calculating the mean population size of 2026 hartebeest, with a standard error of 35.1 and a 95% confidence range of 1957-2095. The standard error is only 1.73% of the mean, which is good evidence of a constant population size through this period. The mean density is 17.8 km^{-2} .

The results of 7 end-of-month total counts of wildebeest and zebra during the study period are available:

month	wildebeest numbers	zebra numbers
December 1970	419	1302
March 1971	707	2205
February 1972	253	165
March	345	171
April	445	557
May	249	108
June	193	156

Table 6.2. The population estimates ($\hat{Y}$), their 5% confidence intervals (S.E. ($\hat{Y}$)), and mean estimates and confidence intervals for 10 hartebeest censuses, 5 censuses of wildebeest and zebra, and 3 censuses of cattle.

Date	Hartebeest $\hat{Y}$, S.E. ($\hat{Y}$), 5% confidence interval	Wildebeest $\hat{Y}$, S.E. ($\hat{Y}$), 5% confidence interval	Zebra $\hat{Y}$, S.E. ($\hat{Y}$), 5% confidence interval	Cattle $\hat{Y}$, S.E. ($\hat{Y}$), 5% confidence interval
26.1.71	4756 + 634			
5.3.71	4775 + 1994			
5.5.71	6104 + 1545			
7.7.71	6178 + 3149			
1.9.71	2830 + 1386			
9.11.71	3353 + 1320	8842 + 2458	4609 + 3244	
13.1.72	5716 + 1980	15800 + 6182	10540 + 5047	
6.3.72	6928 + 2523	12755 + 4298	9063 + 4051	47858 - 25284
27.4.72	4887 + 1571	14584 + 3443	7882 + 3606	44729 + 9761
25.9.72	3396 + 1686	16051 + 9041	3963 + 2407	53008 + 14612
Mean	4892 + 1882	13606 + 5592	7211 + 3775	48531 + 17775

Even in this short series of counts, the numbers of wildebeest and zebra in the park fluctuate widely. Numbers of both were highest in the extremely dry conditions of March 1971 (p. 11), but were also high in the dry season of April 1972. Although the number of zebra in the park can equal that of hartebeest, the mean figures of 666 zebra and 373 wildebeest are far below the mean population size of 2026 hartebeest.

In September 1972 large numbers of wildebeest and zebra entered the park. During this month rain fell at the stations in the north of the plains, while the long run of rainless months continued further south (Appendix 3). In addition, for the first time in the study, large numbers of hartebeest also immigrated in to the park. The end-of-month counts for August and September 1973 gave the following totals:

species	August	September
wildebeest	398	3606
zebra	2710	4082
hartebeest	2123	3066

These figures show that the influx of zebra from the plains was earlier than that of the wildebeest and hartebeest. My own total count of hartebeest on October 3, 1972, produced a figure of 3406 animals. Comparison with the mean of 2026 shows that approximately 1400 animals had moved in.

The hartebeest population of the plains

Table 6.2 shows the estimates of the hartebeest population from the 8 unstratified and 2 stratified counts, with their attached standard errors $SE(Y_2)$ and their 95% confidence ranges. The estimates from the unstratified counts range between 2830 and 6928. For most counts, the variances are high. These are largely an effect of the clumped distribution of the hartebeest. This occurred despite the fortuitous orientation of transects in a way which would tend to reduce the variance. The flights showed that the density of hartebeest varied along an approximate

east-west gradient, discussed below (p.98). Thus each transect contained a mixture of high and low density 5 km lengths, producing a lower variance between transects than if the transects had been oriented north-south. Not surprisingly, the two single-observer counts (7-7-71 and 1-9-71, Table 6.1), which covered only 8% of the area, resulted in the highest standard errors relative to their population estimates, although these two estimates were the lowest and the second highest.

The use of various aircraft types, piloted by people of varied experience of this work, the censusing of one or several species and the photography of later counts introduced many sources of possible error, which would be extremely difficult to take in to account in an analysis of the flight data. Satisfaction with the counts varied widely, but Bartlett's Test (Bailey 1959) showed that the variances were not significantly heterogeneous ($\chi^2 = 12.55$, d.f. 7, $p > 0.05$). Consequently, there is little objective reason for excluding any particular counts in an attempt to reduce the errors and improve the precision of the population estimates.

The mean population estimate from the unstratified counts is 5080 with 95% confidence limits of ± 1956 . This is higher than the 2 stratified count estimates of 4887 and 3396 (Table 6.2), but the errors of the latter are slightly lower. The similarity in these estimates allows an overall mean to be calculated of 4892 hartebeest with a SE of 960 and 95% confidence limits of ± 1882 .

The populations of other herbivores in the plains

Table 6.2 contains the same information for the counts of wildebeest, zebra and cattle, and the same points concerning their accuracy apply. The relatively low estimates for the wild species on the first count were probably due to the observers' inexperience of counting more than one species. The mean population of the wildebeest is 13606 $\pm$ 5592. Their high variances are the result of their very clumped distribution

(see below). Stratification of the sampling effort according to hartebeest density distribution patterns did not reduce the variance on the last two counts. The same holds for the zebra population with a mean estimate of 7211 ± 3775 individuals. This is again probably a minimum figure for the added reason that the size of the population in the census area in September 1972 had certainly been reduced by emigration in to the park (p. 86).

The mean population estimate for cattle is $48,531 \pm 17,775$. The high 95% confidence limits are largely due to the high standard error of the unstratified count of 6-3-72, caused by the patchy distribution of cattle in large herds. Stratification reduced the variance with little effect on the population estimate. The relatively consistent population estimates may be because most herds on all 3 counts were photographed.

The following densities (km^{-2}) of the 4 most numerous species in the Athi Plains are derived from their mean population estimates. For comparison, the densities of the wild species in the Nairobi Park are also shown, calculated from the mean population sizes on p. 85-6.

species	Athi Plains	Nairobi Park
cattle	27.3	0
wildebeest	7.7	3.3
zebra	4.1	5.8
hartebeest	2.7	17.8

Hartebeest population structure

The proportion of immature animals in the plains is calculated from the results of the total counts in the 6 blocks in March, June and September 1972. The results for each month are pooled and compared with those of the park study area count for the same month. Comparisons are made using the following expression (Sokal and Rohlf 1969):

Table 6.3. The number of immature haretebeest in 3 categories as a fraction of the number of adult females in both the Nairobi Park and Athi Plains in 3 months. t_s compares the fractions between areas, and its significance is shown.

Month	Area	Newly-born	t_s	sig.	juvenile	t_s	sig.	, Subadult	t_s	sig.
March	Park	.103	2.52	*	.486	4.47	***	.451	4.26	***
	Plains	.046			.304			.275		
June	Park	.023	.173	n.s.	.530	2.22	*	.411	4.95	***
	Plains	.021			.452			.231		
September	Park	.010	.72	n.s.	.446	2.25	*	.266	2.09	*
	Plains	.006			.376			.210		

The number in each class as a fraction of the number of adult females.

n.s. not significant, * $p < .05$, ** $p < .01$, *** $p < .001$.

$$t_s = \frac{\arcsin p_1 - \arcsin p_2}{\sqrt{820.8 \left(\frac{1}{n_1} + \frac{1}{n_2} \right)}}$$

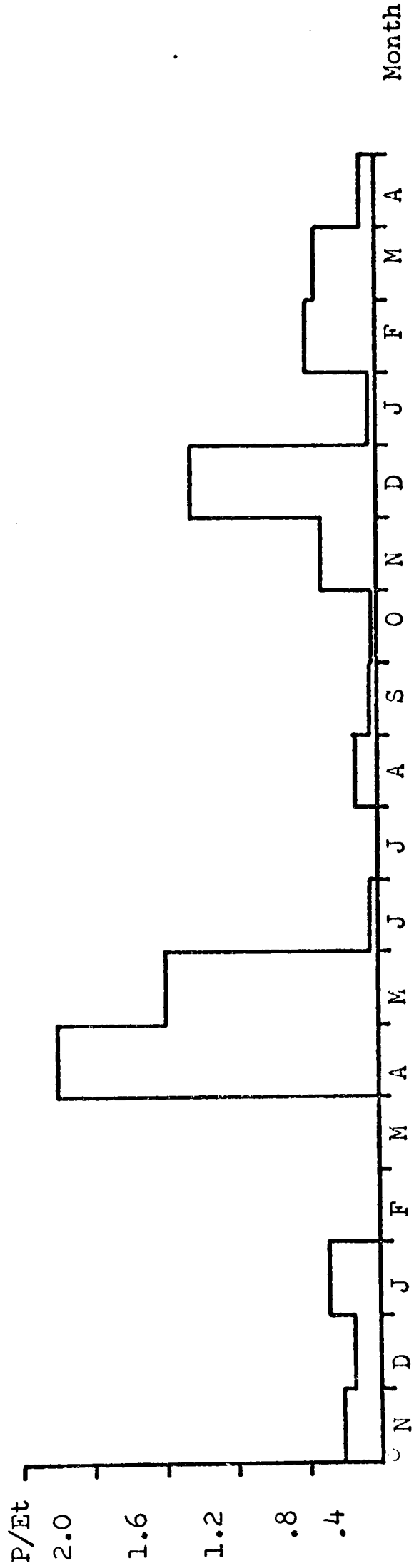
where p_1 and p_2 are the proportions of an age category in the two populations, and n_1 and n_2 are the respective sample sizes. The proportions are transformed with the arcsin function. 820.8 is a constant. Statistically, the comparison is between the number of females in the two populations with or without, for example, a juvenile. The sample sizes are, therefore, the number of females.

The number of each class of immature animals (newly-born calf, juvenile and subadult) as a fraction of the number of females is shown in Table 6.3, with the value of t_s for each comparison between the populations, and its significance. With the exception of March, the proportion of newly-born calves is not significantly different in the two areas, and evidence is presented later (p. 243) to suggest that the park figure of .103 in this month is inflated. The proportions of juveniles in both areas was high in June, which probably reflects the recruitment in to this age class of the relatively large number of calves born in March. The highly significant difference in the number of subadults drops in September, through the decline in the number of subadults seen in the park. This change was coincident with the presence of large numbers of immigrant hartebeest from the plains (p. 86). If the proportion of subadults in the immigrants was the same as in the whole plains in March and June, the number in the park would be depressed to approximately this extent.

The two sets of proportions show that the park contains significantly more immature animals. There may have been factors causing disparate birth rates in the two areas when the animals which were subadult in 1972 were born. On the other hand, if the birth rates in these 3 months of 1972 are considered typical, the differences in age structure appear

Fig.6.2. The selection of 9 vegetation zones by hartebeest on 8 censuses, with the mean effective rainfall of the current month from 6 stations (see text).

Date.	26.1.71	5.3.71	5.5.71	7.7.71	1.9.71	9.11.71	13.1.72	6.3.72	% of area
Veg. Zone				Selection index.					
I	1.34	2.46	1.17	.95	.67	1.67	1.19	1.08	13.2
II	1.01	1.18	.99	1.58	1.32	1.01	1.11	.63	19.7
IVA	.45	.79	.77	.87	.30	1.32	.41	1.07	11.8
IVB	1.88	.48	.82	1.74	.14	1.14	1.07	1.20	6.6
VA	1.23	1.83	1.96	.89	2.28	2.90	3.32	2.58	5.3
VB	1.31	.92	1.85	0	0	.46	.08	.31	1.3
VI	.59	.07	.33	.25	.88	.02	.59	.26	26.3
VII	1.44	1.09	1.97	1.42	1.75	1.05	1.15	2.14	14.5
VIII	0	2.31	.46	2.0	0	2.23	.46	.61	1.3



to be due to differences in post-natal mortality in the first two years of life, rather than to differences in the birth rate. This is discussed later (p. 96).

From the results of 12 study area counts in 1971-72, males form 43.9% of the adult population of the park ($n = 5045$ adults). Although the results of sequential counts in the same place are not strictly independent, this is less restricting when the sample sizes are large, as here. Comparison of the park and plains populations are made on the pooled data from counts in the same 3 months in both places. In these months, the male proportion in the park is 41.2% ($n = 2116$ adults) which is significantly different from a ratio of 50 males:50 females ($d = 8.10$, $p < 0.001$). In the plains, males comprise 59.2% of the adult population ($n = 4244$ adults), which is significantly greater than equality ($d = 12.33$, $p < 0.001$). The Nairobi Park therefore contains a significantly higher proportion of females.

The distribution of hartebeest within the plains

The distribution data from the unstratified counts are shown in Fig. 6.2 as the selection indices for the vegetation zones (Fig. 5.1) of the plains, with the monthly effective rainfall. The 8 counts spread between 15 months cover all seasons, but the degree of selection or avoidance of vegetation zones does not vary significantly ($\chi^2 = 30.378$, d.f. 56, $p > 0.05$).

On the basis of their utilisation by the hartebeest, the zones fall in to three groups. The first contains the Kapiti Plains (zone VI) which are consistently avoided, and the short, Upper Athi Tuffs grassland (IV A) which rarely supported more hartebeest than would be expected by chance. The second group includes the zones which are consistently selected: the Upland and Lowland Acacia drepanolobium grasslands (zones I and II), the Ololokitigoshi grassland (zone V A)

Table 6.4. The selection indices shown by hartebeest, wildebeest and zebra for 9 vegetation zones in each of 3 months, November (N) 1971, January (J) and March (M) 1972.

Vegetation Zone	Hartebeest		Wildebeest		Zebra	
	N	J	N	J	N	J
I	1.67	1.19	.47	.44	2.42	.51
II	1.01	1.11	.04	.18	.47	.18
IVA	1.32	.41	1.16	1.17	.37	1.42
IVB	1.14	1.07	.09	.11	.30	3.45
VA	2.90	3.32	.55	.15	6.17	.26
VB	.46	.08	.05	0	.35	0
VI	.02	.59	2.26	2.32	.19	1.41
VII	1.05	1.15	1.02	.92	.98	.80
VIII	2.23	.46	.96	.77	0	0

and the Basement system grassland (zone VII). The remaining zones of IV B, V B and VIII are selected or avoided to varying extents in different months. For none of them is there evidence of a regular pattern of occupation in the wet or dry seasons. A large amount of this variation is probably due to the sampling error associated with their small areas (Fig. 6.2).

These results show that in all seasons the vegetation zones favoured by the hartebeest change little. Their avoidance of zones VI and IV A, together forming 38.1% of the area of the plains, leaves them distributed along the west and north edges of the plains, with the greatest numbers in zones I and II, V A and VII.

The distribution and movements of wildebeest and zebra in the Athi Plains

The results of the unstratified counts of November, January and March 1972 allow comparison of the distributions of hartebeest, wildebeest and zebra. These are shown in Table 6.4 as the selection indices shown by these species for the 9 vegetation zones. Relative to those of the hartebeest, detailed above, those of the other species fluctuate more, both in the range of index values and in the values for individual zones in different months. This is evidence that both species are, locally, more concentrated and are more mobile.

Fig. 6.2 shows that the short rains broke in November 1971, while January 1972 was very wet following further rain in December. Conditions were slightly drier in March. The wildebeest's selection of vegetation zones was almost identical in the two wet months, with the Kapiti Plains (zone VI) supporting most of the population, and a slight selection for the Upper Athi Tuffs grassland (zone IV A). In both months, the Basement grassland (zone VII) carried the proportion of the population to be expected without selection or avoidance. During the dry month, March, the Lowland Acacia drepanolobium (zone I), the Athi Tuffs grassland (IV A)

Table 6.5. The results of recent aerial censuses over the Athi Plains. With the exception of Stewart & Zaphiro (1963), Casebeer (Pers. Comm.) and the results of this study, the figures are from Modha (1969).

Date	type of census	hartebeest	wildebeest	zebra	cattle	Authority
pre-1961	100%	5400	8800	5400	-	Stewart & Zaphiro (1963)
post-1961	100%	1700	5000	3800	-	Stewart & Zaphiro (1963)
Oct-Nov 1967	100%	2475	7393	5540	-	Modha & Hughes
Oct-Nov 1967	100%	3732	6475	5951	-	Modha & Hughes
Nov 1967	25%	3288	7878	7810	-	Casebeer
March 1968	50%	8366	12220	10874	-	Modha & Hughes
June 1968	25%	5044	11892	8448	-	Modha & Hughes
Nov-Dec 1968	25%	7740	13240	16376	-	Modha & Hughes
Jan 1969	25%	6369	15252	15408	28576	Casebeer & Modha
Jan 1969	25%	5620	17080	14536	28216	Casebeer (pers. comm.)
July 1969	25%	6424	24252	11900	30800	Modha & Hughes
Sept. 1969	25%	7220	10008	10732	56108	Peterson & Isavwa
1971-72	16%	4892	13606	7211	48531	This study

and the Olcoloitigoshi grasslands and bushland (V A and B) were selected to varying extents, while the Kapiti Plains were almost empty. This shows a north-westerly movement away from the wet season areas.

Changes in the zebra distribution were not as marked. The high proportion of the population in Zone I after the November rain was probably a residual effect from their previous dry season distribution. The Olcoloitigoshi (Maasai, "the place of the zebras") grasslands (zone V A) were heavily selected in the less wet months of November and March. In January, most zebra were, like the wildebeest, on the Kapiti Plains. By March they had moved back in to the dry season areas of Lowland A. drepanolobium grassland (I), the Upper Athi Tuffs grassland and bushland (V A and B), and Olcoloitigoshi grasslands (V A).

If these censuses had been flown at the height of the wet and dry seasons, the differences in the seasonal distributions of these herbivores would have been more accentuated. Nonetheless, these results are consistent with the distribution patterns described by Peterson and Casebeer (1972) who show the results of 9 reconnaissance flights over the Athi Plains between August 1970 and October 1971, and summarize the results of a further 9 censuses between 1959 and 1969. It is clear that the movement patterns observed between November 1971 and March 1972 were part of the regular migrations of wildebeest and zebra, which can take place twice a year in response to the start of each rainy season. The general pattern is one of their concentration on the Kapiti Plains in the wet season. This is followed by their gradual northerly and north-westerly movement in to the Olcoloitigoshi grasslands and the Upper Athi Tuffs grassland, until the dry season is spent in the Lowland A. drepanolobium areas. The information from the 8 hartebeest censuses show that they are less concentrated and are not migratory. In addition, their preference for the vegetation zones along the north and west side of the plains means that their distribution patterns are particularly different from those of the migratory species in the wet season.

Discussion

Although systematic aerial sampling may be theoretically less satisfactory than a census method with randomly-located transects (p. 82), it provides population estimates and, in addition, distribution maps as a basis for ground work. The biases in the counts through using a variety of aircraft and pilots are incalculable, but by using the same pair of observers on all counts, one bias was hopefully kept relatively constant.

After investigating some of the biases in aerial sampling, Penny-cuick and Western (1972) recommended a strip width of 300 m and a flying height of 300 ft (91 m) as the best compromise for counting 16 species in a partly wooded habitat. As the Athi Plains are far more open and never more than 4 species were censused, the combination of a 400 m strip and a height of 400 ft is probably a nearly optimum combination for maximising the sampling fraction without missing animals or misidentifying them.

Most aerial counts underestimate population sizes because animals are not seen (Graham and Bell 1969). Observer skill undoubtedly improved during the counts, but reduction in this source of error may have been offset by new errors introduced by counting more species. The same errors presumably decreased as the proportion of animals which were photographed increased.

The large variances attached to the mean population estimates show that the precision of the counts was low. Large variances occur if a species is distributed patchily and their reduction is the purpose of stratifying the sampling effort. The variance of the hartebeest population estimates was reduced only slightly. Two factors may have been responsible. First, stratification is most effective if the transects are oriented parallel to the density contours (Norton-Griffiths 1973). Even within the high density stratum, the effect of the east-west gradient

of hartebeest density (above) along which the transects ran at 90° to the density contours, was probably considerable. Second, the transects in the medium and low strata numbered only 5 and 3 respectively, and some were very short (Fig. 6.1). Sinclair (1972) arbitrarily decided to allocate a minimum of 10 transects to each stratum with the object of keeping the variance low, and the precision of the hartebeest counts undoubtedly suffered for this reason.

The high variances of the wildebeest and zebra estimates, with and without stratification, emphasize the fact that if several species are to be censused and they are distributed non-uniformly in different ways, stratification cannot be optimal for all of them (Sinclair loc. cit.). Under these circumstances, stratification after a count is permissible (Norton-Griffiths 1973). Stratification of the Athi Plains counts also reduced the variance of the cattle estimates (Table 6.2) suggesting that the 3 strata also coincided with parallel variations in their density distribution. This indicates that the distributions of hartebeest and cattle are similar. This is considered in more detail in the next chapter.

The results of recent counts over the Athi Plains are shown in Table 6.5. The increase in the numbers of the wild species between "post 1961" and, approximately, 1968 reflects their build-up after the heavy mortality caused by the drought of 1960-61. The wide confidence limits of the 1971-72 hartebeest counts (Table 6.2) allow nothing to be said about the apparently slight decrease in their numbers in the Athi Plains between 1969 and 1971-72. The results of all the counts of the hartebeest, wildebeest and zebra suggest that their movements are contained within the plains. This confirms the identity of the plains as an ecological unit (Stewart and Zaphiro 1963). On the other hand, the number of hartebeest in the park, unlike those of wildebeest and zebra, stays remarkably constant. Dry season immigration is clearly exceptional.

For ecological purposes, the hartebeest of the plains and the park can be regarded as separate populations.

The seasonal selection of different vegetation zones by wildebeest and zebra confirms their well-known migratory habits (e.g. Kruuk 1970, Pennycuik 1974). The pattern of vegetation zone occupancy by hartebeest is remarkably constant. The impact of the extremely adverse conditions prevailing in April 1971, following the failure of the short rains of 1970 (Fig. 6.2) is apparent only as a slightly increased selection for Zone I, the Lowland Acacia drepanolobium grassland, where water remains well in to the dry season (p. 56). The population movements of hartebeest are no more than an "ebb and flow" of slightly changing density, which is in marked contrast to the "all or none" distribution and migrations of the more concentrated wildebeest and zebra. The relationship between the hartebeest and other herbivores is considered further in the next chapter. The vegetation zones used by the hartebeest occupy the north and west of the plains, lying in the higher rainfall areas (Fig. 4.4). Their sedentary existence in this ecological unit may only be possible where rainfall and primary production are higher than the average for the plains, although many other factors must also be important.

The Nairobi Park has a higher rainfall than most of the plains (Fig. 4.4). This may be partially responsible for its density of 17.8 hartebeest/km², which is 6.6 times higher than the overall plains density of 2.7/km². Females predominate amongst the adults of the park, while the position is reversed in the plains population. There is no evidence of a preferential female ⁺mortality in the plains, ^{and} the sex ratio at birth is approximately unity (Gosling 1974). The predominance of males in the plains is difficult to explain unless males move from the park to the plains. The social behaviour of the hartebeest of the park is characterised by extremely aggressive interactions between adult males within a tightly-packed territorial system (Gosling loc. cit.). This might cause some males to leave the park in favour of the lower density plains

where male territoriality is less consistently developed (personal observations). If this emigration was a continuous but small drain on the male population of the park, its existence might not be detected from the results of total counts in the park. The lower proportion of males in the park is also likely to be a consequence of their greater susceptibility to predation (Rudnai 1973, Gosling loc. cit.).

The lower proportion of immature animals in the plains appears due to lower calf survival (Table 6.3). Approximately 70% of the calves born each year in the park survive to the end of their first year (Gosling loc. cit.), despite predation by lions (Rudnai loc. cit.), cheetah (McLaughlin 1970) and jackals (Gosling 1969), all of which are scarce or absent from the plains. Calf survival is lower in the plains, nonetheless. During the first 2 - 3 weeks of life, the calves lie-out (Gosling loc. cit.) while their mothers feed. Frequent disturbance during this period by the many herds of cattle in the area might make the calves more susceptible to separation from their mothers or to predation by the accompanying Maasai dogs.

The availability of adult males is not a factor limiting the rate of increase of the hartebeest in the park (Gosling loc. cit.). Therefore, the higher proportion of females in the park indicates that this population has a potentially greater rate of increase. In addition to being relatively more numerous in the park, the number of young animals with each female is also higher. The high survival rate of the young animals seems associated with the high densities in the park. The ecological factors which allow this density are the subject of subsequent chapters.

Chapter 7.

COMMUNITY STRUCTURE AND DIVERSITY

7.1 Community diversity and evenness

In the last chapter I described the major differences in the densities and distributions of the common large herbivores within the plains, and, for the hartebeest, between the plains and the Nairobi Park. Any attempt to explain these differences in causal terms first requires some method of describing the structure of the two communities. In this chapter their structures are compared on a year-round and a seasonal basis, and the same methods are extended to the ecology of the individual species.

Communities of living animals differ in such parameters as the total number of species, the number of species relative to the number of individuals, and the relative abundance of these species. These parameters are the basis of various measurements of species diversity such as the species:individual number ratio, the rarefaction method (Sanders 1968) or the log series (Fisher et. al. 1943, Williams 1964). The results from each are dependent to varying extents on the sample size, and in the case of the last method it is assumed that the species are distributed according to a log series, and are sampled in the proportions in which they occur naturally. Because of these and other limitations, a different approach using information theory methods is employed here.

The recent interest shown by ecologists in information theory methods is partly because other methods attempt to fit natural distributions to mathematical expressions (Margalef 1957). No assumptions about the type of distribution are made with the information theory measure of diversity. Diversity is interpreted here as the degree of uncertainty attached to the taxonomic identity of any randomly chosen individual (Pielou 1966). Thus in a community containing few species with a low

diversity, a relatively short series of individuals provides a reasonable state of knowledge or predictability about the community. In a larger community of more species, the identity of more individuals must be known before the degree of uncertainty about the identity of the next individual drops to acceptable levels (Margalef loc. cit.).

The basic expression for calculating the diversity of a community or an individual is the Shannon-Weiner function

$$H' = - \sum_{i=1}^s p_i \cdot \log p_i \quad (\text{Margalef 1957}).$$

where H' is the diversity, p_i is the proportion of individuals falling in the i -th species and s is the total number of species. This expression is suitable when the collection of organisms is so large that a random sample has to be taken for identification, but the total number of species is known (the type B collection of Pielou (1966)). Thus H' is only an estimate of the true population community diversity. When the collection is small enough for all its members to be counted and identified (the Type A collection), it is preferable to use Brillouin's expression (Pielou loc. cit.),

$$H = \frac{1}{N} \log \frac{N!}{N_1! N_2! N_3! \dots N_s!}$$

where H is the true diversity, N_i is the number of individuals in the i -th species and N is the total number of individuals. Both methods, though, are "equivalent" (Margalef loc. cit.).

For practical reasons it was not possible to count all the individuals of the large herbivore community of the park. Thus the study area was used for sample counts. Because the total number of species was known, this appears similar to the type B distribution although the sample of animals was far from random because of the considerations affecting the location of the study area. Pielou (1966) says that this sort of collection can be treated as a finite population rather than as a sample from

some larger population, in which case the Brillouin expression would be most appropriate. However, the Shannon-Weiner formula has been used to allow valid comparison with the diversity of the plains community.

Each of the plains blocks is equivalent to the park study area in that they are sample areas of something larger. But to compare the whole plains with the park, the diversity of the communities occupying all 6 blocks must be calculated. If, by the reasoning of the paragraph above, the sample from each block is regarded as a separate entity, it seems unsatisfactory to compare the diversity of one community (the park) with the combined diversities of 6 communities (in the plains). It is more reasonable to regard the data from the blocks as samples of something bigger (i.e. the whole plains) even though the latter are also located non-randomly. Thus, the diversities of both communities have been calculated using the Shannon-Weiner expression. This is permissible (Pielou 1969) if the extent of the parent populations is known, which is true for the common large herbivores because the Athi Plains comprise a distinct ecological unit (p. 94).

The communities considered in most diversity studies usually contain only a fraction of the total number of species in an area (e.g. MacArthur and MacArthur 1961, Kricher 1972). There is little point in determining the diversity of an entire community because of the over-riding effect of a few taxa or species such as the bacteria (Hurlbert 1971). For these purposes Pielou (loc. cit.) defines a community as "all the organisms in a chosen area that belong to the taxonomic group being studied", but recommends intuition for determining the community boundaries. In this study the "community" of the park and Athi Plains is restricted only to the large herbivores, approaching the ideal of a taxocene (Deevey 1969) - "the members of a taxocene are likely to be of about the same size, to have similar life histories, and compete over both evolutionary and ecological time". All the members of the community belong to the same trophic level, and they are all ungulates with the exception of the ostrich. Although a

bird, the ostrich's ecology converges on those of the ungulates. As a large and common herbivore it fulfills the conditions for inclusion in the taxocene in all but phyletic position, and is therefore included in the community.

The park community considered here consists of the following 11 species: hartebeest, wildebeest, zebra, Thomson's and Grant's gazelles, ostrich, warthog, waterbuck, eland, impala and giraffe. A further 6 species have been excluded. These are Mountain and Chanler's reedbuck, rhinosceros, klipspringer, steinbuck and duiker, which are found in very small numbers in the park study area. Their numbers were not recorded on ground counts because of their rarity and the difficulty of seeing them. All the species, with the possible exception of the rhinoceros, are retiring by nature, and in the 12 counts in the park, probably no more than 20 individuals of all these species were sighted. Although the effect of rare species on community diversity seems to depend on the type of community (e.g. Tramer 1969, Sager and Hasler 1969) the calculated park diversities will always be smaller than the true diversities by a probably negligible amount.

In the plains the species list is added to by cattle, sheep and goats. The last two present a problem in that they are herded together. Their co-existence in the same flock is probably linked with the fact that the goat browses predominantly while the sheep grazes more. In this, they behave as two species, but from the point of view of spatial distribution, they are effectively one species. Because of this they are treated here as a single, compound species, the "shoat", which has a broad spectrum diet. With cattle and "shoats" the park community numbers 13 species.

The Shannon-Weiner function includes the two diversity components of species numbers and the relative abundance of the species (Lloyd and Ghelardi 1964). The second component of equitability or evenness, is at

a maximum when all species contain the same number of individuals. It is at a minimum when all but one species contain one individual each, and this one species contains all the remaining individuals. Although equitability based on the Broken Stick model of species abundance may be more realistic (Lloyd and Ghelardi 1964), it is influenced more by the number of species than is Pielou's (1966) measure of evenness, J (Sheldon 1969). The latter is, therefore, preferred for measuring evenness. It is defined as the calculated diversity as a fraction of the maximum possible diversity:

$$J = \frac{H}{H_{\max}}$$

If the number of species in the community is known exactly, the maximum diversity occurs when each species has $1/s$ of the total individuals, in which case $H_{\max} = \log s$. Thus the evenness is calculated as

$$J = \frac{H}{\log s}$$

The diversity expression is flexible in its application. In this chapter it is used to measure the diversities of the communities occupying different areas - the park study area, the individual blocks in the plains, and the whole plains. Using the same data the index is then used as a measure of the diversity exhibited by each species in its occupation of different areas or vegetation types or areas with a range of grass biomasses. The diversity expression can be used with data from single sampling occasions or with their summed data to produce an overall diversity index. From these indices, the degree of seasonal variation can be assessed by the method described below (p.103).

7.2 Relationships between species

Calculation of the various types of diversity displayed by a species takes no account of its relationships with other species. When analysing the structure of the large herbivores component of a community, the

most interesting relationships are probably those showing the degree of similarity or difference between species in their distribution, food choice, vegetation preference etc. This can often be done by measuring the degree of association between the species' distributions in relation to some environmental parameter. The coefficient of association (Cole 1949) has been used to measure the degree of spatial association between species (e.g. Bell 1970, Sinclair 1970), and this method is particularly appropriate where a grid system of squares can be superimposed over the area concerned, and the species' distributions are recorded on a presence or absence basis. Data furnished by systematic aerial sampling are, therefore, particularly suitable for analysis by this method. In this study the data used here were collected by ground-counting (p.18), and although each sighting of animals was located in a grid square of 1 km^2 , the information theory method of Horn (1966) for measuring overlap (R_o) was preferred for a number of reasons:

1. Within any area, the actual numbers of animals are used (see below), making greater use of the data.
2. Because a grid system is unnecessary, a possibly arbitrary choice of grid size is avoided.
3. Horn's method allows the combination of data from the 6 blocks of the plains. Because the 6 areas lie in 6 different vegetation zones, they could not be regarded as repeated samples for use in Cole's expression.
4. With no grid system, the information theory method is more flexible so that the same distributional data can be used to measure overlap at the level of the block (large, unequal sized areas), the vegetation type (smaller, unequal sized areas) or standing crop value (an arbitrary and interval scale based on a continuous variable measured in unequal sized areas).
5. R_o , the degree of overlap, is not affected by sample size and

it is particularly appropriate when the differential choice among items, rather than their differential availability, is important (Horn loc. cit.).

On the other hand, a probability can be attached to Cole's coefficient because the use of grid squares allows the calculation of the amount of co-occurrence of two species that would occur by chance, so that the values of the coefficient show the magnitude of association or avoidance between the two species. Horn's method only calculates a percentage overlap, and the statistical significance of this cannot be assessed. In this, the measure of overlap resembles the Shannon-Weiner expression for diversity as "quantitatively descriptive" only, assessing the degree of overlap in terms of the maximum and minimum possible diversities and the observed diversities of the two species. This is described algebraically below (p. 106).

7.3 Seasonality

Aerial counting over the Athi Plains (Ch. 6) showed the distribution patterns of the major herbivore species from month to month. However, there are no comparable data for any species other than wildebeest, zebra and hartebeest. To assess seasonal distributions for all the species, the ground count data has been used again in the Shannon-Weiner expression to obtain an index measuring the degree to which the plains blocks and the park study area are used seasonally.

Indices obtained from samples collected from increasingly large areas at a point in time may be combined to measure the heterogeneity of the community through space (Margalef 1957). Here a measure of the temporal heterogeneity of the herbivore community is obtained by combining the indices calculated for the same areas on different occasions. The seasonality index compares the mean diversities of an area at each season with the overall diversity measured through the year. Thus

Table 7.1 The seasonal, mean and overall diversity indices and seasonality indices, evenness (J) and number of species in the 6 study area in the plains, the whole plains and the Nairobi Park study area.

Block	SEASONAL H(s)				H(s) $\bar{x}$	H(s) overall	Seasonality index	Evenness	No. of species
	Wet	Medium	Dry						
15	1.482	2.209	1.977		1.889	2.226	.849	.643	11
22	1.987	2.448	2.327		2.254	2.370	.951	.685	11
30	2.364	1.651	1.888		1.968	2.106	.934	.702	8
35	1.745	1.714	1.226		1.562	1.669	.936	.526	9
39	2.211	2.609	0.724		1.848	1.939	.953	.612	9
62	2.386	2.473	2.003		2.287	2.496	.916	.722	11
WHOLE PLAINS	2.422	2.780	2.094		2.432	2.429	1.000	.678	12
NAIROBI PARK AREA	2.734	2.611	2.534		2.626	2.629	.999	.760	11

$$\text{Seasonality index} = \frac{\text{Mean seasonal diversity}}{\text{Overall diversity through all seasons.}}$$

This is demonstrated in the models in Fig. 7.1. In these, the letters A-L represent 12 species occupying an area. For the sake of simplicity the areas in (a), (b) and (c) can only support 4 species in each of the three seasons (wet, medium and dry), and each species, when present, is represented by 100 individuals. In the three models the areas have different patterns of occupation by the species. In (a) the area supports the same species through all seasons, while in (b) two of the 4 wet season species are still resident in the medium season, and 2 of these are subsequently there in the dry season. In (c) the study area has a completely different community in each season. Common sense suggests that (a) has the least seasonal variation in community diversity, while (c) has the most and (b) is intermediate.

In these models the Shannon-Weiner diversity for each population of 400 animals is the same for each season in all 3 models because the equitability of their distributions has been held constant. This diversity is calculated to be 2.000. The mean diversity between seasons is therefore also 2.000 in each model. However, the overall diversities vary because the distributions of the 1200 animal sightings are different in the 3 cases. Thus the overall diversity, $H(s)$, in (a) is calculated as 2.000, in (b) $H(s) = 2.918$ and in (c) $H(s) = 3.585$, and the seasonality indices, as defined above, are then 1.0, 0.685, 0.558 for models (a), (b) and (c) respectively. A low index demonstrates a non-uniform, hence highly seasonal occupation of the vegetation types in the models, and a maximum value of 1.00 indicates absolutely no seasonal variation in distribution. The index cannot exceed 1.0 because the mean seasonal diversity of a population can never be greater than its overall diversity. The equal mean diversity and overall diversity in model (a) show that index values are independent of the actual number on animals in the sample,

but concerns their proportional distribution between the vegetation types and the equitability of these distributions. Thus, more complicated models in which the equitability changes seasonally can be constructed, and these are obviously more realistic. Also, depending on the data input, the index can measure the seasonal species diversity of different areas or the seasonal diversity of occupancy of different areas by each species at the level of the block or the vegetation type.

The seasonality index calculated for a rare species may be misleading because of the sampling error due to the small number of observations on each sampling occasion. This causes the index to be too low, indicating a highly mobile species. The chance of the sampling error being appreciable depends to some extent on the number of sightings (rather than individuals) relative to the number of categories in to which the observations are put.

In the absence of any guideline, a sample of observations is considered too small for a seasonality index to be calculated if the number of observations is smaller than the number of available categories. For example, if a species is sighted on a total of 4 occasions in counts of 6 areas, the sample would be considered too small for further calculations. In practice it is found that if a species sample is inadequate on one occasion it is usually too small on the other occasions. When only one sample out of a series is too small, the seasonality index is calculated nonetheless.

7.4 Data collection and computation

The data on species' numbers and distributions were collected by total ground counts (p. 18). As 12 monthly counts covering two cycles of wet and dry seasons were carried out in the Nairobi Park study area, the months have been divided into three seasons and the data pooled within each season: Wet season (December, May, June, July), Medium wet (January, February) and Dry season (November, March, April, August, September and October). The moisture content of the grass was used as the

criterion for division to allow combining months from the short and long dry season (p. 23). Counts were done in the 6 plains blocks in 3 months which were chosen to represent as nearly as possible the same three seasons.

To compute the diversity indices, a programme was written in BASIC. The indices were calculated by the "easier" form of the Shannon-Weiner expression (Lloyd and Ghelardi 1964):

$$H' = C (\log_{10} N - (\frac{1}{N} \sum_{i=1}^s n_i \log_{10} n_i))$$

where n_i is the number of individuals in the i -th species, N is the total number of individuals, s is the number of species, and c is the conversion factor to change the logarithms from base 10 to base 2, which are more commonly used. Here, $c = 3.3219$.

Horn's overlap is defined in terms of maximum and minimum diversities and that observed, as:

$$R_o = \frac{H_{\max} - H_{\text{obs}}}{H_{\max} - H_{\min}}$$

and this is calculated as

$$R_o = \frac{(X_i + Y_i) \log (X_i + Y_i) - X_i \log X_i - Y_i \log Y_i}{((X + Y) \log X + Y) - X \log X - Y \log Y}$$

where the population of each species is partitioned between n categories (e.g. blocks), and the number in the i -th category of species "X" and species "Y" are x_i and y_i respectively. The sum of $x_i \dots x_n = X$, the total number of animals of species "X", and the same holds for species "Y". The calculated values of R_o have limits of 0, when the distributions of the two species are completely different, and 1.0 when the distributions are identical.

The large number of R_o values were also calculated on a Nova computer with a BASIC programme. The programme was verified first by confirming

that a distribution had an overlap of 1.0 with itself, and then with an example that was also worked out by hand.

For the plains community, three sets of calculations were made on the data for each season:

1. The overlap between each pair combination of the 11 species was calculated using their distribution between the 6 blocks.
2. On the basis of the results of (1), the overlaps of distribution between vegetation types for 15 species-pairs were calculated.
3. Because the distribution between the standing crop categories of a large proportion of each species was known (p. 19), and the standing crop measurements form an interval scale, a Kolmogorov-Smirnov 2-sample test (Siegel 1956) was performed on these same 15 species pairs, and their overlap then calculated. The rationale behind this was that whereas the K-S test would show whether any two species had distributions which differed significantly, it could not be used to measure the actual degree of difference or similarity. The data used in all these computations are the same as used earlier.

For the park community, the data on animal distributions have been added for similar months to obtain the equivalent data for seasonal distributions. However, interpretation of the calculated overlaps between species is subject to the reservation that the data were not collected on one sampling occasion representing a point in time. If the species' distributions are very different in the months of the same season, a measure of overlap results which may be meaningless in terms of the simultaneous co-occurrence of the two species. This will always happen to some extent unless the species' distributions are identical in each month of the season, which they are obviously not; alternatively, the problem could be avoided by looking at the overlaps for each month. As there are

Fig.7.1. Model of area with 3 patterns of seasonal utilisation to demonstrate seasonality index.

(a)				(b)				(c)				
SPECIES	WET	MED	DRY	TOTAL	WET	MED	DRY	TOTAL	WET	MED	DRY	TOTAL
A	100	100	100	300	100			100	100			100
B	100	100	100	300	100			100	100			100
C	100	100	100	300	100	100		200	100			100
D	100	100	100	300	100	100		200	100			100
E						100	100	200		100		100
F						100	100	200		100		100
G							100	100		100		100
H							100	100		100		100
I											100	100
J											100	100
K											100	100
L											100	100
TOTAL	400	400	400	1200	400	400	400	1200	400	400	400	1200
Seasonal div.	2.000	2.000	2.000		2.000	2.000	2.000		2.000	2.000	2.000	
Mean diversity	2.000				2.000				2.000			
Overall diversity	2.000				2.918				3.585			
Mean/overall = Seasonality index	1.00				.685				.558			

data for 11 species for 12 months for the park, this would be a prohibitive task.

The overlaps of each species-pair have been calculated only for the species' distributions between vegetation types. The standing crop of one vegetation type can be in a different category each month, making any comparison with overlap between vegetation types almost impossible. This comparison is more meaningful for the plains community because the data for each season refer to one month only.

The seasonal distributions of each species between the vegetation types of the Park and the standing crop categories are given in Appendices 7 and 9.

7.5 The diversity and equitability of the large herbivore communities of the Nairobi Park and the Athi Plains

By using the numbers of each animal species in an area as $n_1 \dots n_j$ in the Shannon-Weiner formula, an index of that community's diversity is obtained. To compare the communities of the park and the plains, diversity indices have been calculated for the park study area, each block in the plains and for the whole plains by summing the data for all the blocks. The distribution data are given in Appendix 5. Table 7.1 shows the community diversity indices for each block or study area in each season and for the whole plains. The year-round evenness, J , is included with the number of species seen in each area.

All the animal species are not consistently present in each block (Appendix 5). Cattle, sheep and goats are obviously absent from the park, but more remarkable is the absence of warthog from all the plains blocks. Waterbuck are also absent apart from the sighting of 2 individuals out of a total count of 32,224 animals; these were seen in Block 15, which is the nearest block to the Nairobi Park and lies in the same vegetation zone (Fig. 5.1). As the contribution of the waterbuck to the diversity is negligible, the plains community is effectively composed of only

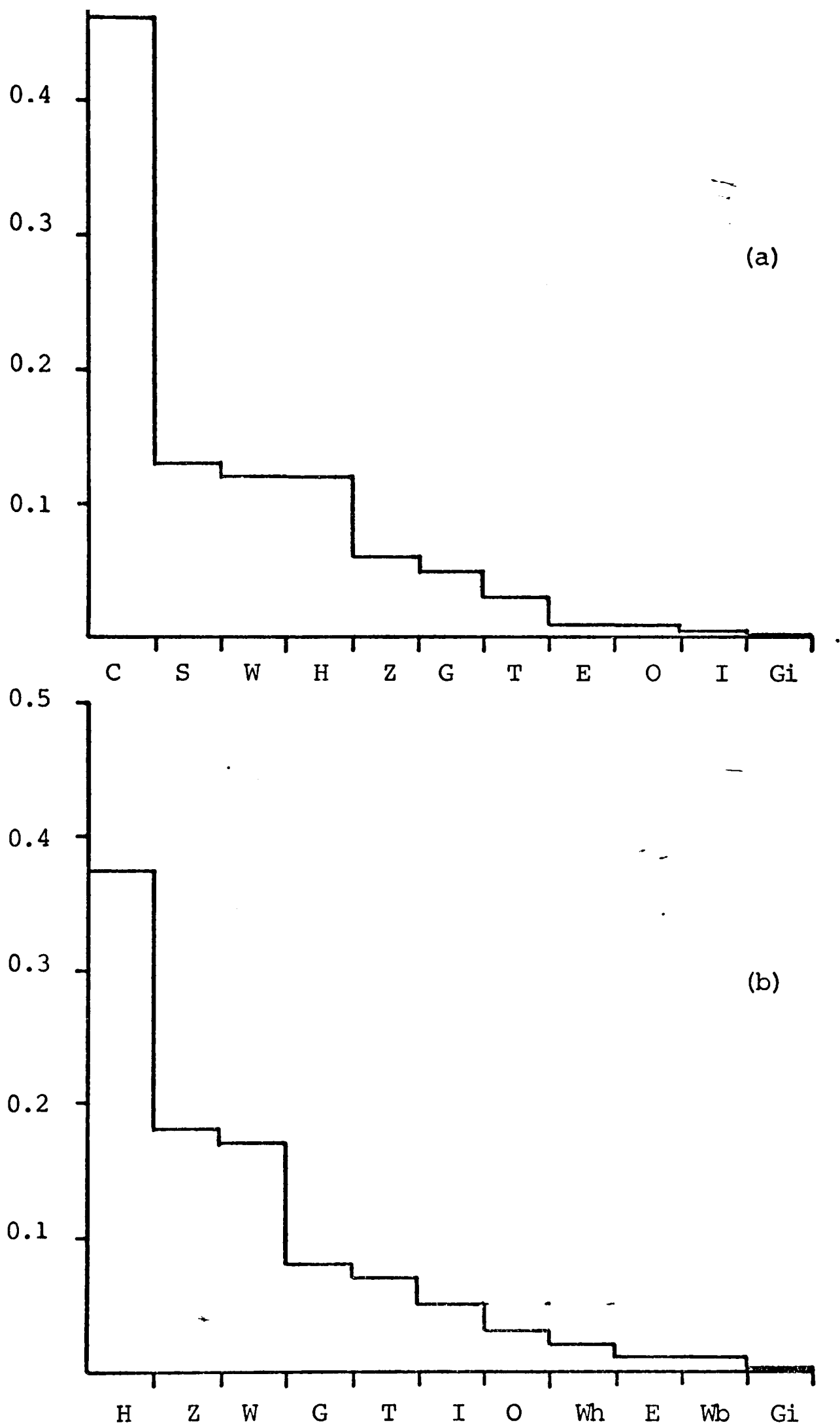


Fig.7.2.The proportion of the total animals in each of 11 herbivore species in (a)the Athi Plains and (b) the Nairobi Park.

C	cow	Z	zebra	O	ostrich
S	"shoat"	G	Grant's gazelle	I	impala
W	wildebeest	T	Thomson's gazelle	Gi	giraffe
H	hartebeest	E	eland	Wh	warthog
				Wb	waterbuck

11 species of large herbivores, although composed differently.

Table 7.1 shows that the Nairobi study area has a more diverse community than does any of the plains blocks, of which Block 62 has the greatest diversity. The community of the whole plains unit is more diverse than that of any single block with the exception of Block 62, but it is still less than the park's.

The evenness of the species numbers varies similarly, with the park community the most equitably distributed ($J = 0.760$). Although three of the plains blocks also support 11 species, their equitabilities are all lower. For the plains as a whole, $J = 0.678$, which is less than the values of three of the single blocks. This uneven distribution of numbers between the species is mostly due to the preponderance of cattle in the plains community (Fig. 7.2), and the small contribution of eland, ostrich, impala and giraffe.

Breaking the indices down by season shows that the park community is evenly diverse in all three seasons, resulting in a seasonality index of 0.999.

The seasonal diversity of the blocks in the plains shows considerable variation: thus, Block 62 has the most diverse community in the wet and medium seasons, and the wet season coincides with its time of greatest animal numbers (Appendix 5). Block 39 exhibits its greatest diversity in the medium dry season, dropping drastically in the dry season, while Blocks 30 and 35 support the most diverse communities in the wet season. The community of Block 22 is uniformly fairly diverse while that of Block 15 reaches its lowest value in the wet season. Although the Shannon-Weiner index is independent of the actual numbers of animals, this pattern of changing diversity approximates to the changing pattern of animal numbers described in the last chapter (p. 92). It seems, therefore, that an influx of large herbivores into an area is accompanied by an increase in the diversity of the community.

Table 7.2. The seasonal, mean and overall indices of diversity and seasonal index for occupation of the 6 study areas in the plains.

Species	SEASONAL H(s)			H(s) $\bar{x}$	H(s) overall	Seasonality index
	Wet	Medium	Dry			
Cattle	2.254	2.384	2.035	2.224	2.313	.962
Wildebeest	1.968	1.587	0.576	1.357	2.190	.620
Zebra	2.297	1.309	1.278	1.628	2.024	.804
Thom. Gaz.	1.929	1.915	1.939	1.928	2.004	.962
Grant's Gaz.	2.175	2.438	2.424	2.346	2.448	.958
Hartebeest	2.177	2.255	1.666	2.033	2.219	.916
Impala	-	-	-	-	1.381	-
Giraffe	-	-	-	-	0.982	-
Eland	-	-	-	-	1.107	-
Ostrich	2.217	2.437	2.295	2.316	2.410	.961
Shoat	1.668	1.500	2.065	1.745	1.871	.933

The seasonality indices of the 6 blocks are all less than that of the park, indicating that the diversity of their communities varies seasonally. However, when the animal data from all blocks are combined to represent the whole plains, the seasonality index is 1.00, which is effectively the same as that of the park. This shows that the plains community as a whole shows an even diversity throughout the year, in which it resembles the park, but this overall diversity is obtained by the changing diversities of its component areas, rather than by a uniform seasonal diversity as in the park community.

7.6 Occupance diversity of the vegetation zones of the plains

The 6 blocks in the plains were chosen as sample areas of the main vegetation zones (p. 17). To look at the differential use made of these areas by the herbivores their distributions between the blocks have been used to calculate diversities of occupance. It is assumed that this is equivalent to measuring the macro-habitat tolerance of each species. The diversities were calculated with the Shannon-Weiner function where $n_1 \dots n_6$ represent the numbers of a species in the 6 blocks.

The distributions of animals between blocks in each season and through the year are given in Appendix 5 . Table 7.2 presents the seasonal diversity indices, their means and overall values, and the seasonality indices. Because distribution between 6 categories is involved, seasonality indices have not been calculated for species with less than 6 observations in each month. This excludes impala, giraffe and eland.

When the species are ranked in order of decreasing diversity (or increasing macro-habitat selectivity) the following order is obtained from the year-round figures:

Grant's gaz.> Ostrich> Cow> Hartebeest> Wildebeest> Zebra> Thomson's gaz.> "Shoat"> Impala> Eland> Giraffe.

Using the actual values of the indices, 3 main groups of species appear. Grant's gazelle, ostrich, cattle, hartebeest and wildebeest utilise

Table 7.3. The number of observations of each species in each season, and their total number in the Nairobi Park study area and the Athi Plains blocks.

Species	Wet		Medium		Dry		Total	
	Park	Plains	Park	Plains	Park	Plains	Park	Plains
Cattle	-	31	-	16	-	38	-	85
Wildebeest	88	137	53	148	176	65	317	350
Zebra	44	37	16	34	115	32	175	103
Thom. Gaz.	101	61	35	58	135	67	271	186
Grant's Gaz.	93	79	39	77	129	70	361	149
Impala	25	3	8	4	43	2	76	9
Warthog	44	-	26	-	74	-	144	-
Eland	23	10	7	3	15	2	45	15
Ostrich	48	26	23	25	71	26	142	77
Giraffe	11	6	3	6	5	2	19	14
Waterbuck	22	1	2	1	28	0	59	2
Hartebeest	276	218	122	206	434	119	832	628
Shoat	-	7	-	7	-	10	-	24

these habitats diversely on an all-season basis. Zebra and Thomson's gazelle have a less diverse use, while the remaining species - "shoat", impala, eland and giraffe - are relatively selective in their choice of vegetation zone. Within each season the relative habitat diversities of the species are similar to this order of overall diversity, but the wildebeest and hartebeest both show large drops in diversity in the dry season, suggesting the concentration of their populations. This is particularly marked in the wildebeest for which fewer sightings were obtained (Table 7.3), but the total number of animals counted was almost the same (Appendix 5), as in the wet and intermediate seasons. The habitat diversity of zebra is low in both the middle and intermediate seasons, but as their number of sightings is nearly constant, this reflects a genuine dispersal in the wet season. Of the other species, the habitat diversity of shoats increases in the dry season, but this is almost certainly due to the large increase in the number of observations compared to the marginally large enough totals of the other months. The remaining species - cattle, both gazelle species and ostrich - all exhibit approximately even diversities in all seasons, but that of Thomson's gazelle is most constant.

The seasonality indices (Table 7.2) separate the species in to two groups. All species have indices of more than 0.900 except for wildebeest and zebra. The low indices are the result of low habitat diversities at any one season but much greater diversities over the whole year, confirming that they are migratory (p.95). Eland are also known to be highly migratory in the Athi Plains unit (Hillman pers. comm.), but there are insufficient observations on this species to calculate its seasonality index.

7.7 The numbers and seasonal diversity of the species in the Nairobi Park study area

It was shown above that the diversity of the park community stays essentially constant through the year, and the purpose of this section is

Table 7 .4. The mean population sizes, their S.E.'s and S.E./ $\sqrt{x}$'s of 11 species in the Nairobi Park study area, from 12 or 8 monthly counts.

Species	Mean Popn.	No. of Counts	S.E.	S.E./ $\sqrt{x}$
Wildebeest	265.6	12	63.5	.24
Zebra	292.3	12	103.4	.35
Thom. Gaz.	107.9	12	9.9	.09
Grant's Gaz.	125.3	12	11.3	.09
Hartebeest	595.3	12	48.5	.08
Impala	79.9	12	8.9	.11
Warthog	33.6	12	4.3	.12
Waterbuck	19.7	12	2.6	.13
Giraffe	5.2	12	1.5	.30
Eland	21.2	12	5.2	.25
Ostrich	43.9	12	7.3	.17
Wildebeest	159.9	8	11.2	.07
Hartebeest	544.4	8	28.5	.05

to see how the sizes of its herbivore populations change through the year. This provides a comparison with the occupancy of the vegetation zones of the plains, and this is taken further by looking at the seasonality indices for vegetation type occupancy.

Whereas a diversity index could be used to look at the changing distributions of animals between habitats, this method cannot be used for the park because the main interest is the extent to which the populations vary through the year in the one area. Because the results of 12 monthly counts are available for each species, the standard errors have been used to measure the variance of these population sizes (Watt 1965); for convenience the S.E.'s have been expressed as a fraction of the mean population of each species ($S.E./\bar{x}$).

Table 7.4 gives the mean population sizes of each species in the park, with their standard errors (S.E.) and the $S.E./\bar{x}$. The full results of each monthly count are given in Appendix 6. The values of the $S.E./\bar{x}$ fall in to two groups divided by the value of 0.20. Wildebeest, zebra, eland and giraffe have high $S.E./\bar{x}$ values, indicating that their population levels change considerably through the year, provided the counting bias is constant between months (p. 18). The high value for zebra is caused by their use of the park in the dry season (Appendix 6) which is an annual or bi-annual event under normal circumstances. The influx of wildebeest in to the park in late 1972 was a rare event, and the effect of this on their population mean size is shown by removing the results of the counts of July, August, September and October. When this is done the $S.E./\bar{x}$ drops to 0.07. As the 8 months used for this calculation include the normal dry season of March-April, it is apparent that the population size of this species usually shows very little variation, which the park records confirm. This behaviour is in marked contrast to the migratory habits of the wildebeest of the plains (p. 92).

Eland numbers show considerable variation, and their dry season use

of the park is very marked (Hillman, pers. comm.). The numbers of giraffe also fluctuate greatly, but as the numbers observed varied from a maximum of 17 to a minimum in 2 months of 0, the variation is probably due to these very small and variable sample sizes. Their population size in the park varies little (Foster and Kearney 1967).

Of the remaining species, the ostrich has a fairly high $S.E./\bar{x}$ value. Again, there is no evidence of any exchange with the plains (Foster and Kearney 1967), and the high variance is probably the result of the seasonal occurrence of large chick groups. Thus of a total of 92 ostrich counted in October, 36 were in one group, and of 88 in December, 48 were in one group. This variance could obviously be reduced by using biomass.

The other species - hartebeest, both gazelles, impala, warthog and waterbuck - all have comparatively low $S.E./\bar{x}$ values, and it is concluded that the sizes of their populations vary little through the year, although the hartebeest population was swollen by immigrants from the plains in late 1972 (Appendix 6 and Park records). However, if the relevant months are excluded, as done for wildebeest, the $S.E./\bar{x}$ drops only to 0.05 from .08, showing that the effect the extra animals was only slight (Table 7.4).

7.8 Occupance diversity of the vegetation types of the park and the plains

Within the two communities the habitat tolerance of each species at the vegetation type level has been investigated by calculating the diversity by each species in its occupance of vegetation types.

The Shannon-Weiner function is used to calculate the seasonal and overall diversities necessary for calculating the seasonality indices. Here, $n_1 \dots n_j$ represent the numbers of a species in vegetation types 1 to j, in the manner of Harris (1972). The distribution data are presented as Appendices 7 and 8 for the park and plains respectively.

The overall species diversities are discussed first, and the seasonal diversities and seasonality indices are then described for each community.

Table 7.5. The seasonal, mean and overall diversity indices and seasonality indices for the occupation of vegetation types by each species in the Athi Plains.

Species	SEASONAL H(s)			H(s) $\bar{x}$	H(s) overall	Seasonality index
	Wet	Medium	Dry			
Cattle	3.240	2.736	3.117	3.031	3.403	.891
Wildebeest	2.961	2.828	1.666	2.485	3.315	.750
Zebra	2.948	2.312	2.018	2.426	2.981	.814
Thom. Gazelle	2.705	2.450	3.154	2.770	2.835	.977
Grant's Gaz.	2.849	3.526	3.135	3.170	3.414	.923
Impala	-	-	-	-	1.938	-
Ostrich	2.883	3.009	2.949	2.947	3.375	.873
Eland	-	-	-	-	2.023	-
Giraffe	-	-	-	-	1.749	-
Shoat	-	-	-	-	2.470	-
Hartebeest	3.293	3.394	2.923	3.203	3.519	.910

Table 7 .6. The seasonal, mean and overall diversity indices and seasonality indices for the occupation of vegetation types in the Nairobi Park.

No. of Months	Species	SEASONAL $H_{(s)}$				$H_{(s)} \bar{x}$	$H_{(s)}$ overall	Seasonality Index
		Wet	Medium	Dry				
12	Wildebeest	2.334	1.809	2.601		2.248	2.658	.846
12	Zebra	2.086	2.020	2.936		2.347	3.136	.748
12	Thom. Gaz.	1.626	1.520	2.121		1.756	2.126	.826
12	Grant's Gaz.	2.541	2.019	2.844		2.468	2.788	.885
12	Hartebeest	2.318	2.441	2.876		2.545	3.060	.832
12	Impala	-	-	-		-	1.608	-
12	Warthog	2.980	2.448	1.946		2.458	2.768	.888
12	Waterbuck	-	-	-		-	1.621	-
12	Ostrich	2.645	2.638	2.593		2.625	2.724	.964
12	Eland	-	-	-		-	2.283	-
12	Giraffe	-	-	-		-	1.423	-
10	Wildebeest	2.334	1.809	2.423		2.189	2.471	.886

Seasonality indices have not been calculated for impala, giraffe, eland and "shoat" in the plains because in each month the number of observations on each is lower than the number of available categories (19 vegetation types of the 6 study areas). For the same reasons, there are no seasonality indices for impala, waterbuck, giraffe and eland in the park.

Because the seasonality indices from the park suggest marked patterns of vegetation utilisation, the species distributions are considered in more detail. The raw distribution data (Appendix 7) do not show which vegetation types are selected for or avoided by a species because they are not of equal size. A vegetation type is said to be selected if the proportion of the population using it is greater than its fractional contribution to the total area. This is the basis of the comparative grazing index (c.g.i.) (Hunter 1954) which is defined as:

$$\frac{\% \text{ of population of species A using veg. type X}}{\text{proportion of total area covered by veg. type X}} \times 100$$

Thus, a c.g.i. of more than 100 shows selection for a vegetation type, and one of less than 100 shows its avoidance. When the c.g.i. = 100, the number of animals in type X is the fraction of the population which would be expected according to its area. Table 7.7 shows the c.g.i. values for each species in the Nairobi study area in each season. In the counting methods used, animals were assigned to the vegetation type in which they were seen, whether feeding or not. Thus the values are strictly measures of comparative occupance intensity, but as all counting was done in the early morning when most species feed, these figures are assumed to be equivalent to true c.g.i. measurements.

7.9 Overall diversity in both communities

Tables 7.5 and 7.6 include the overall diversity indices for each species in the two communities. Because the distributions of animals between 14 vegetation types in the park and 19 types in the plains are

being considered, the actual values of these indices from the two communities cannot be compared directly. But when they are ranked from the species with the most catholic occupation of vegetation types to that with the least, the following orders are obtained:

<u>Park</u>	Zebra > Hartebeest > Grant > Warthog > Ostrich > Wildebeest > Eland > Thomson > Waterbuck > Giraffe > Impala
<u>Plains</u>	Hartebeest > Grant > Cow > Ostrich > Wildebeest > Zebra > Thomson > "Shoat" > Eland > Impala > Giraffe

With 9 species in common, the two orders are substantially the same. In both the park and the plains, the hartebeest and Grant's gazelle show comparatively ubiquitous distributions, followed by the ostrich and wildebeest. Thomson's gazelle, eland, giraffe and impala occupy the lower ranks in both communities, indicating their rather narrow tolerance of, or greater selectivity amongst, the vegetation types of the areas. The position of the zebra is the only one to be substantially different in the two orders. Whereas it is found in a fairly restricted number of vegetation types in the plains, because of its clumped distribution but smaller population than the wildebeest (p. 88), it is the most diverse species on this criterion in the park (see later). This result is due to the influx of zebra in to the park during the dry season of late 1972 (see later), during which these animals occupied a large number of vegetation types.

Of the 4 species which are found in only one community, it is clear from the rank orders above that each species that is unique to one community has a rank position similar to a species that is unique to the other community. Thus cattle and warthog, and "shoat" and waterbuck lie in positions 3 and 4, and 8 and 9 in the park and plains communities respectively. The significance of this apparent replacement of two indigenous species by two domestic species is discussed later.

7.10 Seasonal diversity in the plains community

Typically for migrating species, wildebeest and zebra show the greatest seasonal variation in their occupation of vegetation types (Table 7.5). For the other more sedentary species, one of two basic patterns of utilisation is possible. If a species occupies the same vegetation zones through the year but utilises the vegetation types sequentially, it would have a low seasonality index. On the other hand, if all the same vegetation types were occupied throughout the year, then the index would approach unity. Of the sedentary species considered, ostrich have the lowest index, but as the numbers of observations are low although consistent (Table 7.3), no firm conclusions are possible. The same is true of cattle because their low seasonality index is largely due to their low vegetation type diversity in the medium-wet season when there were only 16 observations (Table 7.5). However, seasonal occupation of vegetation types is certainly lacking in the hartebeest on which there were large numbers of observations in all three seasons (Table 7.3).

7.11 Seasonal diversity in the park community

For the 7 species for which there were enough observations, the seasonality indices (Table 7.6) are ranked in the following order of descending value:

Ostrich > Warthog > Grant's gaz. > Wildebeest > Hartebeest > Thomson's gaz. > Zebra.

This shows that the distribution of ostrich between the vegetation types is the least variable from season to season, while that of zebra changes most. Comparing the seasonality indices from the two communities, hartebeest and Thomson's gazelle use the vegetation of the park differentially between seasons, whereas in the plains they were seen in almost the same types on each sampling occasion. The reverse is true of ostrich and wildebeest where the vegetation used in the park varies little between seasons compared with the plains. The zebra populations are highly

mobile in both areas and show marked seasonal differences in the vegetation occupied, while at the other extreme, only Grant's gazelle shows a relatively unchanging choice of vegetation in both areas.

If genuine, these differences in behaviour in the two areas might be responses to the different conditions of the park and plains. In this case, the use of particular vegetation types at certain times of the year might be an adaptation by the herbivores to enable year-round survival in the park study area. To look at these patterns of utilisation the comparative grazing intensity method (p.114) was employed. This also made it possible to describe the distributions of those species for which seasonality indices were not calculated.

The seasonal c.g.i. values for each vegetation type and each species are given in Table 7.7.

Ostrich, warthog and Grant's gazelle all have high $H_g (\bar{x})$ (Table 7.6) values showing that all three occupy a large number of vegetation types, and this catholicity varies little through the seasons. The actual vegetation used by ostrich changes considerably but this may only reflect their wide-ranging behaviour. However, types 02 and 06 are consistently avoided. Warthog show a consistent selection for the shortest plains grassland (01), and for its unburnt and longer equivalent (04) in the medium and dry seasons. Only the shortest A. drepanolobium grassland (35) is selected, and only in the rains. They also avoid the long grass of the steep valley bottoms (02). Their diversity decreases in the dry season which might be due to a counting bias if they were using the low grass areas, where they would be less visible. However, as there is little evidence that this is the case (Bradley 1968), this reduction in the number of vegetation types used must be real.

Wildebeest have a lower seasonality index and thus greater seasonal utilisation of the vegetation. In the wet season they select the open grasslands (01, 04), the ecotone (03) and the A. drepanolobium areas with the shortest grass (35). In the intermediate months they are mostly on the short grass plains (01), the bush grassland (05) and, again the short

whistling thorn grassland (35). Their dry season vegetation type diversity is higher, largely because of their selection for all open grassland types (01, 03, 04), the bush grassland (05) and again the short A. drepanolobium grassland (35). Although there are considerable numbers of wildebeest in type 02 in the dry season (Appendix 7) their c.g.i. for this longer grassland on steep slopes is 99, showing that it is being neither selected nor avoided.

The high mean number of wildebeest counted in the dry season (Appendix 6) was caused by immigration from the plains. Because the population usually varies little between wet and dry season (Foster and Kearney 1967), the impact of the larger population was assessed by excluding the months of high wildebeest numbers (September and October) and recalculating the diversity indices for wildebeest for a dry season consisting of only November, March, April and August. The new dry season mean and overall indices and seasonality index are included in Table 7.6. With this modification both the dry season and overall diversities drop by similar amounts, but the mean diversity decreases by a relatively small amount. The new seasonality index is therefore higher than the original and is now slightly greater than that of Grant's gazelle. Therefore, when the number of wildebeest varies little through the year, which has been the normal situation since 1962 (Foster and Kearney loc. cit. and park records) they show only very slight differential use of the vegetation between seasons. The c.g.i. values for this modified dry season ("Dry (2)", Table 7.7) show that the same types are selected with the short A. drepanolobium grassland (35) being more favoured, and the long sump grass (02) more avoided.

The seasonality index of the hartebeest is considerably lower than the wildebeest's, especially if the modified dry season is used for the latter. Thus, hartebeest distribution varies more between seasons. In the wet season they select the short grass A. drepanolobium areas (06, 35) and the ecotone with the open plains. There is some slight selection

for the bush grassland (05). In the intermediate months this last type is most selected but the open plains (01, 04) are also favoured, and the numbers of hartebeest in the sumps are as one would expect on a random basis (c.g.i. = 102). This situation changes in the dry season with three sump or lower slope vegetation types being selected (02, 07 and 08), although the ecotone (03), the longer grass plains (04) and the bush grassland (05) are also selected. The only extensive types that are avoided are the shortest grass plains (01) and all the A. drepanolobium types (06, 10, 35). The large number of favoured types causes the increases in the calculated vegetation type diversity in this period. Although this description of hartebeest movements is adequate for comparative purposes, their movements are considered in greater detail later (Ch. 14).

Thomson's gazelle show a comparable seasonality in their distribution, with a pattern of movements which are similar though not as extreme as those of the hartebeest. In all three seasons the shortest grassland (01) is selected. In the wet season the shortest A. drepanolobium grassland (35) is favoured, but in the intermediate months the longer grass plains (04) and bush grassland (05) are selected. Their high seasonality index is largely due to the increase in number of vegetation types occupied in the dry season when types 02 and 03 are also selected. Although this increase is matched by a larger number of observations, its occurrence in the months when the animal biomass is greatest and the grass is shortest (p. 125) is not surprising in view of the propensity of this gazelle for short grass (Western 1973).

Of the 7 species for which seasonality indices have been calculated, zebra appear to have the greatest seasonal use of the vegetation (Table 7.6). In the wet and intermediate months their numbers and the number of observations are both low (Table 7.3) and the species shows a low vegetation type diversity. The longer burnt A. drepanolobium grassland (06) and its ecotone (03), and the longer plains grassland (04, 05) are selected in these seasons, respectively. Their large increase in diversity in the dry

Table 7.7. Seasonal comparative grazing intensity (c.g.i.) values for each species in each occupied vegetation type in Nairobi Park study area.

PERCENTAGE OF AREA		9.4	15.0	2.0	10.8	4.2	24.9	15.3	13.2	1.4	0.9	0.3	2.1	0.2	0.2
Species	Season	VEGETATION TYPE													
		1	2	3	4	5	6	10	35	7	8	9	11	12	13
Wildebeest	Wet	257	3	580	155	9	38	1	278	-	14	-	-	-	-
	Medium	663	40	0	84	250	1	-	64	-	344	-	-	-	-
	Dry (1)	178	99	360	284	345	4	5	102	65	-	-	-	-	-
	Dry (2)	185	13	395	334	193	12	14	291	-	-	-	-	-	-
Zebra	W	-	7	1040	93	-	198	44	76	-	-	666	-	-	-
	M	61	55	-	355	850	39	-	47	-	-	-	-	-	-
	D	45	160	610	182	209	26	106	37	121	44	333	-	50	-
Thomson's Gazelle	W	547	4	10	64	74	3	-	273	-	-	-	-	400	-
	M	730	33	20	112	202	-	-	41	-	-	-	-	-	-
	D	334	136	110	337	100	28	-	30	-	-	-	-	350	-
Grant's Gazelle	W	284	29	90	121	145	91	3	180	-	22	166	-	250	-
	M	537	77	-	181	262	16	-	26	-	-	-	-	-	-
	D	147	185	340	171	274	32	27	66	36	33	-	-	100	-
Hartebeest	W	69	33	215	21	114	199	33	156	28	22	3	-	550	-
	M	174	102	-	231	781	8	17	23	14	22	-	-	1250	-
	D	69	209	525	211	357	20	37	18	171	155	-	-	400	400
Impala	W	6	393	-	8	293	-	-	107	286	-	-	-	-	-
	M	12	457	-	-	193	-	-	167	-	-	-	-	-	-
	D	34	544	-	58	131	-	-	-	-	355	-	-	-	-
Warthog	W	203	17	870	81	476	24	28	119	64	100	1433	-	-	-
	M	255	60	-	213	404	16	26	68	-	-	-	-	-	-
	D	356	69	295	310	76	6	18	61	-	-	367	-	-	-
Waterbuck	W	46	290	-	10	583	-	-	73	1143	-	-	-	-	-
	M	-	-	-	-	1428	-	-	-	2857	-	-	-	-	-
	D	-	567	-	29	-	-	-	-	842	-	-	-	-	-
Ostrich	W	191	40	-	259	238	88	3	72	-	55	167	-	-	-
	M	286	51	-	80	183	27	163	123	-	-	-	-	500	-
	D	258	54	310	275	77	16	40	140	-	-	-	-	-	-

Table 7.7 continued.

PERCENTAGE OF AREA		9.4	15.0	2.0	10.8	4.2	24.9	15.3	13.2	1.4	0.9	0.3	2.1	0.2	0.2
Species	Season	1	2	3	4	5	6	10	35	7	8	9	11	12	13
Eland	W	-	60	800	111	71	157	6	152	-	-	-	-	-	-
	M	-	179	-	143	183	31	25	204	-	-	-	548	-	-
	D	24	578	-	21	52	-	-	-	57	-	-	-	-	-
Giraffe	W	-	95	-	-	283	38	389	36	-	-	-	-	-	-
	M	-	-	-	-	1190	-	327	-	-	-	-	-	-	-
	D	-	125	-	-	-	-	531	-	-	-	-	-	-	-
No.of c.g.i. values		16	13	13	18	25	3	5	13	6	3	6	1	8	1

season results from their increased numbers (App.6 .), with selection for types 02, 03, 04, 05 and 07. The longer burnt A. drepanolobium grassland is avoided, and although they are almost the only species apart from giraffe to use the unburnt A. drepanolobium areas (10), they only occur here in the proportion to be expected on a random basis (c.g.i. = 106).

This high diversity in one season because of a large increase in numbers is similar to the wildebeest situation, but because the zebra immigrate in to the park regularly (Foster and Kearney loc. cit.), this increase in diversity is considered to represent the normal situation, which was not the case with the wildebeest. It is worth pointing out, though, that the highly seasonal use of the vegetation by zebra arises for reasons that are different from those described for hartebeest and Thomson's gazelle. The area supports populations of these two species which are essentially constant in size through the year (Table 7.4) and display distinct cycles of vegetation type occupancy.

Of the 4 species for which there are no seasonality indices, a certain amount can be deduced from their c.g.i. values (Table 7.7). The number of giraffe seen is low but in each season they show a consistent choice for vegetation type 10, which contains the densest A. drepanolobium, although the bush grassland (vegetation type 05) is also selected in the wet and intermediate months.

Impala, waterbuck and eland all exhibit the same basic pattern of being on the upper slopes in the wet season and retreating to the valley bottoms in the dry season. In the wet months eland occur in low numbers, but select the open plains (04), their ecotone with the thorn areas (03) and the shorter A. drepanolobium areas (06, 35). Impala show a slight selection for type 35 (c.g.i. = 107), while most are found in types 02, 05 and 07. Waterbuck show even less movement away from the valley bottoms, selecting only these last three types. The few data for the intermediate months suggest little changes in these distributions, but in the

dry season all three species show powerful selection for type 02, the Cymbopogon-Hyparrhenia grassland, although impala also select types 05 and 08, and waterbuck also choose the sump vegetation of type 07. Although it is not apparent from Table 7.5, the number of eland in the park usually increases in the dry season (Park records), and, during this period of high numbers, the steep-sided gorges (type 11), which replace type 02 lower down the valleys, are used extensively. As the searching efficiency for eland in this terrain was undoubtedly lower, the apparently strong preference of eland for type 02 in the dry season may be inflated because of this counting bias.

7.12 The distribution of herbivore species in relation to the standing crop of grass

There are many factors which may operate to determine whether a vegetation type is a suitable habitat for a herbivore species. Some of these factors, such as the availability of surface water, may be extrinsic to the actual vegetation, but there is evidence (e.g. Western 1973), that the height of the grass of a vegetation type largely determines which species are found in it.

In order to test whether the various diversities of the herbivore species amongst the vegetation types might be related to their tolerance of different grass heights, the numbers of each species were broken down in to categories of grass standing crop for the vegetation type in which they were seen. It is assumed here that grass height is directly related to the grass biomass, which was measured. When the numbers seen in each crop category are used in the Shannon-Weiner expression, the resulting index of diversity may be equated with the degree of tolerance of each species to the range of available standing crops. This index has been calculated for all the species of the park community and for the 6 most numerous species in the plains, namely, cattle, wildebeest, hartebeest, zebra, Grant's and Thomson's gazelles. Although numerous, "shoats" have

Table 7.8. The overall diversity indices for the utilisation of areas of different standing crop values for species in the park and plains communities.

Rank	H(s) Nairobi Park	Species	H(s) Athi-Kapiti Plains	Rank
1	2.766	Ostrich	-	
2	2.744	Hartebeest	2.787	1
3	2.662	Grant's Gazelle	2.748	2
	-	Cattle	2.695	3
4	2.564	Eland	-	
5	2.534	Zebra	2.539	4
6	2.532	Warthog	-	
7	2.382	Giraffe	-	
8	2.335	Wildebeest	1.905	5
9	2.262	Thomson's Gaz.	1.847	6
10	2.190	Waterbuck	-	
11	1.793	Impala	-	1

been excluded because of the small number of observations (Table 7.3).

Grass biomass was measured by clipping quadrats in each of the more extensive vegetation types in each month (p. 19). The calculated standing crops were then grouped into the following categories:

Standing crop kg/ha	category	S.C kg/ha	category
0-400	1	20-2400	6
400-800	2	24-2800	7
800-1200	3	28-3200	8
12-1600	4	>3200	9
16-2000	5		

The divisions of 400 kg/ha were chosen to provide an adequate number of categories over the range of observed biomasses. For, practical reasons, quadrats were not clipped in 7 of the 19 vegetation types in the plains blocks, and in 6 of the 14 types in the park study area. Thus, animals seen in these vegetation types are not included in the calculations of diversity between standing crop values. For 10 out of the 11 species in the park, less than 10% of the observed animals are excluded by doing this; the exception is the waterbuck for which 19.5% were excluded. Of the 7 species of the plains considered here, there are no standing crop measurements for 11% of the observed zebra, and the corresponding fractions for the other species are all smaller. Because this fraction is consistently so small, I consider that the indices of diversity amongst standing crop values allow comparison with the indices of vegetation occupation.

The distribution of individuals of each species broken down by standing crop are given in Appendices 9 and 10 for the park and plains respectively. Table 7.8 contains the indices for each species in the two areas. To compare the two communities, the species' indices have been ranked. Thus, in Table 7.8 the rank order of the 5 species common to both communities are exactly the same. In both, the hartebeest and Grant's gazelle display

a relatively broad tolerance of the standing crop of grass, while zebra, wildebeest and Thomson's gazelle increasingly prefer certain grass biomasses. Although cattle occupy third place in the plains order, their index suggests a tolerance only slightly less than that of the hartebeest and Grant's gazelle.

These indices suggest that the 13 herbivore species differ in their tolerances to the spectrum of grass conditions, measured as standing crop, and that the relative tolerances of those species which are found in both areas are very similar, although the areas differ considerably in other respects. If grass volume is an important parameter in herbivore distribution, then a broad tolerance might allow a species to occupy a larger number of vegetation types. This hypothesis was tested by comparing the rank values for crop diversity and the diversity of vegetation type occupation (Tables 7.5, 7.6) for the 11 species in the park and the 7 species in the plains. With a Spearman rank correlation test the species orders for the two indices for the park are significantly correlated with $r_s = 0.822$, $p < 0.05$, $n = 7$. It seems, therefore, that even though the vegetation types may differ in other respects than grass volume, a herbivore's tolerance of a wide range of standing crop values enables it to occupy more vegetation types.

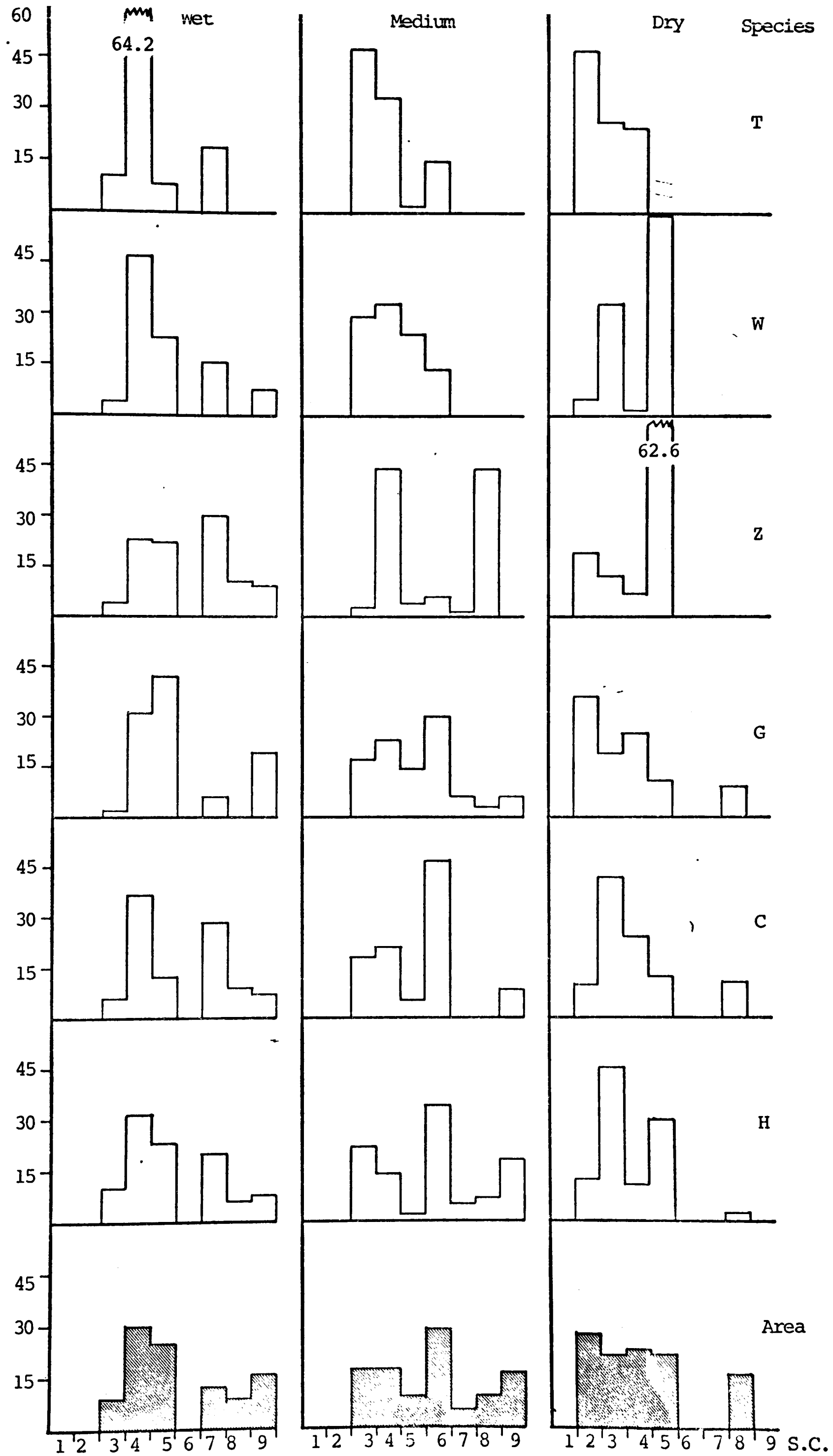
7.13 The seasonal distribution of herbivore species between areas of different standing crops of grass

The overall diversity of 11 species in the park and the 6 most common species of the plains was examined above in relation to the standing crop of grass, and if these data are broken down by seasons, seasonality indices can be calculated for each species. However, while this procedure only measures the relative tolerances of each species to a variety of grass volumes, it would be more instructive to know how this results from the distribution of the animals in relation to the available standing crops.

As the area of each vegetation type was known (p. 26), the area

Fig.7.3. The percentage distribution of 5 herbivore species between 9 categories of grass standing crop (S.C.) in the Athi Plains in the wet, medium and dry seasons.

Area	the percentage of the total area covered by each standing crop category.
C	cow
H	hartebeest
W	wildebeest
Z	zebra
G	Grant's gazelle
T	Thomson's gazelle



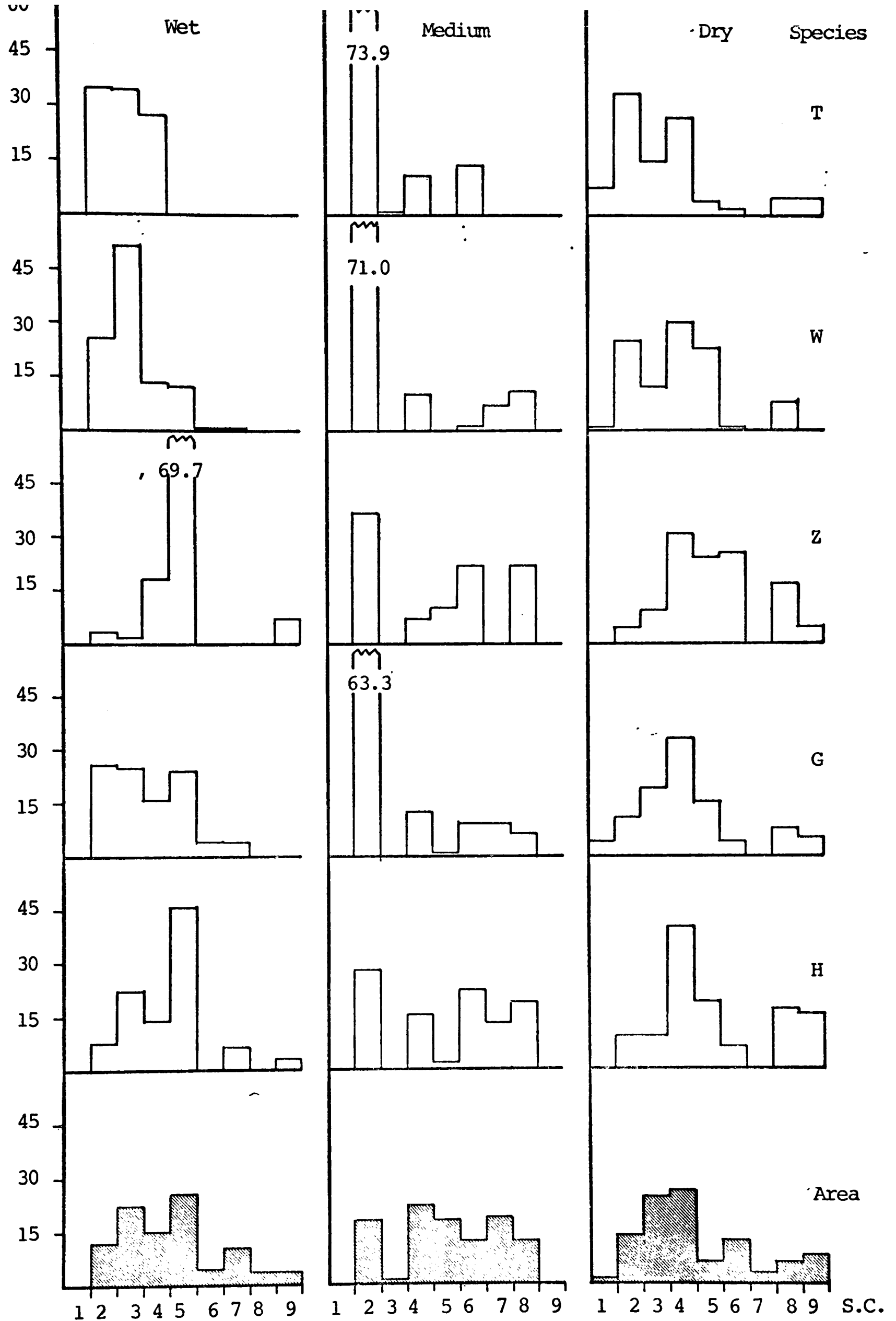


Fig.7.4. The percentage distribution of 5 herbivore species between 9 categories of grass standing crop (S.C) in the Nairobi Park in the wet, medium and dry seasons. Species' symbols as for Fig.7.3.

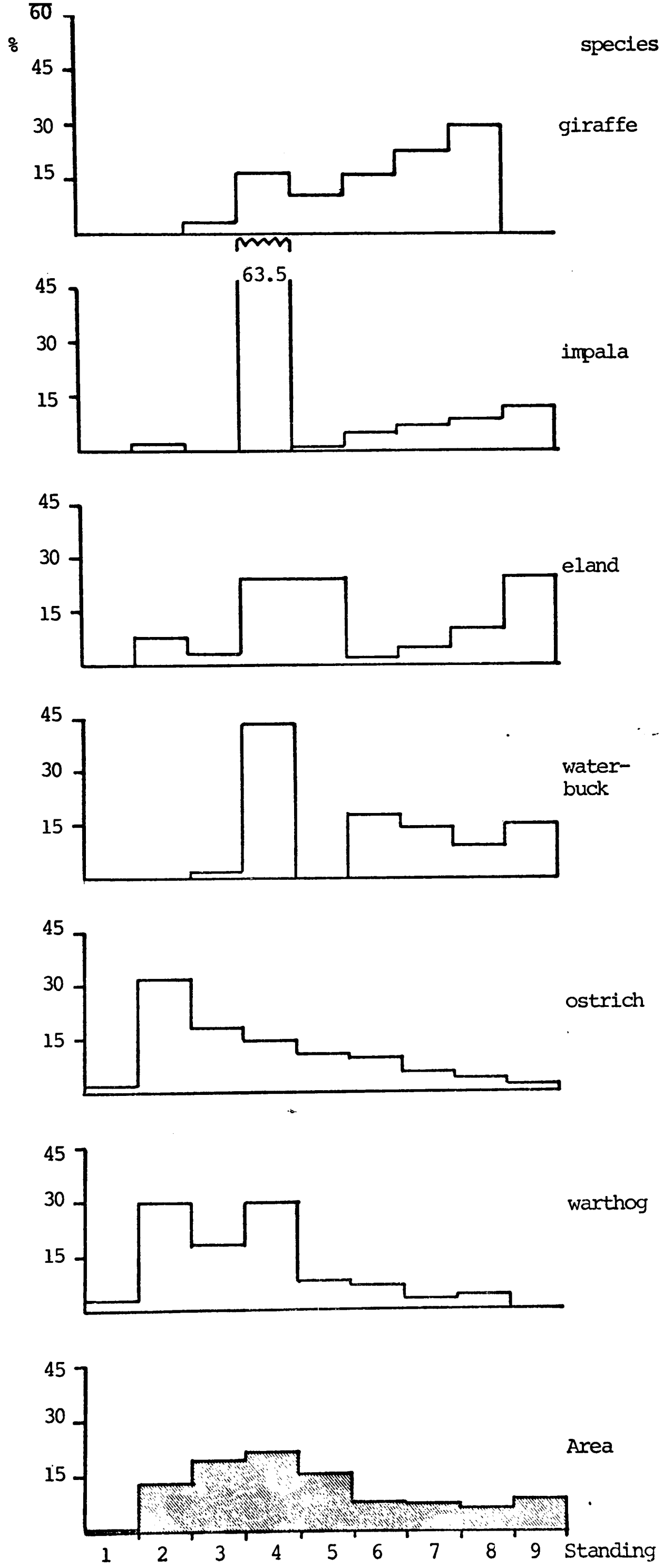


Fig.7.5. The percentage of the populations of 6 herbivore species in each of 9 categories of grass standing crop, with the percentage of the area covered by each category, through 12 months in the Nairobi Park.

covered by each standing crop category was calculated as a percentage of the total area. If the animals of a population were to distribute themselves randomly, the number associated with each standing crop value would be proportional to the area covered by that crop value. Thus the standing crop distribution by area can be used as an expected distribution against which the actual animal distributions can be compared, using the Kolmogorov-Smirnov One-sample test (Siegel 1956).

This comparison has been made on a seasonal basis for the 6 most abundant species in the plains and all the species in the park. The distributional data are presented in Appendices 9 and 10 for the park and plains respectively.

The histograms of Fig . 7.3 show the distributions between standing crop values of the 6 plains species in each season with the percentage of the area covered by each standing crop category. Fig . 7.4

shows the same data for the 5 most abundant species in the park, and Fig. 7.5 is the equivalent for the 6 less common species with their data summed over all months.

With the Kolmogorov-Smirnov one-sample test, the distributions of all the plains species are significantly different at the 0.05 level from the expected distributions, although the hartebeest distribution in the wet season approaches a condition of no significant difference from the expected. For the park, all species show significantly different distributions from the expected distributions in each season. Therefore, no species in either area is distributed at random with respect to the range of available grass biomasses.

In both areas, the amount of grass varies in the three seasons in the same way. In the wet months, categories 3 and 5 (800-1200 and 1600-2000 kg/ha) in the park, and 4 and 5 in the plains are most abundant (Figs. 7.4, 7.3). In the medium season the categories of standing crop which occur are more evenly represented, indicating a higher

overall standing crops after a longer period of production. The volume of grass is reduced between this period and the dry season when the available grass distributions are skewed to the left (Figs. 7.3, 7.4) because of the prevalence of short grass. This skewness is particularly marked in the plains distribution. In relating and comparing the animal frequency distributions to those expected, a species is said to be selecting for a grass crop category if the percentage of its population in a category is greater than the contribution of that category to the total herbage. Similarly, if the herbivore proportion is less than would be expected on a random basis, the species is said to be avoiding grassland of that crop category. This distinction is the basis of the comparative grazing index (c.g.i.) used earlier, but the actual values have not been calculated here.

Considering the plains community, the hartebeest frequency distributions are very similar to the distributions of standing crop by area in the wet and intermediate months, so that their greatest numbers are in the most common crop categories - 4(1200-1600 kg/ha) and 6(2000-2400 kg/ha) respectively. In the dry season, their distribution departs from the expected, and there is selection for crop categories 3 and 5. The cattle distribution of the wet and medium seasons are very similar to the expected ones (and hence to the hartebeest's), with the same high proportions in the modal categories. In the dry season, their distribution resembles the expected one more than the hartebeest's does but, again, the two species show a similar degree of selection for category 3.

Apart from occurring in category 3 grassland in the wet season in the proportion in which it occurs, Thomson's gazelle is consistent in its selection for the shortest grass. Its distribution is highly skewed to the left in each season. Wildebeest are mostly found in the short grass areas, but their tolerance of longer grass is greater than the gazelle's, and in March their most selected category is one higher (4 cf. 3). Unlike the gazelle, in the dry season, however, most of the population is

in much longer grass, although the proportional occurrence of higher categories has decreased.

Grant's gazelle are found in almost all the available crop categories, but they select medium-length grass (categories 4 and 5) in the wet season and occur most frequently in the most abundant category (4) in the intermediate month. Their distribution in the dry season is almost exactly the same as would be expected if they were distributed according to the area of each grass category. The zebra distributions show little resemblance to the expected distributions, and the categories selected vary between seasons: 7 in June, 4 and 8 in March, and 5 in September. Although inconsistent, the overall picture is of a tendency to select the longer grass categories. In the dry season, the majority of both wildebeest and zebra are in grassland of category 5 (1600-2000 kg/ha).

In the park, the hartebeest distributions again resemble the expected distributions in the wet and medium seasons. In both, grassland of category 5 biomass is the most utilised; in the wet season it is the most extensive category, covering 26% of the area and supporting 45.5% of the population, while in the medium months it only covers 22% of the area but is used by 47% of the hartebeest. In the dry season, the hartebeest distribution departs more from the expected one, with a pattern of avoidance of the shortest grassland, and strong selection for category 4 areas, which are also the most extensive.

As in the plains, wildebeest and Thomson's gazelle are found predominantly in the short grass categories, although in the wet and dry months the wildebeest are again in slightly longer grass than the gazelle. The wildebeest's occupation of longer grass areas in the dry season is not as marked as in the plains (Fig. 7.3). In the intermediate months both species show almost identical, very strong selection for grassland of category 2 (400-800 kg/ha). Grant's gazelle also shows this selection in this season with a distribution which is very different from those of

other months. In the wet season this species avoids the areas of longest grass but again selects for areas of category 2 standing crop, and uses areas of categories 3, 4 and 5 to an extent approximately equal to the amount in which they occur. Their dry season distribution is more similar to the expected distribution, in that the whole range of standing crop categories is used, but the species shows a considerable degree of selection for category 4.

The zebra distributions in the park are very variable, as they were in the plains, with strong selection for category 5 in the wet season and for category 2 in the intermediate months. Their numbers are much higher in the dry season and their distribution is more similar to that expected, but with some selection for the areas of longer grass (4, 5, 6 and 8).

Of the less numerous species in the Park (Fig.7.5), impala and waterbuck show a year-round selection for category 4 grassland, which is also the most abundant category. Their discontinuous distributions are the result of the very low vegetation type diversities of these species (Table 7.6). Giraffe also have a low diversity, and their selection of the longer grass areas is a consequence of their preference for areas of dense Acacia drepanolobium (vegetation type 10). Eland have a bimodal distribution with slight selection for medium length grass (categories 4 and 5) and greater selection for the long grass areas (categories 8 and 9), which suggests a considerable tolerance of standing crop values. Warthog only occur in any numbers in categories 2 to 4, showing a strong selection for the shortest grasslands, with the exception of category 1 which is only just represented. Ostrich are more tolerant of grass length, occurring in all the standing crop categories, but most of the population selects for category 2 with the proportions decreasing through the higher categories.

7.11 Overlaps between the plains species

An array of 11 species produces a matrix of 11 x 11 overlap (R_o) values covering all possible species-pairs combinations. But as the

overlap between species A and species B is the same as between B and A, the 66 unique values halve the full matrix along the diagonal. Table 7.9 gives the seasonal values of R_0 for distribution among the 6 blocks. The seasonal measurements of overlap between vegetation types in the plains for 15 species pairs are given in Table 7.10. Using the K-S 2-sample test, the cumulative distributions amongst standing crop values for each of the 15 pairs were significantly different in each season at the 0.05 level, although the distributions of wildebeest and hartebeest in March, and cattle and hartebeest in September approached states of no significant differences.

In Table 7.10 the R_0 values for distribution between 6 blocks, 19 vegetation types and 9 standing crop categories are summarised for the 15 species-pairs. As the chance of obtaining two identical distributions between 6 blocks or 9 crop categories is much greater than between 19 vegetation types, a significant overlap between vegetation types will be obtained with a far lower R_0 value than would be required for either of the other overlaps, even though it is impossible to attach a probability to an R_0 value. As overlaps calculated at the levels of block and vegetation type are significantly correlated ($r = 0.834$, $p < 0.001$, $n = 45$) (Fig. 7.6), the degree of overlap of two species between blocks changes only slightly when the more detailed data of distribution amongst vegetation types are used. Consequently, "spatial overlap" can refer here almost equally to either R_0 , but those between block and standing crop are used because of their similar number of categories (6 and 9).

In the following analysis of these results, a distinction is made on the basis of the number of observations between the "important" species of the community (wildebeest, zebra, cattle, hartebeest, Thomson's and Grant's gazelles) and those which are relatively minor - "shoats", impala, giraffe, eland and ostrich. Considering the vegetation zone overlaps between species of the latter group and all other species (Table 7.9), giraffe

Table 7 .10. The seasonal overlaps in distribution (Block, Vegetation type) and grass standing crop for 15 pairs of species in the Athi Plains.

Species pair	WET SEASON			INTERMEDIATE SEASON			DRY SEASON		
	Block	Veg. Type	Stand. Crop	Block	Veg. Type	Stand. Crop	Block	Veg. Type	Stand. Crop
Cow-Wbst	.793	.774	.950	.691	.624	.840	.454	.360	.760
Cow-Zebra	.766	.688	.947	.680	.510	.504	.569	.568	.766
Wbst-Zebra	.831	.812	.920	.445	.399	.592	.884	.827	.921
Cow-Thom.Gaz.	.764	.736	.929	.838	.707	.872	.789	.587	.874
Wbst-Thom.	.926	.774	.928	.937	.813	.917	.286	.261	.561
Zebra-Thom.	.759	.616	.798	.447	.358	.560	.322	.364	.666
Cow-Grant Gaz.	.833	.716	.862	.921	.734	.911	.928	.733	.938
Wbst-Grant	.902	.617	.936	.833	.715	.887	.350	.280	.626
Zebra-Grant	.943	.466	.840	.534	.518	.633	.553	.413	.756
Thom-Grant	.868	.509	.740	.921	.660	.820	.774	.553	.911
Cow-Hbst	.852	.832	.963	.613	.576	.656	.888	.750	.903
Thom-Hbst	.791	.688	.889	.776	.598	.825	.537	.453	.785
Grant-Hbst	.807	.508	.906	.871	.772	.917	.703	.547	.857

have an apparently high overlap in their distribution with zebra and Thomson's gazelle in the medium-wet season and with impala in the dry season, but this is probably a consequence of the small number of giraffe seen. The same is true of the high overlap between eland and hartebeest in September ($R_o = 0.945$), when only 6 eland were seen. Only the ostrich shows a consistent degree of overlap with any species, which it does with cattle and Grant's gazelle in all three seasons, with hartebeest in the wet and medium months, and with zebra and wildebeest in the wet season. Ostrich are found in almost all 6 blocks in each season (Appendix 5), as are cattle and Grant's gazelle, while hartebeest are widely dispersed in all but the dry season, and zebra and wildebeest are only in the wet season (Table 7.2) . These patterns are responsible for the observed overlap with the ostrich distributions. For all the other species combinations, the values of R_o cover a wide range without any notable high values.

The spatial and standing crop overlaps for the 15 combinations of "important" species pairs are dealt with individually: (Table 7.10).

Cattle/Wildebeest: All overlaps are fairly low, but they exhibit a strong overlap of crop values in the wet season although they are spatially separate at this time. Spatial separation is at its greatest in the dry season.

Cattle/Zebra: A pattern similar to that of cattle/wildebeest, but their spatial separation in the dry season is not quite as great.

Wildebeest/Zebra: Their crop distributions overlap very highly in June, although their distributions are fairly separate. Overlap drops to a minimum in the medium month, but in the dry season their crop overlap is almost as great as in the wet month and they are spatially more coincident.

Cattle/Hartebeest: In the wet season their distributions overlap by 96% and their crop selection by 98%, but both are lower in March. In the dry

season their standing crop preferences are again 94% overlapping, but their spatial overlap is at its lowest.

Wildebeest/Hartebeest: Their standing crop distributions overlap by 96% in the wet season, although their ranges are only 85% similar. Again, these overlaps drop in the intermediate month and increase in the dry season, but compared to the wet season the standing crops selected by the two species are not quite as similar although their spatial distributions are 89% coincident.

Zebra/Hartebeest: Their standing crop preferences are very highly similar in the wet season, although they are spatially separate. Both overlaps are lower in the intermediate month, rising again in the dry season to medium levels (i.e. less than 90% similar), but their crop overlap is then less than their spatial overlap.

Cattle/Thomson's gazelle: In all three seasons their overlaps are consistently fairly low, but they show a 93% overlap in standing crop preference in the wet season.

Wildebeest/Thomson's gazelle: In the wet and intermediate seasons their distributions are extremely similar (93% and 94% respectively) and their standing crop preferences overlap by similar amounts (93% and 92% respectively). This results from the preference of both species for areas of short grass in these months (Fig . 7.3). Overlap on both measures is minimal in the dry season (29% and 56% respectively) because of the changed standing crop selection of the wildebeest at this period (Fig.7.3).

Zebra/Thomson's gazelle: Both overlaps are consistently low, caused by the selection of the latter species for short grass and for longer grass by zebra (Fig . 7.3).

Table 7.11 Species pairs with vegetation overlaps (R_o) of at least 0.800 in each season (taken from Appendix 11)

R_o	WET	MEDIUM	DRY
≥ 0.950		Wildebeest/Thomsons gaz Grant's/Warthog Thomson/Grant	Hartebeest/Zebra Thomson/Warthog Grant/Hartebeest Impala/Eland Warthog/Ostrich
0.900-0.949	Eland/Zebra Grant/Ostrich Impala/Waterbuck Hartebeest/Eland	Wildebeest/Grant Hartebeest/Zebra Hartebeest/Warthog	Wildebeest/Thomson Wildebeest/Grant Wildebeest/Warthog Wildebeest/Ostrich Zebra/Grant Grant/Ostrich Waterbuck/Eland
0.850-0.899	Wildebeest/Thomson Wildebeest/Grant Zebra/Hartebeest Grant/Hartebeest	Wildebeest/Warthog Thomson/Warthog Grant/Hartebeest Warthog/Ostrich	Wildebeest/Hartebeest Ostrich/Zebra Grant/Thomson Ostrich/Thomson Grant/Warthog Impala/Waterbuck Warthog/Hartebeest
0.800-0.849	Thomson/Grant Hartebeest/Grant Eland/Grant Hartebeest/Warthog Hartebeest/Ostrich	Zebra/Warthog Hartebeest/Ostrich	Wildebeest/Zebra Warthog/Zebra Giraffe/Zebra Hartebeest/Thomson Hartebeest/Ostrich Hartebeest/Eland

Cattle/Grant's gazelle: Unusually, both overlaps are at their lowest in the wet season, but are both very high in the intermediate and dry seasons, although their vegetation type overlaps are low. The high overlaps between two such ubiquitous species (Table 7.2) are not surprising.

Wildebeest/Grant's gazelle: Their overlap on both measures is greater than 90% in the wet season, thereafter declining to very low values in the dry season. This drop is due to the concentration of the wildebeest in the dry season while the gazelle is consistently more dispersed (Table 7.2).

Zebra/Grant's gazelle: Both overlaps are highest in the wet season, and although at this time their spatial distributions overlap by 94%, their standing crop selection is essentially different (84% overlap).

Thomson's gazelle/Hartebeest: In all seasons the overlaps are low, probably because of the intolerance of the hartebeest for the shortest grass (Fig . 7.3) which the gazelle favours. Their spatial distributions are most distinct in the dry season.

Grants gazelle/Hartebeest: Both species tolerate a wide range of standing crop values and their overlaps are high on this measure in the wet and intermediate seasons, although they are geographically fairly separate. Both overlaps drop in the dry season because of the relative concentration of the hartebeest (Table 7.2).

7.15 The overlaps between the species of the park

Appendix 11 gives the 66 unique values for the seasonal overlaps between every combination of the 11 species in the park. Those species-pairs with overlaps of more than 0.800 have been extracted to form Table 7.11.

It is clear from Table 7.11 that the number of overlaps which exceed

0.800 is highest in the dry season and lowest in the wet season. If an overlap of at least 0.900 is taken to be of some biological consequence, there are 4 such species-pairs in the wet season, 6 in the medium, and 12 in the dry period. These overlaps are now considered by season.

Wet season.

Eland/Zebra and Eland/Hartebeest: Although only present in small numbers, eland occur in a wide range of vegetation types from open plains (Type 04), the A. drepanolobium ecotone (03) and in this dwarf tree grassland (06, 35). The zebra distribution is similar, while the hartebeest are predominantly in the short A. drepanolobium grassland (06, 35). Thus, eland overlap with both species, but the zebra and hartebeest distributions are less similar ($R_0 = 0.855$).

Grant's gazelle/Ostrich: Both species are ubiquitous (Table 7.6), and are found in most of the extensive types.

Waterbuck/Impala: Although both species have low diversities of vegetation utilisation (Table 7.6), they are at their highest in this season when both species move away from the valley bottoms, and are found together in types 02, 05 and 07.

Medium wet season

Wildebeest/Grant's gazelle, Wildebeest/Thomson's gazelle, Thomson's/Grant's gazelles: Unlike in the wet season, there are few wildebeest in the tree grassland types of 06 and 35, and they are concentrated on the very short grass type 01. The majority of both gazelle populations are also in this vegetation type in these months producing very high overlaps between the three species-pairs.

Hartebeest/Warthog, Grant's gazelle/Warthog: The warthog is relatively

widespread (Table 7.6), and is found in the fairly long grass of type 05. It, therefore, overlaps with Grant's gazelle (but with Thomson's to a much lesser extent), and with the hartebeest which is most abundant in vegetation type 05. Hartebeest and Grant's gazelle overlap less because of the greater selection of the gazelle for type 01.

Hartebeest/Zebra: Although their numbers are low, zebra overlap highly with hartebeest because of their occurrence in types 04 and 05, those most selected by the hartebeest.

Dry season

The 12 species-pairs with overlap values of 0.900 or greater are summarised in Table 7.11.

Wildebeest/Thomson's gazelle, Wildebeest/Warthog, Wildebeest/Ostrich, Thomson's gazelle/Warthog, Warthog/Ostrich, Wildebeest/Grant's gazelle.

The key species is the wildebeest because of its abundance in the open grasslands (types 01, 04), the valley bottoms (02), the bush grassland of the middle of the catena (05), the shortest A. drepanolobium grassland (35) and its ecotone (03) with the plains. This distribution causes the high overlaps with Thomson's gazelle, warthog and ostrich - species which frequent the open plains, rather than the steeper lower slopes. These patterns of occupancy also result in the high overlaps between Thomson's gazelle and warthog, and between warthog and ostrich. Thomson's gazelle and ostrich have a lower overlap because ostrich also use the A. drepanolobium types (06, 10, 35), which the gazelle scarcely does. Wildebeest have a very similar distribution to Grant's gazelle because the latter is ubiquitous, although most abundant in type 02.

Ostrich/Grant's gazelle: Although their utilisation of type 02 is very different, their distributions overlap highly because of their use of the A. drepanolobium types. Both species have high diversities of vegetation

type occupancy (Table 7.6).

Grant's gazelle/Hartebeest, Grant's gazelle/Zebra, Hartebeest/Zebra: These three species form a group because the bulk of their populations use the lower slopes of the catena in the dry season (type 02), producing high overlaps. These species also have the three highest vegetation type diversities of occupancy in these months (Table 6.6), being found together in most of the common vegetation types.

Impala/Eland, Waterbuck/Eland: These three species are restricted to the vegetation types of the lower slopes of the catena (02, 07, 08), although impala range further up the slope (01, 04, 05). Their diversities are appropriately low (Table 7.6), and this means that their overlaps with the group containing Grant's gazelle, hartebeest and zebra are all much lower.

The overlaps values found show clearly that the 11 species are most separated by their choice of vegetation in the wet season, while in the dry months the proportion of highly overlapping species increases and the magnitude of overlap also increases. In the dry season there are four main groups of species within which most high overlaps occur.

1. The short grass, open plains species (Thomson's gazelle, warthog, ostrich and wildebeest) usually selecting types 01, 03 and 04, although wildebeest also select the lower type 05 and ostrich the shortest A. drepanolobium grassland (35).
2. Grant's gazelle, zebra and hartebeest which have large numbers in the valley bottom types (05, 02) (Appendix 7), but like the last group's species they also select the Themeda ecotone (03) (Table 7.7).
3. Eland, impala and waterbuck which only use the lowest vegetation types of the sequence (types 02 and 07).
4. Giraffe alone because of their selection for type 10 with its dense A. drepanolobium (Table 7.7) in each season.

At this stage the following points can be made:

1. 10 out of the 11 species involved have very similar distributions in some season to at least one other species. The exception is the giraffe. Its selection for type 10 is the result of A. drepanolobium being its main food plant in the park (Wyatt 1969). Thus, its diet is very different from those of the other 10 species, which accounts for its low distributional overlap with them.
2. Although the calculated overlaps between the Grant's gazelle, zebra and hartebeest group and that of waterbuck, impala and eland are not high in the dry season, the majority of individuals of all 6 species are in type 02; although this is only part of the range of the species of the first group, it is almost the only type used by the second group. In functional terms this means that the eland, waterbuck and impala are being very highly overlapped by the other species, while overlapping them to only a slight extent.
3. Considering that the hartebeest has the highest mean monthly population among the 11 species (Table 7.4) of the study area, and it has fairly high vegetation diversities in each season (Table 7.6), it is remarkable that its distribution is rarely more than 90% similar to any other species. Even in the dry season, it has high overlaps only with zebra and Grant's gazelle.
4. Table 7.7 shows that through the year the number of occasions on which a vegetation type has been selected (c.g.i. > 100) by the animal species is far from constant. The bush grassland type 05 is by far the most highly selected. Floristically, the grass species of this type are a mixture of those of the open plains (type 04) which lie further up the slope and of type 02 which lies below, and its bush variety and cover is greater than the latter's (p. 58-59). It is thus an area of great heterogeneity which is selected by all the herbivores in at least one season of the year (Table 7.7). Part of its attraction for ostrich and warthog which are

rarely seen on steep ground, may be that the grass species characteristic of type 02 occur in an area where the gradient is slight compared to 02 itself. These features associated with ecotonal vegetation are common manifestations of the edge-effect (e.g. Odum 1959).

Types 03 and 35 are both ecotones between the A. drepanolobium grassland (06, 10) and the plains (01, 04), but selection for them is no greater than for several other types, although 35 is favoured by 7 species in the wet season, and 03 by 7 species in the dry months. Although type 03 is an edaphic ecotone between the Black Cotton and lateritic soils areas (p. 59), its vegetation of almost pure Themeda triandra is a distinct type rather than being intermediate, and distinguishes it from 05. The soil of 35 is superficially similar to that of 06 despite its surface brechia. Its vegetation composition is nonetheless very different and some of its species e.g. Digitaria macroblephara are characteristic of the plains. Thus type 05 is far more of a mixture between two contrasting types than either 03 or 05, resulting in its greater selection by the herbivores.

7.16 Discussion

Community diversity

The structures of the two communities and the differences in their diversities and species' behaviour raise important questions, such as why is the park community so much more diverse than any of the areas of comparable size in the plains which have been looked at? How is this diversity maintained through-out the year? Why do both communities, as defined here, contain 11 species? What can one say about the relationship between the species?

It is an ecological truism that varied environments contain more species than relatively simple ones (e.g. Simpson 1964), and this has been observed on the global scale from polar to tropical regions (e.g. Fischer 1960). The usual explanation for this phenomenon is that a varied environment provides more habitats, so that unless the species of an area are totally unselective at the level at which the habitats are distinguished,

a varied environment will support more species. MacArthur & MacArthur (1961) show that bird species diversity is correlated with the foliage height diversity of a variety of habitats.

The vegetation map of the Nairobi Park (Fig. 5.9) shows it to be more diverse than any of the 6 blocks (Figs. 5.2, 5.4 to 5.8), containing an unmatched variety of vegetation types or habitats. The reasons for this variety have been put forward (p.77), but it depends for the most part on the relatively steep topography producing well-differentiated vegetation types which are vertically zoned. The resulting variety was improved upon during the study period by the local occurrence of fire. As there are few fires in the plains (p.75) and the vegetation types cover relatively larger areas, the habitat diversity in the plains is lower, and there are fewer species per unit area.

The variety of vegetation in the plains obviously increases when all 6 blocks are taken together to represent the major vegetation zones of the plains. One might then expect the diversity of their animal community to be greater than that of the park because of the occurrence of the same 11 indigenous species found in the park and the exotic species of cattle, sheep and goats. For present purposes, sheep and goats are considered as one species because they are herded by the Masai in mixed flocks. However, warthog were never seen in the plains, and waterbuck accounted for only 2 out of more than 30,000 animals counted, so the plains community effectively also contains 11 species. Thus, in the comparison of the two communities, the species number component (Lloyd and Ghelardi 1964) is constant, and differences in diversity reflect differences in the evenness of the numbers of the species.

Without any knowledge of their biology or evidence of direct persecution, the absence of warthog and waterbuck from the plains might be explained, by saying that only 11 herbivore niches are available to be filled, rather than 13. Tables 7.5 and 7.6 might appear to confirm this because

it shows cattle and warthog to be similar in their high vegetation type diversities, while "shoats" and waterbuck have much lower diversities.

Waterbuck have a low vegetation type diversity in the park because of their heavy utilisation of the vegetation of the lower slopes (types 07, 08, 02). In the plains type 02 is hardly found because of the lesser development of the steep, red-soil lower valley slopes which support this Cymbopogon-Hyparrhenia grassland (p. 77). Although these particular grass species may not be essential, the main habitat requirement of the waterbuck is tall grass within a short distance of a river-course (Hanks, Stanley Price, Wrangham 1969, Kiley-Worthington 1965). Apart from being a dry season feeding and night-time area (Kiley-Worthington 1965) this grassland is used by female waterbuck to leave their offspring in during the day for the first 3 - 4 weeks of their life while the female moves further away to feed. This requirement for long grass can rarely be met in the Athi Plains because the riverine grasslands are much shorter and are those used heavily by "shoats". Watson (1972) used the river courses and a strip of 800 m on either side as a separate high density stratum in his aerial counts of the Athi Plains, and gives a density of 39.2 sheep and goats km^{-2} in this stratum and a density of 5.9 km^{-2} over the rest of the plains. As grazers and browsers, the impact of sheep and goats on the vegetation at these densities must be very great. Although there may be edaphic reasons for the shorter riverine vegetation in the plains, it would seem that the large numbers of "shoats" have effectively displaced the waterbuck by their severe modification of the latter's original habitat.

The same cannot be said of the apparent replacement of warthog by cattle, because the former is found in a large number of vegetation types in the park (Table 7.6) and tolerates standing crops up to 1600 kg/ha (Fig.7.4) Thomson's gazelle selects even shorter grass and thrives both in the park and the plains, so there is no suggestion that the grasslands of the plains are unsuitable on these grounds. The diversity of vegetation

types used by warthog for feeding suggests a broad habitat tolerance, but it also has one very specific habitat requirement, which is the necessity to use a burrow at night (Bradley 1971). In the Nairobi Park, the burrows are probably modified by warthog after being started by aardvarks (Orycteropus afer Pallas) for feeding purposes (Bradley 1971), so the warthog appears to be dependent upon the presence of this animal for its own survival. Aardvarks are nocturnal and secretive, and little is known of their biology. Whether they are absent from the Athi Plains, and if so why, is unknown, but there appear from personal observations to be few holes that might be suitable for warthog, and this may be the reason for their absence. Thus, the parallels between the addition of cattle to the community and the loss of warthog are probably no more than coincidental.

The plains community is characterised by the migratory habits of wildebeest and zebra. This is shown by the highly variable seasonal diversities of the 6 blocks (Table 7.1) and by the changing vegetation zone and type occupancies of these species (Appendices 5 and 8). The numbers of wildebeest and zebra within one zone or type fluctuate widely, producing low seasonality indices (Table 7.2). By comparison, the hartebeest has a rather higher seasonality index for vegetation zone occupancy but its index for vegetation type occupancy is very high indeed (Table 7.5). Its movements between zones is therefore, far less and is slight enough for the same vegetation types to be used through the year. The same picture resulted from the results of aerial censuses (p. 95).

The seasonal utilisation of different areas in the plains is characteristic of areas which are relatively unpredictable in climate and resources (Tramer 1969). The opposite situation occurs in the park where a higher rainfall (Fig. 4.4) and artificial water supplies (see below) remove some of this unpredictability, thereby supporting a community whose diversity varies little through the year. The herbivores of the park community are also more evenly divided between the species than in any of the plains

blocks or the whole plains blocks or the whole plains (Fig. 7.1). Again, a higher equitability (J) is characteristic of organisms like birds living in a stable environment, where J is increased by factors such as territoriality (Tramer loc. cit.). Community diversity in the park, and hence its evenness (because 11 species are always present) both drop in the dry season because of the immigration of wildebeest and zebra. Kricher (1972) noted a similar effect of immigrant feeding flocks of birds on the resident, breeding birds of an area.

The two main requirements of an animal are food and water, and it is perhaps these that the park is able to provide so continuously. The water resources of the park have been increased considerably by the construction of dams, and the study area alone contained three. The importance of these dams is discussed in Chapter 14, but even in a normal dry season they contained 99% of the water available to the herbivores. The presence of permanent water has, therefore, almost certainly helped the same community of water-dependent species to occupy the park through the year.

Although the park community is more diverse and for the most part composed of populations which are resident through the year, this measure of diversity takes no account of the parameter of biomass. The following table gives the mean biomass densities for each block and for the park study area.

The biomasses are calculated from the data given in Appendix 5 and the species weights used are given in Appendix 2.

Block	Mean biomass density (kg/km ²)	
15	25	745
22	20	374
30	13	982
35	14	551
39	26	436
62	8	105
Nairobi	6	476 n = 8
Nairobi	11	584 n = 12

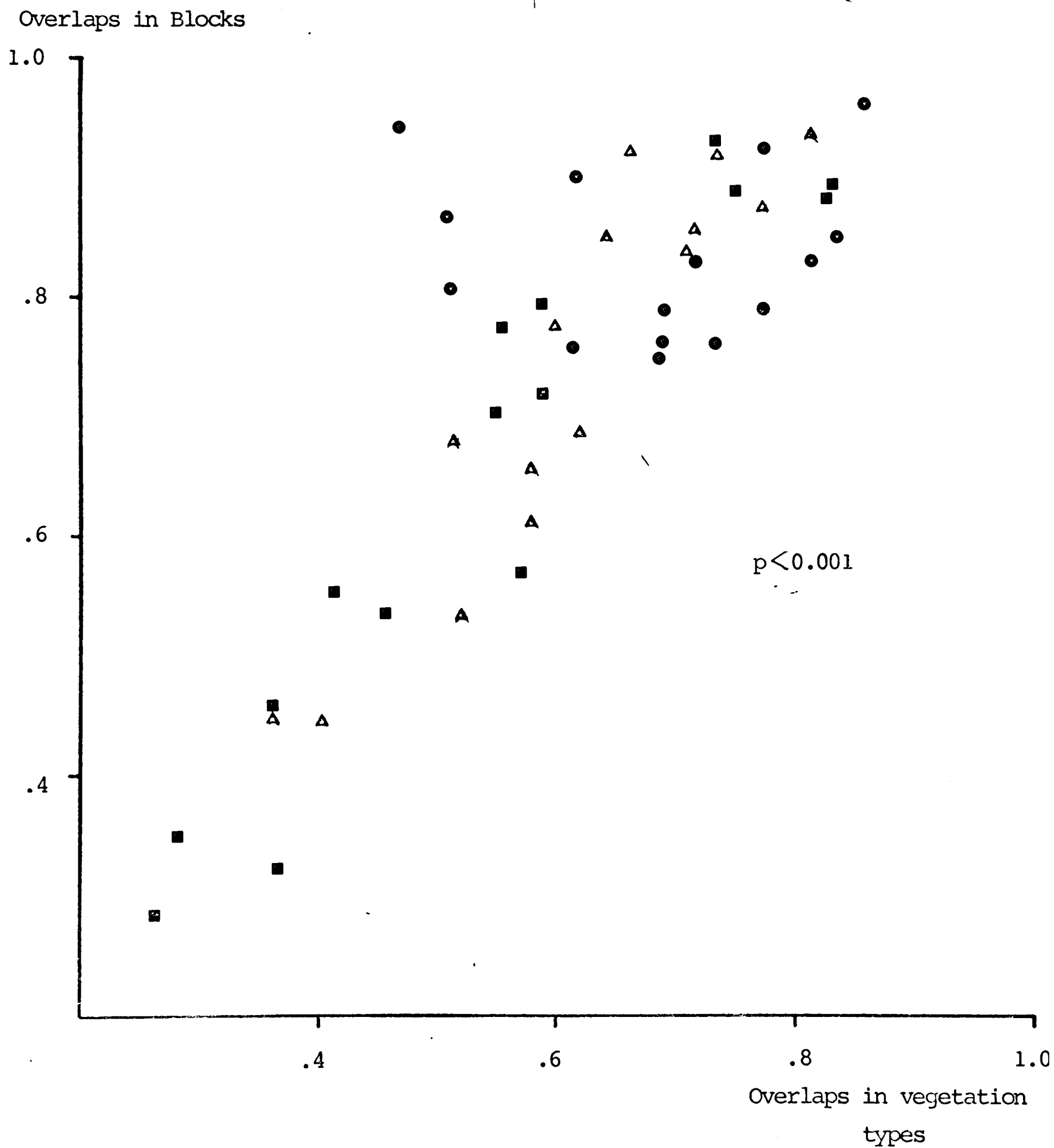


Fig.7.6. The overlaps in distribution of 15 species-pairs between Blocks and between vegetation types in 3 seasons.

● wet, △ medium-wet, ■ dry season.

The figure of 11 584 kg/km² for the park includes the months of unusual wildebeest immigration in late 1972. When 4 months are excluded to represent the normal situation, the biomass density is less than 7,000 kg/km². Even if the higher figure is used, the mean biomass density of all the blocks except 62, is greater than the park's. It appears, though, that although the park has a diverse, resident community with a high evenness, it has a lower biomass density than the plains community which shows less diversity and evenness and contains migratory species. It should be added though, that the bulk of the plains biomass is comprised of cattle. As their present numbers (p. 88) are considerably higher than those of ten years ago (Prole 1967), and there are obvious signs of gully erosion, it is possible that the sustainable carrying-capacity of the plains has been exceeded. As there is nothing to suggest that this state of affairs applies to the park, the comparison of the two biomass densities may not be strictly fair. On the other hand it is unlikely that the biomass exceeds the carrying capacity by as much as the differences between the biomass densities of the park and the 6 blocks.

Species overlaps and diets

Earlier sections of this chapter have shown that the herbivore species of the ecological unit differ in such parameters as their mobility, their tolerance of vegetation types and of the range of grass biomasses encountered. However, these differences are not always sufficient to prevent large overlaps between species' distributions. Under these circumstances, ecological separat^{-ion} may depend upon adequate differences in the diets of the overlapping species, and the remainder of this discussion is devoted to the probable trophic relationships of these species whose distributions are highly coincident.

In the Athi Plains the mean overlap in distribution between 15 species pairs is highest in the wet season, with a range of lower and more dispersed values in the intermediate season (Fig. 7.6). In the dry season

Fig.7.7.Nairobi Park, Dry season, The distribution of 11 herbivore species, their spatial overlaps of at least 0.900, and their diets.

DISTRIBUTION	SPECIES & OVERLAPS 0.900	DIET	REFERENCE
Upper slopes bush areas	Giraffe	Tree browse	Wyatt 1969
Upper slopes short grass plains	Warthog	Grass & roots etc	Field 1970
	Thomson's gazelle	Dicots > grass	Stewart & Stewart 1970, 1971.
	Ostrich	Dicots & grass seed heads	Hurxthal pers. comm.1974
	Wildebeest	Grass	Gwynne & Bell 1968, Stewart & Stewart 1970, 1971.
Lower slopes and dispersed	Grant's gazelle	Dicots>> grass	Stewart & Stewart 1970, 1971
	Hartebeest	Grass	Stewart & Stewart 1970, 1971, This study
	Zebra	Grass	Gwynne & Bell 1968, Casebeer & Koss 1970.
Lower slopes only	Impala	Dicots & grass	Azayedo & Agnew 1968 Ables & Ables 1969.
	Eland	Dicots>> grass	Stewart & Stewart 1970 Wilson 1969
	Waterbuck	Grass>dicots	Kiley 1966, Hanks, Stanley Price & Wrangham 1969.

the overlaps fall in to three distinct groups of very high, medium or very low. On the other hand, in the resident community of the park, the number of high overlaps ($R_o > 0.900$) builds up from the rains to a peak in the dry season. An increase in overlap might be expected in an area where animals concentrate in the dry season (e.g. Lamprey 1964), and Bell (1970) showed that the associations between topi (Damaliscus korrigum) and 6 other species reached peak values in the late wet season and at the end of the dry season. In the Serengeti also, buffalo and wildebeest are most associated in the dry season (Sinclair 1970). To make the differences more striking, I shall only discuss the overlaps of the wet and dry seasons.

The park

In the wet season there are only 4 species-pairs with overlaps of more than 90% (Table 7.11). Eland feed most on grass at this time of year, and overlap with two species, hartebeest and zebra, which graze almost exclusively (Stewart and Stewart 1971) without a high mutual overlap. Impala and waterbuck also both graze predominantly in this season (Agnew and Azavedo 1968, Ables and Ables 1969, Kiley 1966), although dicotyledons are taken by both species. Grant's gazelle and ostrich overlap highly, and as the former grazes most in this season (Stewart and Stewart 1971), while the ostrich diet consists almost entirely of non-woody browse (Muxthal pers. comm. 1974), their diets probably overlap little. However, the grass biomass is greatest in these months so that food is likely to be super-abundant. If this is the case, then the overlap between these species which, except for the ostrich, are predominantly grazing in the wet season may be of little consequence in terms of competition for food.

Diet separation between species is more crucial for survival in the dry season when the herbage biomass is reduced and growth has ceased, the herbivore biomass is greater and the animals are relatively concentrated, as the large number of high R_o values shows (Table 7.11). Fig.7.7 contains the information immediately pertinent to the problem of ecological

separation between the 11 species in the dry season. After the species' name, the second column describes its distribution in terms of the 4 locations distinguished on p.134. The next column shows with which species there are overlaps of at least 0.900 in the dry season. Most of the information in the "Diet" column is taken from the review of Hofmann and Stewart (1972). Ostrich, zebra, giraffe and warthog are not included in this work, but I have classified their feeding habits on the same criteria with information from the sources quoted in the table. If information on a species' diet is confirmed by several sources, the reference(s) shown in the "Diet" column are those with information from as near to Nairobi, or from as similar a habitat, as possible.

Of the 12 species pairs with overlaps of at least 0.900, there are 5 which clearly contain one grazing species and one which browses to some extent - Thomson's gazelle/wildebeest, Grant's gazelle/hartebeest, Grant's gazelle/wildebeest, Grant's gazelle/zebra, Ostrich/wildebeest. These gross differences probably cause a sufficiently large separation to allow co-existence.

Warthog have high overlaps with wildebeest, Thomson's gazelle and ostrich. Warthog and wildebeest are both exclusively grazers of short grass, but the pig has a feeding technique which perhaps enables it to use a food resource that is untapped by any other species. This is its ability to use its snout to collect the tiller bases of grasses (Field 1970) and underground grass shoots (Bradley 1968). These probably act as a food refuge for the warthog, helping it to survive in areas with large numbers of short grass grazers such as wildebeest. With this behaviour, it is unlikely that the warthog diet overlaps to a large extent with those of either wildebeest or Thomson's gazelle, or ostrich which mostly browse.

All but one of the remaining pairs consist of 2 species which are known to both browse and graze. As in the wet season, the ostrich and Grant's gazelle distributions overlap highly. Although the gazelle

tolerates longer grassland (Fig . 7.4) and is found on the lower slopes by selecting types 02 and 05 (Table 7.7), both species are predominantly browsers in this season. However, the ability of the ostrich to use its bill to strip off the seed heads from grass culms (Hurxthal , pers. comm. 1974), would ensure some dietary separation.

The gorges with their rich variety of browse serve as a dry season refuge for eland (Hillman pers. comm. 1974) and probably for no other species. It overlaps with impala and waterbuck may be inflated if only eland uses the gorges in this season.

The only remaining species-pairs with a high overlap is that of zebra and hartebeest. At the level of food habit description of Fig.7.7, these species show the greatest coincidence of distribution (Table 7.11) with least grounds for distinguishing them on their gross diets at the time of year when food is shortest. If food were limiting, then these species might be competing. I therefore, conclude that in this study area the ecological separation between zebra and hartebeest is less than between any other species. This relationship is examined in more detail in Ch. 8.

It is also instructive to see which species have similar diets but are spatially separate, thereby achieving ecological separation. Of the common species, hartebeest and wildebeest are numerically dominant for most of the year and graze exclusively. If both species grazed together in the dry season, competition might occur. As it is, they are separated by their selection of vegetation types of differing grass biomasses. In these months both gazelle species select the same vegetation types (01, 02, 03, 04, 05) but the overlap between their distributions is only 0.871 because Grant's gazelle selects the ecotones 03 and 05 most, while Thomson's gazelle favours types 01 and 04 most. This reflects the former's tolerance of longer grass (Fig.7.4) which achieves a measure of spatial separation at a time when the diets of both contain large amounts of dicotyledonous material (Fig.7.7).

The diet of Thomson's gazelle consists mostly of dicotyledon material in the dry season, but its overlap with the ostrich is only 0.884, although both select types 01, 03 and 04. The ostrich which is relatively water-independent (Western 1973) also selects type 35 while the gazelle moves further down the slope to favour types 05 and 02 whose grass retains slightly more moisture (Appendix 15). Therefore, although both species select short grass areas, the problem of dietary overlap may be avoided because these areas are not always the same ones.

The plains

For the reasons given on p.108, overlaps in the plains have been calculated for both coincidence of spatial distribution and for the selected standing crop values. The data on diets in Fig. 7.7 are assumed to be equally applicable to the same species in the park or the plains. Comparable data for cattle show them to be almost exclusively grazers (Casebeer and Koss 1970, McKay 1971).

In the wet month of June, there are 11 species-pairs out of the 15 combinations of "important" species in this community with overlap values of at least 0.900 for either their distribution between blocks or between standing crop values or both. Table 7.10 shows that of these 11 pairs, both species of 5 pairs are exclusively grazers: cattle/wildebeest. The remaining 2 pairs of the 7 with low area overlaps ($R_o < 0.900$), contain one grazer and one species which grazes and browses: cattle/Thomson's gazelle and Grant's gazelle/hartebeest. However, at this season the two gazelles are taking grass mostly (Stewart and Stewart 1970). Thus the species with the same type of diet are selecting grassland of similar grass weight but in different places.

There are 4 species pairs with high spatial overlaps only (Table 7.10). One pair, zebra/Grant has a low standing crop overlap, meaning that within the same block the two species are selecting areas of different grass

volume, hence different vegetation types. The three remaining pairs have high overlaps for both factors, but it is notable that the grazing wildebeest overlaps highly with both gazelles which also browse to some extent, although minimally at this time of the year. Thus, diet separation would appear possible even if food were not superabundant. Moreover, wildebeest and Thomson's gazelle have a facilitatory relationship in some areas (Bell 1969). Hartebeest/cattle is the only combination to contain two exclusively grazing species, and they also have the highest spatial overlap and grass biomass overlap of any species pair in all three seasons.

In the wet season food and standing water are most abundant, and the herbivores are probably distributed in relatively optimal feeding areas. "Optimal" here includes a variety of factors such as the structure, volume and food value of the sward and the presence or absence of other species, with their multiple effects on the sward. In this situation, I conclude that the areas selected by cattle and hartebeest are more nearly identical than those selected by any other pair of species at this season.

The number of species-pairs with overlaps of more than 0.900 is smaller in the dry month. Only cattle and Grant's gazelle have coincident distributions and selection for the same standing crop values. The gazelle's diet consists almost entirely of dicotyledonous material in the dry season (Stewart and Stewart 1971), thereby distinguishing it from cattle. Four more pairs show selection for the same grass biomasses, but their spatial distributions are less similar. This ensures the separation of 3 pairs of grazers (wildebeest/zebra, wildebeest/hartebeest, and cattle/hartebeest) and one pair of grazer-browsers (Thomson's and Grant's gazelles). The diets of both members of each pair are very similar on the gross classification used here. If their distributions had been more similar, a situation of competition or potential competition might have arisen.

The overlaps between cattle and hartebeest are particularly interesting.

Although their distributions between the 6 blocks are very different ($R_0 = 0.720$), their standing crop overlap is very high ($R_0 = 0.945$). The latter is again higher than for any other pair in this season, which reinforces the conclusion made about these species for the wet season. Their spatial separation in the dry month shows that their distributions are then largely determined by different factors. But within the constraints imposed by these factors, their selection for grass biomass remains nearly identical. Thus, in this community the potential for competition is greatest between these species, or alternatively, cattle and hartebeest approach being ecologically equivalent. The consequences and implications of this relationship are returned to frequently in the chapters which follow on the ecology of the hartebeest.

Chapter 8.

FOOD SELECTION AND THE DIET OF THE HARTEBEEST

8.1 Introduction

Analysis of the large herbivore community of the Athi Plains showed the hartebeest as a grazing species occupying a wide variety of vegetation types. Although it does not show marked population movements, its distribution is highly coincident in some seasons with those of other species, notably cattle and zebra. Under these circumstances, ecological separation depends on dietary differences, even though in practice the extent of the difference needed to avoid competition may be difficult to measure. In this chapter, the diet of the hartebeest is described first in terms of its composition relative to that on offer through the seasons. This, and other information, is then used to compare the hartebeest's diet with those of cattle and zebra.

The diet of the hartebeest population was studied by examination of the rumen contents, a method chosen because animals could be collected, while other methods were not feasible. The direct observation of animals which may furnish quantitative data on animals which browse above the herb layer (e.g. Wyatt 1969, Leuthold 1968, 1970) was not practical, even though the hartebeest could be approached, undisturbed, to within 30 m in the Nairobi Park. Difficulties arose through their grazing in medium-length grass (p.126), and even if the feeding site could be located precisely, identification of the food plants often involved displacing the animal. If feeding was subsequently resumed, it was in a different place, rarely less than 50 m from the previous site, making impossible any continuous quantified recording of the food plants eaten. Moreover, identification of food plants by an observer even only 30 m from the grazing animal is subject to biases (Wallmo et al 1973). Some of these problems can be overcome by using tame animals with or without oesophageal or ruminal

fistulas, but no such animals were available. The method of searching for the grazed species in the sward (van Zyl 1969) is unsatisfactory when the area is used simultaneously by several species of herbivore, as is the Nairobi Park.

Faecal analysis techniques share with observation the advantage that the animals are relatively undisturbed and the same individual can provide information over a period of time or in different places. But, feeding and defaecation may be widely separated in time and space, and because of the mixing and slow passage of food through the ruminant digestive tract (Campling, Freer and Balch 1961), it may be difficult to compare faecal composition with what was on offer in the actual feeding area. Moreover, although most grasses which form more than 3% of oesophageal-fistula samples are recorded in the faeces (Stewart 1970b), the proportions in the diet may be seriously modified as the food particles pass down the gut. Feeding experiments followed by faecal analysis (Stewart 1967) revealed, first, that grasses differ in the degree to which they fragment in the herbivore gut and, second, that the degree of fragmentation of a single grass may vary with the herbivore species eating it. The small size of faecal particles means that species frequencies determined by this method are usually based on sightings of leaf epidermis only (e.g. Stewart et. al. 1971, but cf. Casebeer and Koss 1970).

Analysis of stomach contents overcomes some of these problems. As the samples are taken from higher up the digestive tract, the diet composition is less affected by differential digestion, and the particles are larger. This facilitates identification of each particle in to its species and the part of the plant (see below). The main disadvantage of the method is that animals have to be shot unless material from individuals found dead is used, which may introduce biases. In either case the sample refers only to a short period of time and cannot be repeated on the same animal.

The rumen material was analysed for the parts of the plants it contained, rather than for its species composition. Ideally, the material would be analysed for both, but the parts analysis was chosen for the following reasons:

1. Although plant species differ in their chemical composition, the leaf, sheath and stem fractions of grasses differ in their protein and carbohydrate contents (Appendix 12) and also have characteristic digestibilities (Terry and Tilley 1964). The reported differences in quality between grass species as food may only reflect differences in the proportions of leaf, sheath and stem (Lambourne and Reardon 1962). If the same parts from different species show similar digestibilities, the development of a method for calculating the extent of differential break-down in the rumen, the main site of digestion (Goodall and Kay 1965), might be practical for each of a few classes of particle rather than for each species.
2. A small number of studies have been made in East Africa on the diets of co-occurring herbivore species. Where the plant species eaten have been identified, they may be eaten by several herbivore species (e.g. Stewart and Stewart 1970, Field and Blankenship 1973). This may be due, in part, to the fact that such analyses are based usually only on the leaf epidermis of grasses. On the other hand, considerable separation between species may be apparent if the diets are analysed for their plant parts (Gwynne and Bell 1968). This suggests that the structure of the sward may be more important in determining what is eaten than its species content per se.

A parts analysis, therefore, increased the chances of developing a method of correcting the rumen proportions for the effect of differential digestion on the original proportions of the diet, and of estimating the intake of nutrients at different seasons (Ch. 9). Moreover, the results of this analysis could be interpreted in conjunction with those of other studies on the plant species eaten by the hartebeest and other herbivores in or near the Athi Plains.

8.2 Methods

Materials. Three hartebeest consisting of an adult male, an adult female and an immature animal, were shot in each month between November 1970 and September 1971, although the immature was not collected in some months. This régime was designed to monitor seasonal changes in the animals from small samples taken at frequent intervals. These animals (Series 1) (Fig.3.1) had to be taken east of the Athi River to Kajiado road/in Kenya Hunting Block 68, although the density of hartebeest was low here (p.90). Thus, animals were collected over a large area of suboptimal habitat. To overcome these limitations, permission was granted in 1972 to collect 32 animals from an area SW of Senya where hartebeest were abundant under almost all conditions. To supplement the Series 1 results with larger samples, 8 animals were shot on each of 4 occasions at 2 - 3 month intervals between January and September 1972. Each sample consisted of 3 adult males, 3 adult females and 2 immatures. All 32 animals were shot in an area of 50 km².

To collect samples of rumen digesta, the abdominal cavity of a freshly-killed animal was opened, and the intact reticulo-rumen, omasum and abomasum with the spleen were freed by severing their attachments to the body wall. The entire stomach was rolled out on to a rubber mat at the side of the carcass, where the oesophagus was cut at the cardiac sphincter, and the omasum and abomasum were separated from the reticulo-rumen. The latter is subsequently called the rumen. The spleen and any attached muscle were removed.

The intact rumen was kneaded vigourously to mix its contents before being weighed. The rumen contents were then tipped out on to the mat, and a sample taken immediately from the surface and weighed for estimation of the dry matter fraction. The total weight of digesta was obtained by difference after weighing the empty rumen.

For analysis, approximately four large grab samples were taken randomly

from the surface of the digesta. These were bulked and thoroughly mixed, and then spread in to a circle about 5 cm deep. The circle was divided in to quarters, and a smaller grab sample was taken from each quarter. The total sample of about 250 cc was preserved in 10% formalin to await analysis.

Analysis. The analysis of the samples was performed by Dr. M.D. Gwynne, using the methods of Gwynne and Bell (1968). The sample to be analysed is prepared in the following way: about 40 g is washed with acetic acid to clear the mucus from the particles, and then rinsed in water and drained. The sample is evenly spread across an enamel tray and enough water added to support a perspex sheet overlay without air bubbles being trapped underneath. The overlay is inscribed with fine intersecting lines giving a 11 x 11 cm grid of 1 cm^2 cells, and therefore contains 100 line intersections. A binocular microscope is used to identify the plant part immediately underneath each intersection. The percentage frequencies obtained in this way are closely related to the dry weight of the proportions in the rumen (Gwynne and Bell loc. cit.).

Dicotyledon material was identified as leaf, stem, flower, fruit, seed, bark, wood or root, while grass material was classified as leaf (the blade as far as the ligule), sheath (from the ligule to the node below), stem and seed (including all inflorescence components). Grass was classified as sheath only if free of any stem.

Each determination was carried out with the analyst not knowing the code number of the sample or its date of collection. A random selection of 7 samples was re-analysed after a few days, to check the consistency of observation. The extremely close agreement with the results of the first analysis obviated the need to repeat determinations on all the samples (see below).

Table 8.1. The percentages of plant components in the Series I hartebeest rumens, with the duplicate results for nos. 4, 7, 17, 26, 34.

Sex: M = male, F = female. Age class: A = adult, I = immature.

Month	Number	Sex	Age class	Leaf	Sheath	Percentage stem	Inflorescence	Dicotyledon
Nov. 1970 Dec.	1	M	A	9	52	39	0	0
	2	F	A	40	26	34	0	0
	4		A	18	46	36	0	0
Jan. 1971	5	F	I	18	45	37	0	0
	7	F	A	22	46	32	0	0
	9	M	A	17	61	22	0	0
Feb.	10	F	A	17	59	24	0	0
	11	M	I	9	56	34	0	1
	12	M	A	14	52	32	1	1
April	17	M	A	4	46	50	0	0
	18	F	I	16	47	37	0	0
	19	F	A	17	44	39	0	0
May	20	M	I	26	50	23	0	0
	21	F	A	18	42	40	0	0
	22	M	A	64	21	15	0	0
June	23	M	A	32	36	31	1	0
	26	M	I	31	54	15	0	0
	27	M	A	39	55	5	1	0
July	28	F	A	38	49	12	1	0
	29	F	I	39	48	13	0	0
	30	M	A	43	38	19	0	0
Aug.	31	F	A	45	37	18	0	0
	34	M	A	40	47	12	0	1
	35	F	A	18	39	43	0	0
Oct.				33	42	25	0	0
				21	48	31	0	0
				25	50	25	0	0

Vegetation Sampling. On the last day of each collection of hartebeest in 1972 (Series 2), grass samples were clipped to measure the sward composition. The sampling procedure was that described on p. 19 .

Quadrats were clipped in vegetation type 15, the most extensive vegetation in the collecting area, which ground counts showed to be used by large numbers of hartebeest (Appendix 8). However, on the first collection, in January 1972, the vegetation samples were taken not from type 15 (Vegetation Zone VII), but at the west end of vegetation zone IVb (Fig. 5.1).

Rainfall. The Series 1 animals were shot over a wide area, for which the monthly rainfall is calculated as the mean of that at Stony Athi, Kenplains, Senya, Konza, Kajiado, (Fig. 4.3), although figures for rainfall before October 1970 are available only from Stony Athi, Konza and Kajiado. All the Series 2 animals were taken within 10 km of the rain gauge of Block 39, whose data is therefore used. The monthly rainfall totals are included in Appendix 3 , and are used as effective rainfall (P/E_t) calculated cumulatively for the months preceding sampling (p. 22).

8.3 Results

Series 1 rumen contents

The proportions of the plant components in the rumens of the Series 1 animals are shown in Table 8.1. The 5 duplicated determinations show very consistent results. The dietary proportions could not be calculated by the method of Appendix 12 because sward samples were not cut at the same time. The mean percentages of leaf, sheath and stem are plotted by month in Fig. 8.1 with the rainfall of that month.

Table 8.1 shows that through the year the occurrence of dicotyledonous material as opposed to grass, was so low as to be insignificant.

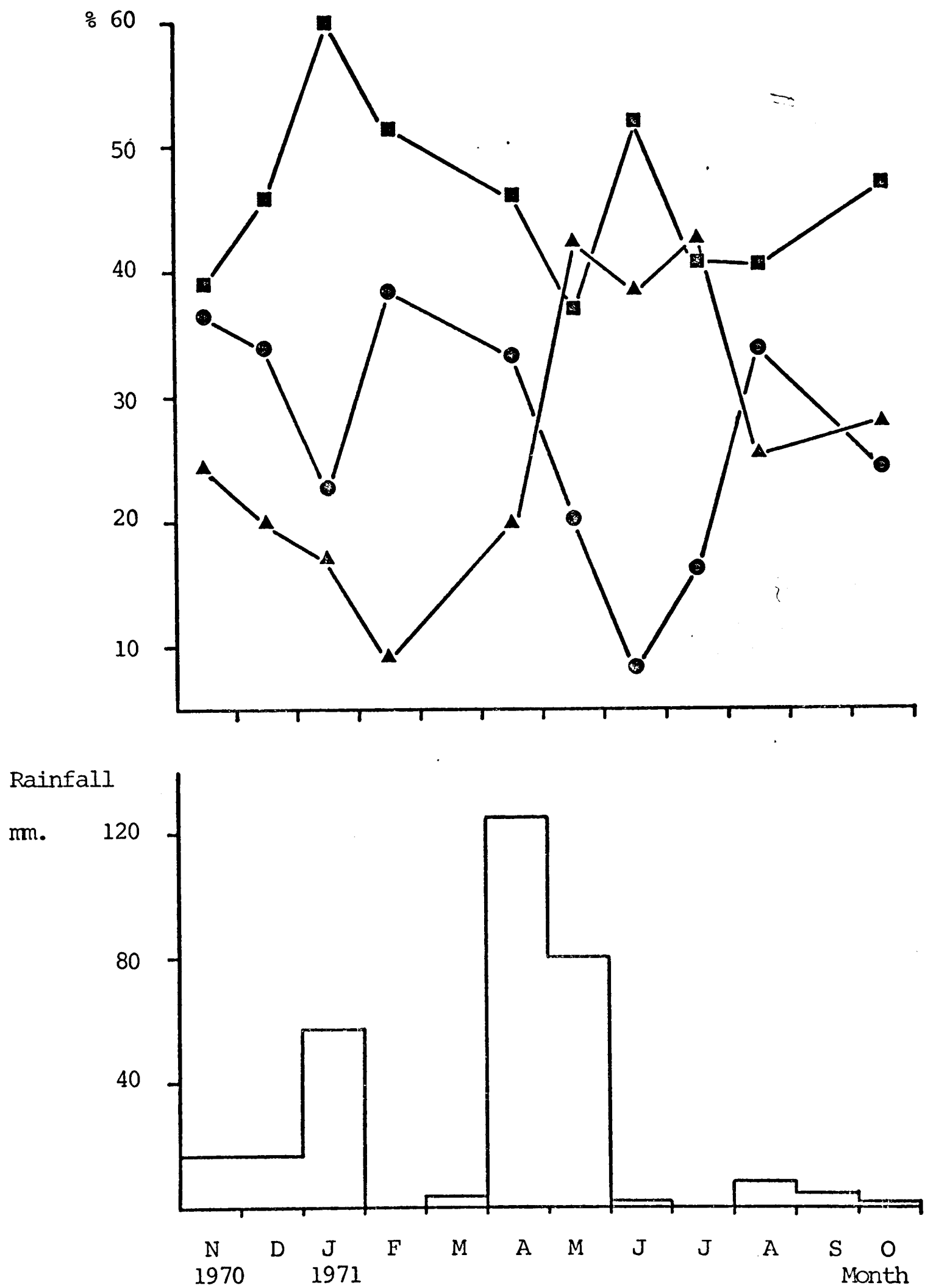


Fig.8.1. The mean proportions of grass components in the rumens of the Series I hartebeest, with the monthly rainfall.
leaf ▲ , sheath ■ , stem ● .

These hartebeest were, therefore, exclusively grazers. Within the grass categories, inflorescences with or without attached stems were rarely found, although they occurred once in both animals in June. This fraction has been combined with that of stem in Fig. 8.1.

In all months except May and July, sheath was predominant in the rumen with a mean of 45.6 out of 100 particles. Within each month it generally showed less variation in its proportion than either leaf or stem. The proportion of leaf reached its minimum mean value of 9% in February, and its maximum of 42% in May and July. The amount of stem in the rumen follows an approximate inverse relationship to the amount of leaf, with a mean maximum of 38.7% in February and a minimum of 8.5% in June. Fig. 8.1 shows that these differences are related to the local rainfall during the same period. The long rains of December 1971 - January 1972 were late and small, and their only apparent effect on the rumen proportions was to increase ^{the amount} of sheath at the expense of stem. The heavier and more prolonged rain of April and May produced greater changes in the rumen contents. The leaf proportion at the end of May was more than double that of April, and this was maintained for a further two months, although June and July were effectively rainless. At the beginning of these rains the proportions of sheath and stem both dropped (May) but the further decrease in the stem fraction in June was matched by an increase in sheath rather than leaf. By the end of July the stem fraction had increased again, but at the expense of sheath, so that the high leaf proportions were maintained. In these months the differences between individuals were slight (Table 8.1).

The amount and distribution of rain clearly affects the nature of the observed changes in the rumen proportions. The rain falling in January 1971 only slowed down the decline in the leaf proportion between November and February. The proportion of stem dropped considerably as that of sheath increased, but this trend was reversed by the end of February.

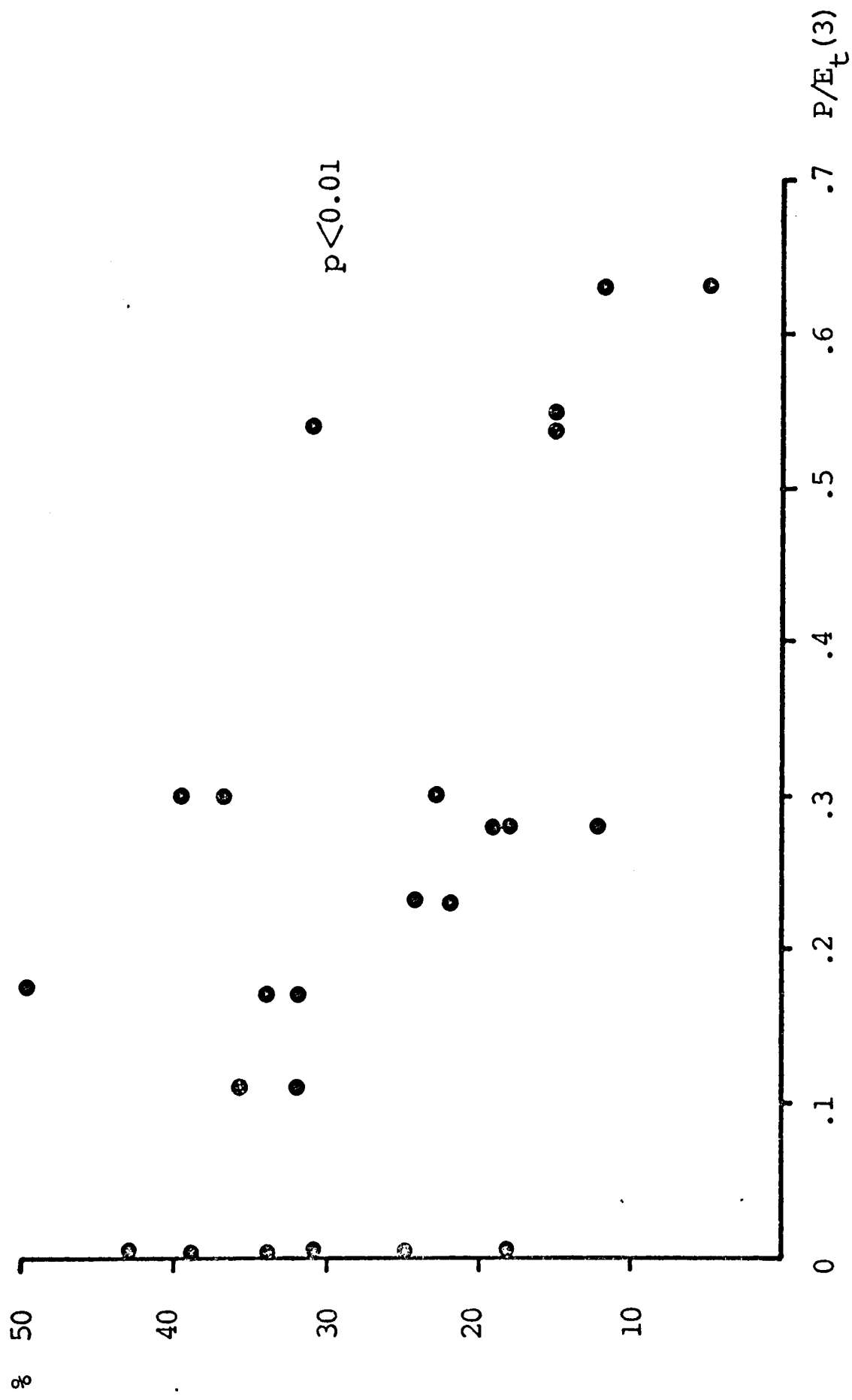


Fig.8.2. Series I hartebeest: the percentage of stem in the rumen and the effective rainfall over the previous 3 months, $P/E_t(3)$.

The higher rainfall of April and May depressed the stem fraction for 3 months, an effect which lasted well in to the subsequent dry season. The reduction in stem and slight increase in sheath in October compared to August is qualitatively similar to the January situation although Fig. 8.1 shows September and October as rainless. During this dry season, however, it was only possible to collect two animals in October because a few hartebeest were attracted to an area of fresh grass in the Kapiti Plains where an isolated shower had fallen. This was too local to be recorded at any of the rain stations. In this area the grass was green and the new growth of grass probably caused the depression of the stem fraction.

The effect of rainfall on the observed composition of the rumen contents was examined by correlating the percentages, first, of leaf and then stem against the effective rainfall (P/E_t) over different number of months, with the following results :

No. of months		correlation coefficients and significance		
rainfall (P/E_t)	% leaf	p.	% stem	p.
1	.070	n.s.	.020	n.s.
2	.251	n.s.	- .209	n.s.
3	.481	<.05	- .597	<.01
4	.577	<.01	- .584	<.01
5	.503	<.01	- .403	<.05

These show that the most prompt effect of high rainfall is in the reduction of the amount of stem in the rumen, rather than an increase of leaf. The stem proportion is most significantly inversely correlated with the rainfall over the previous 3 months (Fig. 8.2). The lesser correlation of the leaf proportion is due to the changing proportion of sheath which varies with rainfall in a less consistent pattern (Fig. 8.1).

Table 8.2

The percentages of plant components in the Series II hartebeest rumens, with the duplicate results for Nos. 48, 65.

Sex: M = male, F = female.

Age class: A = adult, I = immature.

Percentage

Month	Number	Sex	Age class	Leaf	Sheath	Stem	Inflorescence	Dicotyledon
January 1972.	40	F	A	31	30	29	0	0
	41	F	I	35	34	29	2	0
	42	F	A	53	34	13	0	0
	43	M	A	25	40	35	0	0
	44	F	A	31	48	21	0	0
	45	M	A	26	42	32	0	0
	46	M	A	28	35	37	0	0
	47	F	I	44	43	12	1	0
	48	F	A	45	36	17	2	0
				43	38	18	1	0
April	49	M	A	40	38	21	1	0
	50	F	A	32	48	20	0	0
	51	M	A	40	35	24	0	1
	52	M	A	37	46	17	0	0
	53	F	A	46	37	17	0	0
	54	F	I	48	26	26	0	0
	55	F	I	38	31	31	0	0
	56	F	A	49	32	19	0	0
	57	F	A	45	37	18	0	0
	58	F	I	50	35	15	0	0
July	59	M	A	26	40	34	0	0
	60	M	A	25	43	32	0	0
	61	M	I	33	45	22	0	0
	62	F	A	32	41	27	0	0
	63	M	A	41	42	17	0	0
	64	M	A	37	36	27	0	0
	65	M	A	17	31	52	0	0
	66	M	A	18	28	54	0	0
	67	F	A	22	50	28	0	0
	68	F	A	12	41	47	0	0
September	69	F	A	9	37	54	0	0
	70	F	A	23	28	49	0	0
	71	M	I	18	32	58	0	0
					42	40		

Table 8 - 3. The mean percentages and 95% confidence limits of grass parts in the rumen and the diet, and the percentage of parts in the sward.

Month	Part	% in rumen	±	95% conf. limits	% in diet	95% conf. limits	% in sward
January	Leaf	34.1	8.2	25.9-42.3	44.3	36.0-52.4	29.0
	Sheath	38.3	4.8	33.5-43.1	38.5	33.7-43.3	14.7
	Stem	27.7	7.9	19.8-35.6	17.2	9.4-25.2	56.3
April	Leaf	40.8	4.6	36.2-45.4	67.4	62.8-72.0	44.1
	Sheath	37.1	5.2	31.9-42.3	21.0	15.8-26.2	34.2
	Stem	22.0	2.9	19.1-24.9	11.5	8.6-14.4	21.7
July	Leaf	37.6	9.6	28.0-47.2	63.3	53.7-72.9	42.9
	Sheath	39.4	2.9	36.5-42.3	14.6	11.7-17.5	23.5
	Stem	23.0	7.6	15.4-30.6	22.1	14.5-29.7	33.6
September	Leaf	18.5	10.5	8.0-29.0	21.2	10.7-31.7	18.0
	Sheath	37.1	4.8	32.3-41.9	33.9	29.1-38.7	28.1
	Stem	44.4	10.6	33.8-55.0	44.9	34.3-55.5	53.9

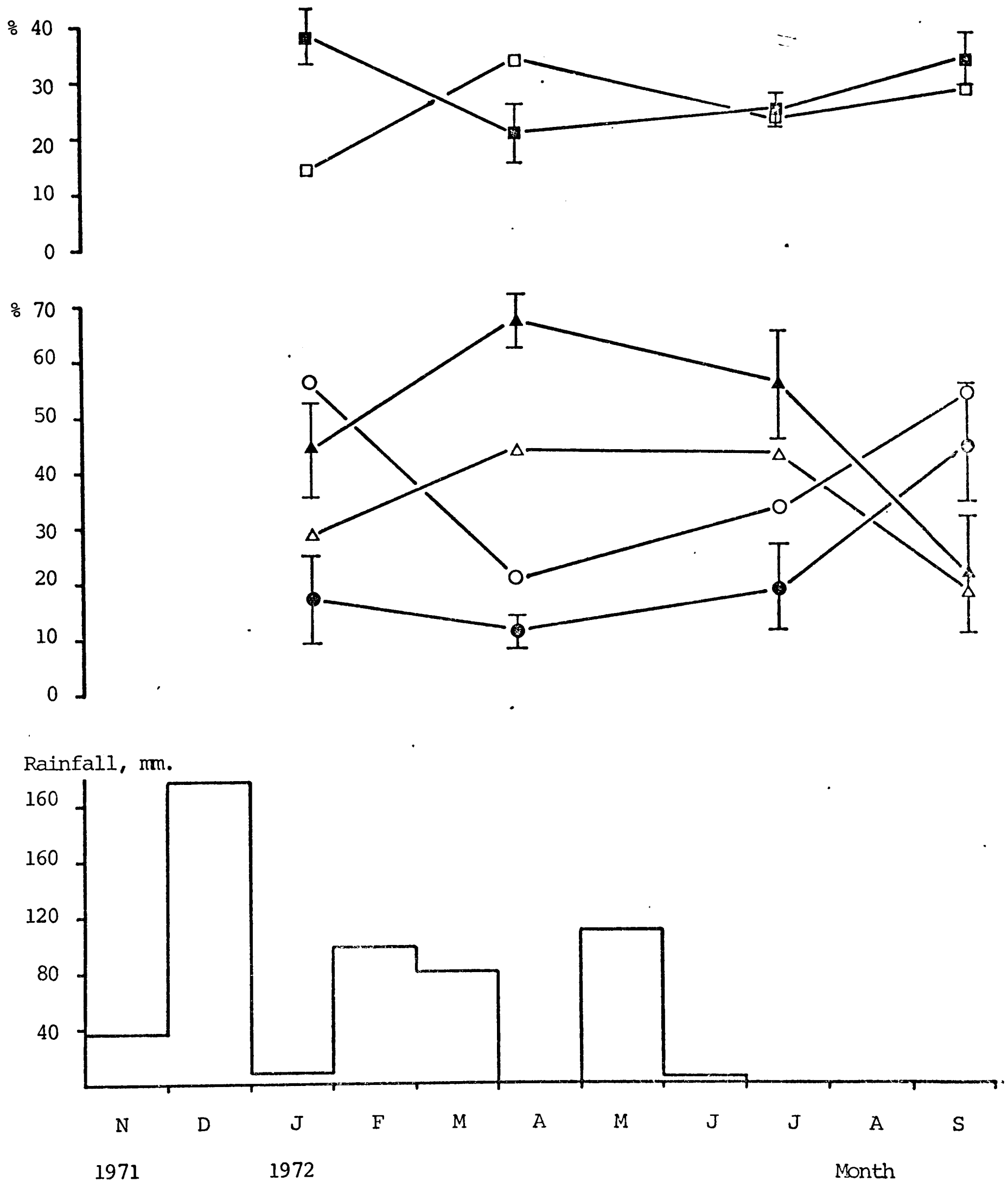


Fig.8.3. Series II hartebeest: the mean percentages of grass components in the diet and the sward, with the monthly rainfall.

	leaf	sheath	stem
sward	△	□	○
diet	▲	■	●

Series 2 rumen contents and diets

The results of the rumen analyses of the 32 hartebeest collected in 1972 are shown in Table 8.2. The frequencies of these parts have been corrected to those at intake by the method described in Appendix 12 .

The monthly mean proportions in the rumen, those at intake and those of the sward are compared in Table 8.3. Fig 8.3 compares the diet and sward proportions with the monthly rainfall measured in Block 39.

These data confirm the results from the Series 1 animals that the hartebeest does not browse, and that the proportion of inflorescence eaten is very low even when, as in July, it formed 5.8% of the sward by weight (see below). Because of this low proportion, the inflorescence fractions have been combined with those of stem for both the rumen and sward measurements, and is subsequently referred to as the stem fraction.

The most obvious sources of variation in the composition of the diets are the month in which the animals were collected, and their age. To assess their relative importance, a two way analysis of variance was performed on the transformed percentages of leaf in the diet in the 4 months and the 2 age classes, of adult and immature. The leaf proportion differs significantly between months ($F=10.611$, $df\ 3,24$, $p=0.01$), but there is no difference between the proportions in adult and immature animals ($F=0.292$, $df\ 1,24$, $p>0.05$). As similar results were obtained with the stem proportions, the diet data of all animals in each month have been combined.

The rainfall pattern during the study period was typical although most of the long rains fell in May rather than June. The half-yearly total of 298 mm between January and June 1972 was average for the area (Thomson and Sansom 1967).

To interpret these diets, the 95% confidence limits of the diet proportions are used to show whether a part is found in a significantly different amount from its sward proportion. The direction of a significant

difference determines whether the part is being selected for or avoided by hartebeest.

The proportion of leaf in the sward reflects the rainfall pattern, so that it reaches a maximum of 44.1% in April (Fig 8.3), due to the cumulative effect of at least 50 mm rain in 3 of the previous 5 months. Its percentage declines gradually until July, but then drops to 18% in September after 4 nearly rainless months. The stem fraction follows the reverse course, while the sheath fraction remains relatively constant, with the exception of January when stem is more abundant (56%) than in the dry season (53.6%), and the sheath proportion is correspondingly depressed.

The very high sheath and low stem proportions in January are probably the result of taking sward samples from a different vegetation type (p.153), characterised by a different sheath:stem ratio. Consequently differences in sward composition between January and April are not necessarily real, and little reliability is attached to any comparison of diet and sward compositions in the former month.

In each month, with the exception of September, correction of the rumen proportions to those of the diet reduces their similarity to the sward percentages. This is shown in the following table by the two sets of fractions of (% in rumen / % in sward) and (% in diet / % in sward). Alongside each fraction is its interpretation in terms of selection, avoidance or neither for each component. Comparison of the 2 columns shows that adjusting the rumen proportions increases the ^{apparent} degree of selection/avoidance practiced by the hartebeest.

Month	part	$\frac{\% \text{ in diet}}{\% \text{ in sward}}$	selection	$\frac{\% \text{ in rumen}}{\% \text{ in sward}}$	selection
January	leaf	1.53	select	1.18	-
	sheath	2.62	select	2.60	select
	stem	0.30	avoid	0.49	avoid
April	leaf	1.53	select	0.93	-
	sheath	0.61	avoid	1.08	-
	stem	0.53	avoid	1.01	-
July	leaf	1.48	select	0.88	-
	sheath	0.62	-	1.68	select
	stem	0.68	avoid	0.68	avoid
September	leaf	1.18	-	1.03	-
	sheath	1.21	select	1.32	select
	stem	0.83	-	0.82	-

The diets show a consistent pattern as the sward composition changes. In the first three months leaf was selected, but was taken as it occurred in September when it comprised only 18% of the sward by weight. Stem was avoided in all months although this is only suggested by the September figures whose 95% confidence limits include the amount on offer. The occurrence of sheath in the diet varied most, from being avoided in April when leaf was most abundant, to being eaten as it occurred in July when the sward stem had increased and leaf was unchanged. In September when leaf was scarce and stem abundant, the hartebeest showed a very slight selection for it. Although little can be deduced from the January figure for the reasons above, the sequence of April - September shows the progressive defoliation of the sward with the amount of stem increasing. The parallel, increasing similarity between sward and diet composition shows that the hartebeest were exercising less selection of their diet in terms of its plant part content.

Table 8 . 4. The occurrence of Themeda triandra in hartebeest faecal material from the Athi Plains.

Location	Season/Sward condition	Abundance of <u>Themeda</u>	No. of samples with <u>Themeda</u> (<u>Max. 10</u>)	Mean frequency in faeces, %	Reference
Nairobi Pk.	early rainy	10% foliage	10	74.6	Stewart & Stewart (1971)
"	end rainy	6% foliage	10	57.0	" "
"	end long dry	frequent/locally abundant	10	64.2	" "
Kajiado	mature, brown pasture	abundant	10	92.1	Stewart & Stewart (1970)
Nairobi	mature, brown	-	10	58.4	" "
Athi Plains	early dry	11% herbage	-	62	Casebeer & Koss (1970)
"	late dry	33% herbage	-	70	" "
"	end short rains	26% herbage	-	60	" "
"	end long rains	25% herbage	-	68	" "

8.4 Plant species in the hartebeest diet.

The species eaten by the hartebeest have been the subject of investigations in the Athi Plains (Casebeer and Koss 1970) and the Nairobi Park and plains (Stewart and Stewart 1970, 1971). All employed the method of faecal analysis. The most striking result is the prevalence of Themeda triandra in the diet in all seasons, even taking into account the fact that it tends to break in to many fragments in the gut which are easy to identify (Stewart et. al. 1970). Table 8.4 summarises these findings, and shows that even when this grass formed only 6% of the foliage, it was found in all the faecal samples with a mean frequency of 57%. Its proportion reached a maximum of 92% when the grass was abundant in a dry season pasture.

Other species e.g. Cynodon dactylon, Ishaemum afrum, Heteropogon contortus were taken in significant amounts at certain seasons in the park (Stewart et al, loc. cit.) and Pennisetum mezianum was utilized in the wet season in the plains (Casebeer and Koss loc. cit.), but in each place and in each season, Themeda predominated in the faecal material. Because of this concentration on one species, the hartebeest used a relatively small range of grass species in the park, and in the plains the species content of the diet was less similar to that on offer than those of cattle, wildebeest, and zebra.

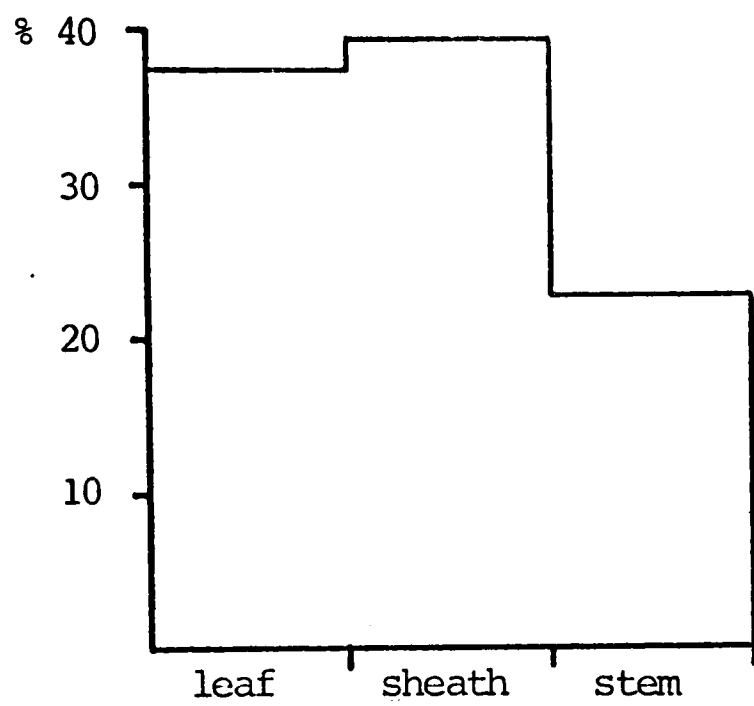
8.5 The dietary relationships of zebra and cattle with hartebeest.

I concluded in Chapter 7 (p.144,147) that when food was least abundant in the dry season, there were very high overlaps between the population distributions of zebra and hartebeest in the Nairobi Park, and between cattle and hartebeest in the plains. All three species were classified as exclusive grazers. I shall now examine these overlaps from the point of view of dietary similarity or difference.

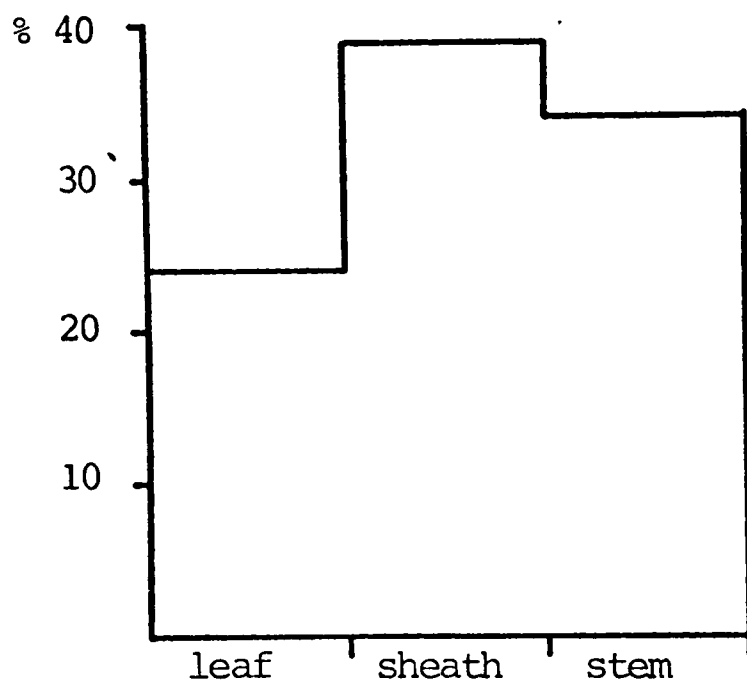
The dry season diet of the zebra in the Athi Plains contained significantly more species than that of the hartebeest (Stewart et. al. 1971). Although Themeda occurred in all zebra samples, its proportion was relatively low. Cynodon dactylon and Ischaemum afrum appeared to be selected. In the plains their dry season diet contained less of the three most common species, T. triandra, P. mezianum and Digitaria macroblephara, although the stemmy P. mezianum was less avoided than by hartebeest, wildebeest or cattle (Casebeer and Koss loc. cit.). Its overall diet composition was the most similar to that on offer. Because the hartebeest was the most selective species (above), the all-seasonal similarity between hartebeest and zebra diets was lower than between any other pair of species.

There is less information on the species eaten by hartebeest and cattle in the same area. Outside the Nairobi park, Stewart et. al.(1970) found that T. triandra and Cynodon dactylon were found in all cow faecal samples with the mean ration of 1:3.4. Further South, near Senya (Fig 3.1), the proportion of Themeda in cattle faeces was higher than in the sward, but lower than in hartebeest samples (Casebeer and Koss loc.cit.). Although the all-seasonal similarity in their diets was lower than between all other combinations of the 4 herbivores except for hartebeest and zebra, I have calculated the degree of similarity using Horn's method of estimating overlaps (p. 102) with the frequencies of the 15 most abundant species in the faecal samples. The overlaps between hartebeest and cattle were 0.951 and 0.890 in the early and late dry seasons respectively. Although other species pairs had greater values, these overlaps are high compared to those in Ch. 7, suggesting great similarity in diets.

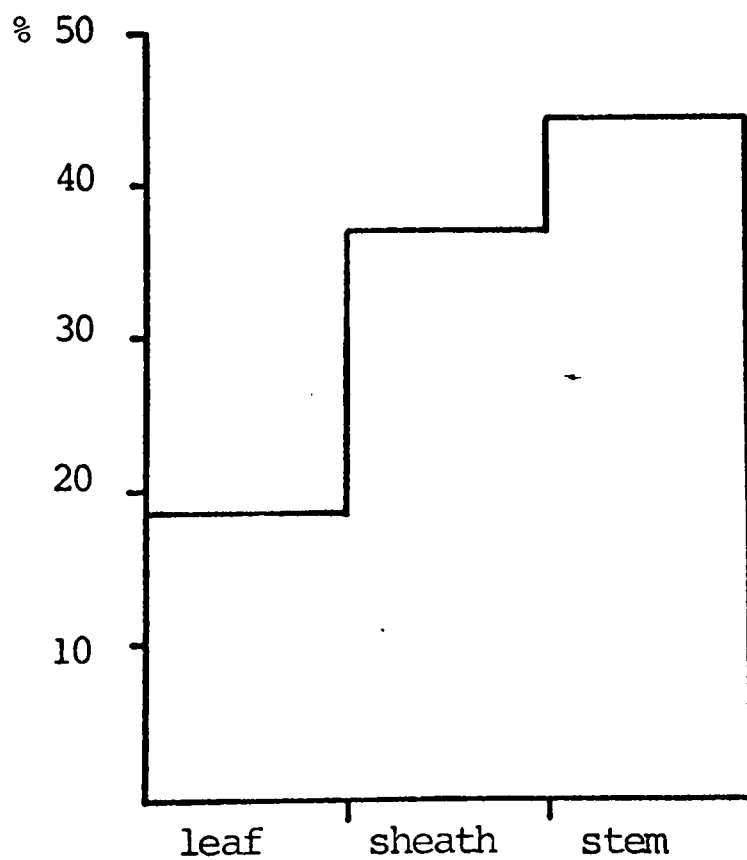
In the Acacia drepanolobium grassland of the Kenyan Rift Valley, 69.2% by weight of ingested material from oesophageal-fistulated cows comprised Themeda, which was approximately 1/3 more than the sward contained (McKay 1971).



Hartebeest, July.



Cattle, July-August.



Hartebeest, September.

Fig.8.4. The proportions of grass components in hartebeest and cattle rumens. Hartebeest, mean of 8 animals in each month. Cattle, mean of 5 animals in July and August.

In comparable vegetation about 15 km away, 67% of the leaf fragments in hartebeest rumens were also Themeda (Field and Blankenship 1973).

The plant components taken by hartebeest and cattle can be compared using information from Owaga (1974). She examined rumen samples from cows which had been grazing approximately 5 km from where the hartebeest were taken. Data on rumen frequencies are available from single animals slaughtered on each of 5 occasions between 29.6.72 and 30.8.72, a period including my July collection and ending 2 weeks before the September collection of Series 2 hartebeest. Through this period the proportion of leaf in the rumens dropped from 35.1% to 18.0% while stem increased from 29.8% to 42.0%. This trend is parallel and similar in extent to that described above for the hartebeest. Fig 8.4 shows how the mean of the cattle proportions is bracketed by the hartebeest proportions of July and September. If samples had been taken from both species at exactly the same time, there is little reason to doubt that they would not have been nearly identical.

8.6 Discussion

Before discussing food selection by the hartebeest, the extent to which the shot animals were representative of the population must be considered. The area in which the Series 1 animals were shot was sub-optimal habitat for the population. The value of these small samples of animals taken over 12 months lies in the fact that they show how the proportions of the grass components in the rumen change with rainfall and the consequent plant growth.

The second series of animals was taken at the edge of an area with a maximum density (see below) equal to the 17.8 hartebeest/km² of the Nairobi Park (p. 95). Although the sampling area had supported high numbers of hartebeest in previous dry seasons their numbers dropped

considerably between the July and September collections, as the following results of ground counts made within two weeks of shooting show:

Location	Area km ²	Month	hartebeest/km ²	cattle/km ²	available water, m ²
Block 39+40	57.5	Jan 1972	17.5	-	-
39	24.9	March	21.3	20.0	17,486
39	24.9	June	22.5	56.4	6,118
39	24.9	Sept	6.6	137.2	134

The drop in density from 22.5 to 6.6 /km² coincided with the failure of the hartebeest to select leaf, because of its scarcity, and a large decrease in the amount of water. Thus the September diets are those of a minority of hartebeest which did not move to areas with more water and/or better grazing (mostly the Lowland A. drepanolobium e.g Block 15, Appendix 8), for which there are no data on diets. However they do describe the diet of hartebeest sharing an area with very high densities of cattle whose water was effectively limitless because of wells in Block 39. Under these dry season conditions, the diets of the shot hartebeest may not be typical of the population.

Although the proportion of stem in the rumen of the Series 1 animals was more closely related to the previous rain than was the leaf fraction, the reverse might hold for the proportions in the diet. This is because the observed proportions have resulted from the differential digestion of food of unknown composition. It is not surprising that the correlation with rainfall is not perfect because of the numerous other factors affecting the composition of the sward. Important amongst these is the influence of other herbivores, modifying the composition of the growth due to earlier rain.

The Series 2 hartebeest show a consistent avoidance of stem in their diets and a slightly less consistent, though perhaps more marked, selection

for leaf. "Selection" and "avoidance" are used to interpret differences between diet proportions, with attached variances, and the single measurement of sward composition. If more samples had been clipped, each sward component would also have a variance and 95% confidence limits in Fig 8.3. As, in this case, selection (or avoidance) would only be shown if the 2 confidence limits did not overlap, the single observation of sward composition clearly increases the likelihood of obtaining significant differences. The size of this effect will depend on the size of the sward variance, but in general, selection would be less marked especially in July and September (Fig 8.3). In the latter month it is unlikely that any of the three components was ingested in significantly different proportions from those on offer.

The importance of sheath in the diet changes most when the rumen proportions are corrected to those of the diet. Instead of being apparently selected in all months (excluding January for the reasons given on p. 157), it was avoided in April and eaten as it occurred in July when the amounts of leaf on offer were greatest, and was selected only in the dry season (September) when leaf formed 18% of the sward. If corrections of this size and direction were applied to the Series 1 rumen proportions (Table 8.1, Fig 8.1) leaf would become the predominant component in the diet in May, June and July when its sward fraction would have been highest following the rain of April and May. The ratio of leaf to sheath in preceding and subsequent months would be relatively unchanged and similar to those of September 1972 when leaf was scarce. However even at the end of a year with little rain, ending in April 1972, stem was less abundant in the diet than sheath, while the reverse occurred in the Series 2 diets of September after only 4 rainless months (Fig 8.3). Part of this difference may be due to the different vegetation structure of the areas where the animals were collected - vegetation zone IVa and VI (Series 1) and zone VII (Series 2) (Fig. 5.1).

This difference in diet over 10-20 km also emphasizes the hazards of extrapolating from such a sample to the population.

When the sward contains at least 30% leaf, hartebeest appear capable of increasing its proportion in the diet. Sheep can select leaf from a sward (Arnold 1960). Their selectivity increased with the maturity and volume of herbage, but on a lucerne sward they exercised no selection at leaf levels of 8 - 12%. For the hartebeest, this point appears to have been reached under natural grazing conditions with a leaf fraction of only 18% (Fig 8.3).

The volume of a diet component is also important. When the yield of green matter (kg dry matter/ha) dropped below a critical level, sheep no longer removed it selectively from dead herbage (Hamilton et al 1973). Although this might explain the failure of the hartebeest to remove leaf at low availability, vegetation type 15 from which the sward samples were taken, supported grass biomasses of 1117, 1171, and 1372 kg/ha respectively in April, July and September respectively. Over the whole Athi Plains in March, June and September 1972, 42.8% of 3766 observed hartebeest were in areas with grass biomasses between 800 and 1600 kg/ha, although this covered only 37.2% of the area. This small degree of selection (p.114) suggests that the absolute amount of herbage available to the shot animals was not critical.

Herbage yield in itself is not a good indicator of the intrinsic availability of herbage to a grazing animal (Allden and Whittaker 1970, Stobbs 1973b). Intrinsic availability measures the accessibility of the food component and the effect of this on food intake under field conditions (Raymond 1966). Thus it obviously depends on the sward structure and the particular herbivore species. As the volume of herbage increases, the bite size of cattle decreases, suggesting that the favoured leaf fraction is becoming relatively inaccessible, (Stobbs loc. cit), although its absolute abundance may be greater. Although this may prevail at

high herbage yields, the situation in the Athi Plains during September appeared to be one of low absolute availability of leaf although the standing crop was nearly optimum, as measured by occupancy (above).

Amongst the range of possible effects, selective grazing produces a greater net intake of energy (or other nutrient). The same principle of increasing food intake per unit effort is central to current optimization models of predator strategies (e.g. Schoener 1971, reviewed by Krebs 1973). Although these are developed for situations where a predator hunts for discrete food items in an environment which is not food, this is not qualitatively different from the herbivore situation where all the grass above ground is potential food, but where different components can be ranked for food value. If the abundance of the "best" food item decreases, the net benefit from selection will decline as the cost of the selection processes required to obtain a unit amount of the "best" food increases. Grazers can partially alter their feeding behaviour to compensate for such changes and reduce the extra cost: as the bite size and bite rate of sheep drop on progressively sub-optimal swards, a constant intake is maintained by increasing the grazing time (Alliden and Whittaker loc. cit), but the scope of these adjustments is limited, and net intake eventually drops. The same principles probably govern the profitability to the hartebeest of selectively removing leaf: at a certain sward abundance it becomes increasingly advantageous to ingest larger proportions of lower- quality food items whose energy cost of collection and, possibly, digestion is lower. Hence the dietary proportion of sheath increases, and one can predict that as this is depleted stem would be taken in greater amounts.

In the preferred medium - length grassland (p.126), hartebeest feed at the base of grass clumps for which the long, narrow face is an adaptation (Frontispiece). The upper and lower lips which are expanded

and highly mobile, remove grass by nibbling in a vertical plane about the long axis of the head. I suggest that this is an efficient means of removing sheath from defoliated swards without detaching and ingesting the stems. Sinclair and Gwynne (1972) show that sheath is the dominant diet component of Serengeti buffalo in the dry season, but conclude nevertheless that it is probably not actively selected because the buffalo's broad mouth and wide incisors are not adapted for this type of feeding behaviour. However, as cattle diets contain abundant sheath in the dry season (Owaga 1974, and Fig 8.4), it seems likely that the buffalo/cow mouth shape and feeding behaviour combine to remove sheath selectively from stem. Cattle gather food by lateral movements of the tongue which encloses a bunch of grass. By applying an appropriate force, sheath might be rasped off the stems by the tongue, causing the high proportions observed in the rumen.

Hartebeest and zebra diets.

The works reviewed above (p. 160) suggest that the hartebeest and zebra diets differ considerably in their species content because of the relatively catholic choice of the latter. Their use of grasses such as Pennisetum mezianum and Ischaemum afrum, which are unpalatable to cattle except when young (Edwards and Bogdan 1950), suggest that zebra can eat and adequately digest coarse material. This is possible because of their equid dentition with upper incisors, and their non-ruminant digestive system which depends on high rates of throughput (Bell 1970). This enables the zebra to include large quantities of stem in its diet: in the Serengeti dry season, the stomach proportions of leaf, sheath, stem were 0.2, 48.7, 51.0% respectively (Gwynne and Bell 1968). Although there was no measure of their available proportions, the comparable figures for wildebeest were 17.2% leaf and only 30.1% stem from the same area concurrently. This suggests a tolerance of stem by zebra, whatever the degree of selection, which is inconsistent with the interpretation of

the hartebeest feeding behaviour in any season. On this evidence it is impossible to conclude that their diets are identical even when large numbers of both coexist in the dry season in the Nairobi Park.

On the contrary, it is more likely that their diets are complementary and that the zebra prepare the sward in the way suggested for the Serengeti (Gwynne and Bell loc. cit.). On numerous occasions in the Nairobi Park, zebra were seen removing grass culms, effectively reducing the stem bulk density (Stobbs 1973b) and perhaps making the lower leaf layers more accessible to the hartebeest.

Hartebeest and cattle diets.

It is apparent that the grass components' proportions in the dry season diets of hartebeest and cattle are very similar (Fig. 8.4). Their dietary separation therefore depends on the extent to which the species eaten are different. Although Casebeer and Koss (1970) concluded that the species eaten were dissimilar compared with most other herbivore pairs, their overlaps were high (Horn's $R_0 = 0.951$ and 0.890 in two dry seasons) and, in fact, all species pairs had overlaps at the same time between 0.839 and 0.956 . These values are all so high and clumped that they are probably of little value for investigating the dietary separation between species, especially in view of the limitations of frequency data from faecal material (Stewart 1967). Moreover, during their study period rainfall was above average and no long dry season occurred (Casebeer and Koss loc. cit.). As hartebeest were abundant in all seasons in their study area in vegetation zone IVA (Fig 5.1), but fewer occupied this zone in 1970 - 72 (p.90), food may have been super-abundant for the grazers, and the stated herbage yield of up to 6700 kg/ha supports this. Under these conditions the diets of hartebeest, wildebeest, zebra and cattle are all very similar, but the results of more direct methods in similar areas under less exceptional conditions confirm that

Themeda is an important component of the diets of both hartebeest (Field and Blankenship 1973) and cattle (McKay 1971).

The diets of these species are, therefore, very similar with respect to both grass species and their parts. Their similarity on the latter criterion is supported by two other lines of evidence. Hofmann (1973) describes the hartebeest ruminal structure as typical of a roughage grazer, in which category cattle also belong. No other wild ruminant in the Athi Plains is included in this group. Second, Hungate et. al. (1959) show that from a variety of antelope, the hartebeest rumen bacteria were most compatible with cattle rumen liquor. The considerable ability of this combination to digest cellulose was due to the similarity between the hartebeest bacteria and Bacteroides succinogenes found in cattle. These represent anatomical and physiological adaptations to diets of the same physical nature, which the parts analysis confirmed to be similar. With at least some species eaten in common, their dietary separation is less than between any other of the grazers of the Athi Plains.

Chapter 9.

THE INTAKE OF DRY MATTER AND ITS REGULATION

9.1 Introduction

Studies of herbivore ecology are largely concerned with the complex relationships between the members of this trophic level and the vegetation which supports them. Although the carrying capacity of an area summarises its ability to maintain a certain herbivore biomass, the impact of these animals on the vegetation and its annual production is more accurately assessed if the amount of plant material eaten by each individual is known.

In a recent review, van Dyne (1968) stated that "the determination of the quantity of forage consumed by grazing animals (as opposed to penned ones) is normally dependent on knowledge of total faecal output". The basis of this statement is the many regressions relating the weight of faecal dry matter or organic matter and its nitrogen concentration with the intake of dry or organic matter by the animal (e.g. Arnold and Dudzinski 1963, Lambourne and Reardon 1963). Such regressions are developed with penned animals and are then applied to free-grazing animals whose total faecal output can be collected. Total collection of the faeces of a free-living, wild herbivore is clearly impractical, with the result that the study of the intake and nutrition of wild herbivores has lagged behind that of other aspects of their biology or of domestic species.

In Appendix 12, I calculated the retention times of the diet components in the hartebeest's rumen. These times are used in this chapter with other information from the same shot animals to estimate the daily intake of the hartebeest under field conditions. The results of a feeding trial and those reported in the literature are used to corroborate the estimates. To test the validity of this approach, the temporal

variation in estimated intake is investigated in terms of some of the factors which regulate the intake of comparable feeds by domestic ruminants. This leads to a consideration of the environmental correlates of the observed variation, thereby introducing a predictive capability for other periods. The results are then generalized further by relating the observed changes in the dead hartebeest to changes in the nitrogen concentration of the faeces. By doing this, the intake and nutrition of the hartebeest become predictable under field conditions without requiring the collection of animals, or measurement of total faecal output.

9.2 Methods

Feeding trials

The only hartebeest available for a feeding trial was a semi-tame male, aged about 2 y 3 m. For the trial he was confined to an outdoor enclosure (c. 14 x 4 m), of bare earth which allowed collection of all the faecal pellets. The only food offered was hay grown at Athi River on irrigated land, containing plant species typical of the Athi Plains. It was provided in a drum 40 cms deep, with a diameter of 80 cms, to catch the food dropped during eating. Water was freely available throughout the trial from a graduated bucket. The amount of water drunk each day was recorded when the bucket was topped up each morning.

At the beginning of a 10-day pre-trial (PT) period, the animal was shut in the paddock and the normal ration of concentrates withdrawn. The hay was chopped in to approximately 4 cm ^glengths to reduce the opportunity for selection of particular parts, and was given twice a day at 0700 and 1900 h. All droppings were removed at the same time. During the second half of PT the weight of food consumed was measured by difference between that given and that remaining at the next feed. About 70% more food than was voluntarily consumed at each meal during PT was supplied during the

trial period (T).

On day PT 10, the hartebeest was weighed to the nearest 1 kg on a cattle weighing station, and was reweighed at the end of the trial, day T11. Known weights of food were given from T1 and T10, while all faeces were collected and weighed between T2 and T11. These were then oven-dried to calculate the weight of faecal dry matter.

At each feeding a sample was taken from the food and from the refusals, and the samples of each were bulked for analysis. About 20% of each day's faecal production was also composited for analysis.

A similar feeding trial was conducted later by Dr. A.N. Said on two 6 y old wether sheep (N.Z. Romney Marsh x Corriedale), fed hay ad libitum from the same source and grown under the same conditions.

Collected hartebeest

The age class and physiological or social status of the shot hartebeest were recorded as described earlier (p.26). The rumen contents of each animal were weighed as described on p.151 . As the rumen was opened, a grab sample of about 200 g was weighed accurately. This was subsequently sun-dried and reweighed to determine the dry matter fraction. The latter was then used with the total weight of rumen contents to calculate the total dry matter in the rumen (RDM).

RDM and faecal samples from the rectum of each animal were analysed for nitrogen at the Dept. of Animal Production, University of Nairobi. The sward was sampled and analysed at the same time as described earlier (p.19).

Rainfall and grass moisture

The monthly rainfall was measured in Block 39, at the edge of the collecting area (p.153). The effective rainfall was calculated as P/E_t , taking in to account the drying power of the atmosphere. Cumulative values have been computed for 1 to 4 months before each month in which hartebeest were shot, in the way described on p.23.

Calculation of dry matter intake

The retention time (RT h) of food residues in the rumen has been measured in domestic animals by slaughter methods (Makela 1956, Ulyatt 1971). When the mean daily intake is known and the total rumen contents are weighed after slaughter, the retention time of dry matter (RTDM h) is

$$\frac{\text{weight of dry matter in rumen at slaughter}}{\text{mean DM intake daily}} \times 24$$

This method makes two assumptions (Makela loc. cit):

1. At constant feeding, the amount of DM leaving the rumen in 24 h is the same as that entering in 24 h.

2. At constant level of feeding, the amount in the rumen is constant.

In Appendix 12 the RT's of the different grass components were calculated to obtain their diet proportions. From these two sets of information a mean retention time for the rumen contents of each hartebeest was calculated. Because the total weight of dry matter in the rumen (RDM) of each animal was known, the same expression allows calculation of the daily dry matter intake (DMI kg/day):

$$\begin{aligned} \text{DMI} &= \frac{\text{RDM}}{\text{RT}} \times 24 & \text{RDM} &= \text{rumen dry matter kg} \\ & & \text{RT} &= \text{retention time h} \end{aligned}$$

Body size effects

To overcome the effects of differences in absolute size between animals of the 4 samples, RDM is subsequently expressed as a percentage of the dead weight.

When calculating intake, the metabolic weight is used, for, as Benedict (1938) showed, the heat production per unit weight of small animals is far greater than the heat production per unit weight of larger animals. Heat production is proportional to some fractional power of

Table 9.1 Composition of hay used in feeding trials on hartebeest
and sheep, with their liveweights and dry matter intake.

	HARTEBEEST		SHEEP
	Dry matter composition		
	Hay eaten	Refused	Hay eaten
crude protein, %	10.6	10.4	8.9
crude fibre, %	36.5	37.7	39.1
ash, %	10.5	10.7	11.2
N-free extract, %	40.6	39.6	38.0
ether-extractive, %	1.8	1.6	2.8
gross energy, cal/g	4135	4120	4038
Liveweight, W kg			
start	108		61.9 (mean of 2 sheep)
finish	107		58.1
weight change	- 1.0		- 3.8
mean dry matter intake, g/day			
	1274		674
metabolic weight,			
$W^{.73}$,kg	30.5		19.9
daily dry matter intake			
g/kg. $W^{.73}$.day.	41.8		33.9

the body weight in the expression :

$$Q_{bm} = C.W^b$$

where Q_{bm} = basal metabolic rate
 C = constant
 W = dead weight
 b = exponent

Although for all practical purposes the mean metabolic rate is $70.W^{.75}$, the exponent of 0.73 is often found in the agricultural literature, and is used here to facilitate comparison.

Analysis

Regressions and correlations are used to test the association between parameters of the environment and the hartebeest digestive tract and DMI. In each case quadratic and linear functions were fitted and their suitability compared with an F-test (Bailey 1958). For each, the amount of variance accounted for was almost the same and the linear equations are presented here.

9.3 Results

Dry matter intake

The composition of the hay used in the feeding trials is shown in Table 9.1 with the same data for the feed refused by the hartebeest. The performance of the two species on these hays is discussed in Ch. 10 . The hartebeest's apparent weight loss of 1 kg over the 10 day trial does not exceed the accuracy of the scales, so its weight is considered to have been constant. The mean weight of the sheep dropped by 3.8 kg over the 17 day pre-trial and trial period.

The mean daily intakes of DM were 1274 and 674 g/day for hartebeest and sheep respectively. Using their metabolic weights ($W^{.73}$) of 30.5 and 19.9 kg, the hartebeest consumed 41.8 g.DM/kg $W^{.73}$. day and the sheep 33.9 g/kg $W^{.73}$. day, so that on this basis the intake of the hartebeest was 23.3% greater.

Table 9.2. Series II Hartebeest: their month of collection, status, dead weight, weight of dry matter in the rumen (RDM g/kg dead wt), retention time of rumen contents (RTh), daily dry matter intake DM g/kg W^{0.73} day , rumen nitrogen (RN%) and faecal nitrogen (FN%) concentrations.

MT - male, territorial, MB - male, non-territorial, FNPNL - female, non-pregnant, not lactating, FPNL - female, pregnant, not lactating, FPL - female, pregnant and lactating, FNPL - female, non-pregnant, lactating, IMM - immature animals, male and female.

Month	No.	Status	Dead weight W. kg	g/kg dead wt. RDM	h RT	g/kg.W ^{0.73} day DMI	RN%	FN%
Jan.	40	FPNL	105.2	20.3	23.2	73.9	2.86	1.16
	41	IMM	85.3	23.9	22.3	85.2	2.87	1.40
	42	FNPNL	101.6	20.2	19.8	84.9	2.87	1.33
	43	MT	128.6	22.6	23.3	86.2	2.75	1.45
	44	FNPNL	94.3	21.6	21.7	81.9	2.90	1.23
	45	MB	134.3	24.3	22.9	95.3	2.66	1.28
	46	MT	132.5	19.8	23.3	76.3	2.63	1.09
	47	IMM	53.5	20.6	20.4	70.5	3.00	1.26
Mean			-	21.7	22.1	81.8	2.82	1.27
April	48	FNPNL	128.8	21.7	34.8	55.3	2.50	1.05
	49	MT	128.8	27.1	36.7	55.9	2.27	1.05
	50	FNPL	110.7	29.4	40.4	62.3	2.43	1.19
	51	MB	111.6	25.3	37.2	58.3	2.32	1.12
	52	MB	153.8	25.0	37.9	61.5	1.95	0.98
	53	FNPL	127.0	28.3	34.4	72.9	1.84	0.91
	54	IMM	100.7	28.3	33.8	69.6	2.30	0.98
	55	IMM	78.5	21.3	37.7	43.8	2.51	0.98
Mean			-	25.8	36.6	59.9	2.26	1.03
July	56	FPL	125.1	27.2	20.4	117.5	2.70	1.16
	57	FPNL	120.2	23.0	21.0	95.5	2.19	1.26
	58	IMM	59.1	16.1	20.3	57.1	2.56	1.19
	59	MB	134.3	29.8	23.9	112.0	2.16	-
	60	MB	137.9	20.2	24.2	75.3	2.45	1.40
	61	IMM	87.1	19.4	23.1	67.0	2.64	1.25
	62	FNPNL	101.2	23.0	23.1	83.2	-	1.36
	63	MT	136.5	21.2	21.8	87.8	2.59	1.20
Mean			-	22.5	22.2	86.9	2.47	1.26
Sept.	64	MB	145.0	30.8	88.0	32.3	1.30	0.84
	65	MB	135.5	32.0	89.7	32.2	1.73	1.05
	66	MT	131.5	31.9	91.0	31.2	1.81	0.98
	67	FPNL	114.7	20.2	91.5	20.1	1.62	0.98
	68	FPNL	131.1	20.3	91.3	19.9	1.71	0.91
	69	FPNL	117.8	29.3	88.3	28.9	1.58	0.98
	70	IMM	57.5	26.4	90.8	20.7	2.26	1.05
	71	IMM	98.2	25.6	90.8	23.2	2.00	1.05
Mean			-	27.1	90.2	26.1	1.75	0.98

Table 9.3 Results of the analysis of variance on dry matter intakes in different months and for different groups of hartebeest.

Factor	treatments	no. of treatments	F ratio	Probability
1. Month	Jan, April, July,Sept.	4	38.860	< .001
2. Status	MT, MNT, FNPNL,FPNL, FPL,FNPL, IMMAT	7	1.454	.234
3. Status	MT + MNT, FNPNL+FNPL, FPNL+FPPL, IMMAT	4	1.071	.378
4. Status	MT + MNT, FNPNL+FNPL, FPNL+FPPL, IMMAT	4	.763	.527

MT = Male territorial

MNT = Male non-territorial

FNPNL = Female not-pregnant,
not lactating.

FNPL = Female not pregnant,
lactating.

FPNL = Female pregnant, not
lactating.

FPL = Female pregnant,
lactating.

IMMAT = Immature animal.

The information from the shot animals used to calculate the dry matter intake (DMI) is shown in Table 9.2. The mean DMI's for the 4 months, with their 95% confidence limits, are :

	DMI g/kg.W ^{.73} .day	95% confidence limits
January	81.8	± 6.55
April	60.0	± 7.53
July	87.5	± 20.9
September	26.1	± 4.7

The results of analyses of variance on these intakes are shown in Table 9.3. The animals have been divided either by the month of collection or in to various groups according to their physiological or social status across months. The small sample size precluded most 2-way analyses of variance by month and status.

The first analysis in Table 9.3 shows that the calculated intakes are significantly different between months. When the data from each month are pooled and broken down by status, significance is lost. The second analysis uses the 7 basic status/age groups, while the third combines all adult males but separates the adult females in to those lactating or dry, irrespective of whether pregnant or not. The last analysis distinguishes females on the basis of their being pregnant or non-pregnant. Because the F-ratio is not significant in any of the latter 3 analyses, daily intake calculated in this way is affected only by the month of collection, and not by the physiological status or age of the individuals. However, single factor analysis rules out detection of any possible interaction effects between month and status.

Dry matter intake, rumen dry matter and rumen nitrogen

The rumen contents consist of liquid and solid fractions. The mean percentage liquid in the sample of fresh digesta taken from 8 animals in

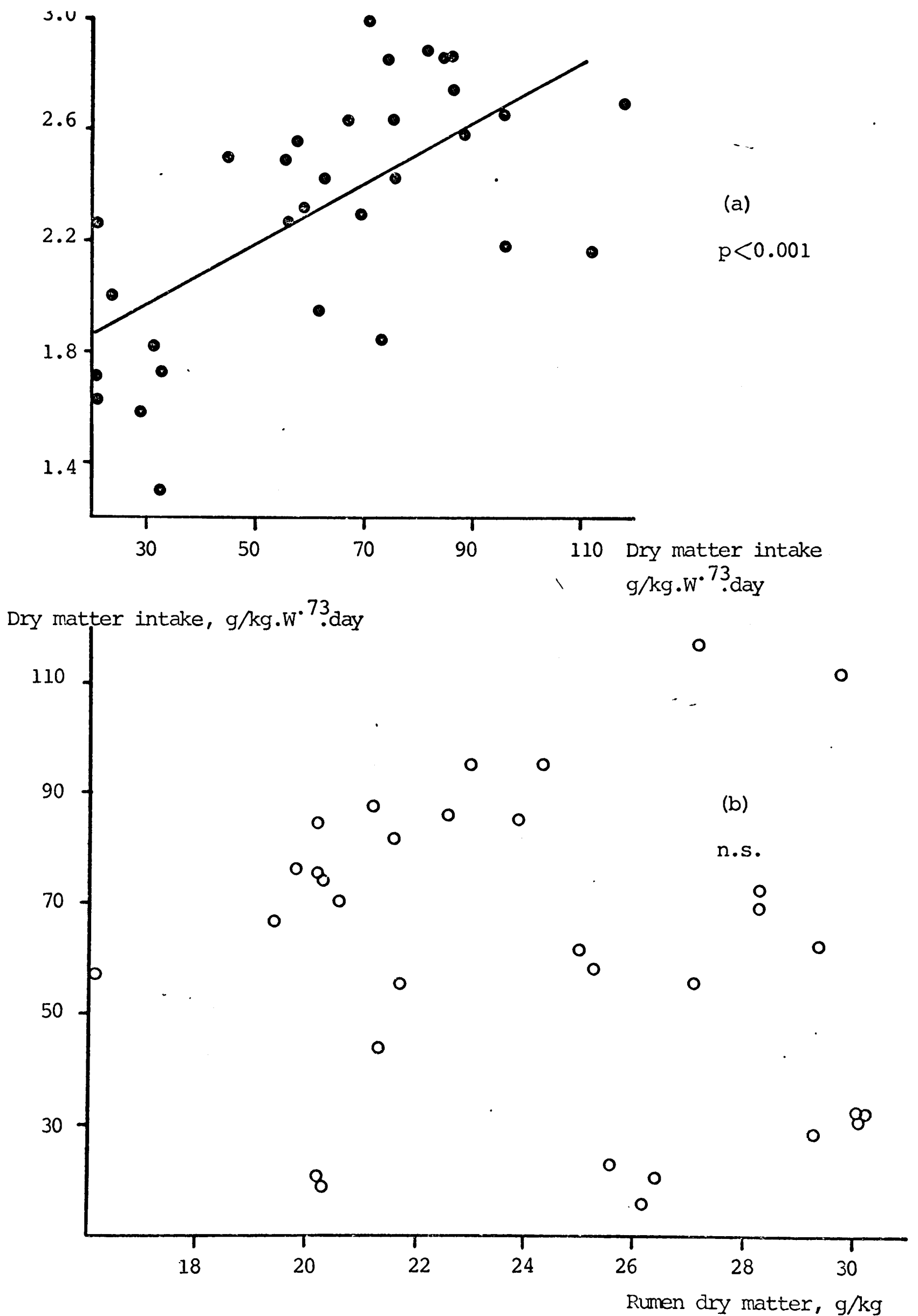


Fig.9.2. The daily dry matter intake (g/kg.W^{0.73}.day) and (a) the rumen nitrogen concentration (%), and (b) the weight of dry matter in the rumen (g/kg dead weight).

each month was :

month	mean percentage of liquid	95% confidence limits
January	83.5	± 0.76
April	84.3	± 0.60
July	83.4	± 1.50
September	82.7	± 0.94

As the liquid proportions are nearly identical in each month, any temporal variation in the weight of the rumen contents is due to differences in the amount of dry matter (RDM).

When food with a longer retention time is eaten, the weight of dry matter in the rumen increases ($r = .456$, $p < 0.01$, d.f. 29) but the relationship is not striking (Fig 9.1a). The low correlation is due to the wide scatter of points, and to the fact that the monthly mean dry matter weights vary between 21.7 and 27.1 g/kg (Table 9.2) whereas the mean retention times vary between 22.1 and 90.2 h. This suggests that the hartebeest's rumen has only a limited ability for expansion to accomodate food which passes through relatively slowly. Thus, the animal must compensate by reducing its intake, which was calculated above to vary between mean values of 26.1 and 87.5 g/kg.W^{.73}. day.

Variations in the amount of dry matter in the rumen (RDM) are accompanied by other changes. Using data in Table 9.2, Fig 9.1.b shows that the nitrogen level in the rumen (RN) is inversely related to RDM by

$$RN = -.059 RDM + 3.767, (r = -.559, p < .001, d.f. 29)$$

The measured ruminal N level is also correlated with the calculated DMI (Fig 9.2.a)

$$RN = .011 DMI + 1.638, (r = .653, p < .001, d.f. 29)$$

On the other hand, the dry matter intake cannot be predicted from the quantity of dry matter in the rumen : ($r = -.161$, $p > 0.05$, d.f. 29) (Fig 9.2.b)

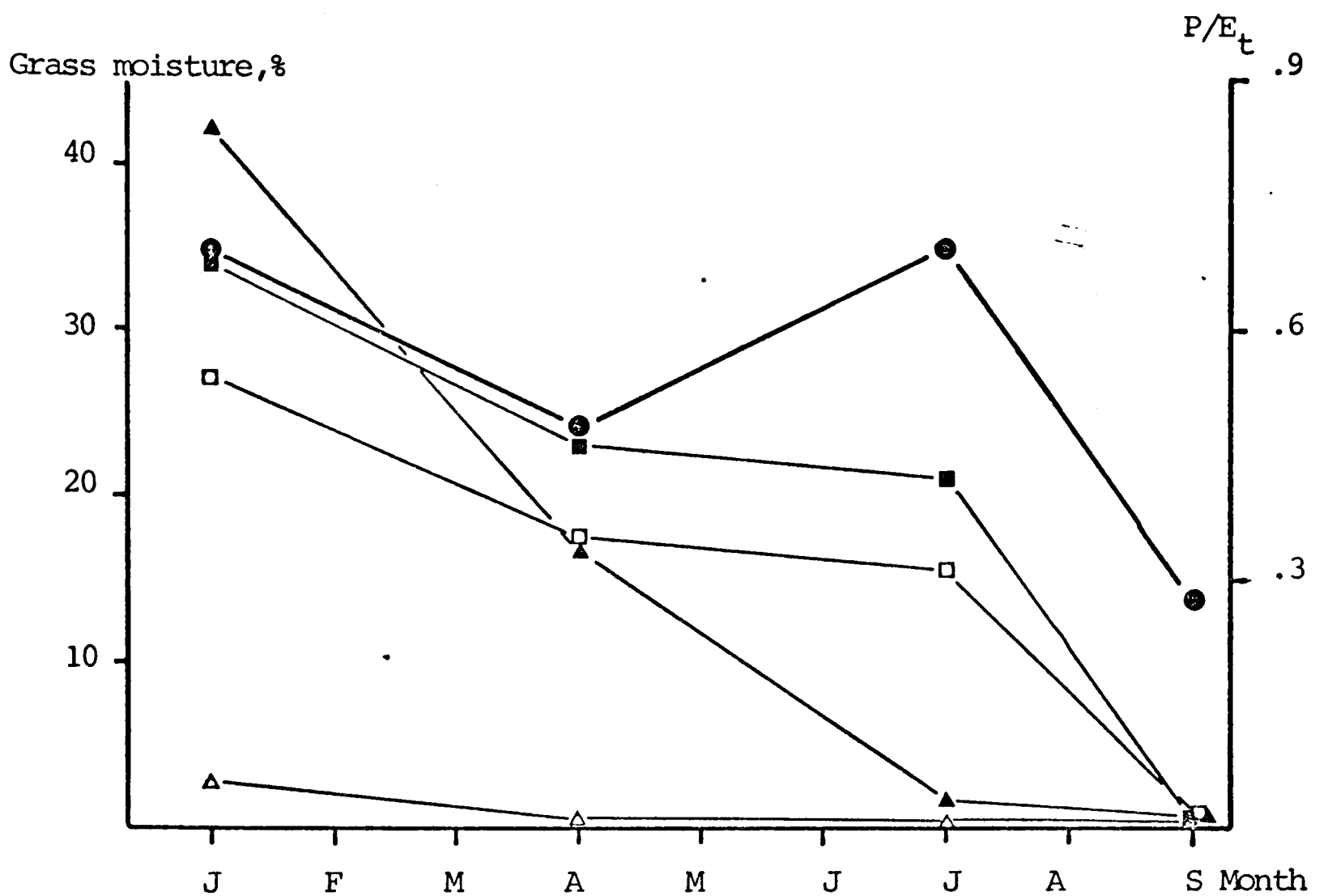


Fig.9.3a. The effective rainfall, P/E_t , over 1 month (Δ), 2 months ($\blacktriangle$), 3 months ($\blacksquare$) and 4 months ($\square$) and the moisture content of the grass (%) ($\bullet$) in 4 months in 1972.

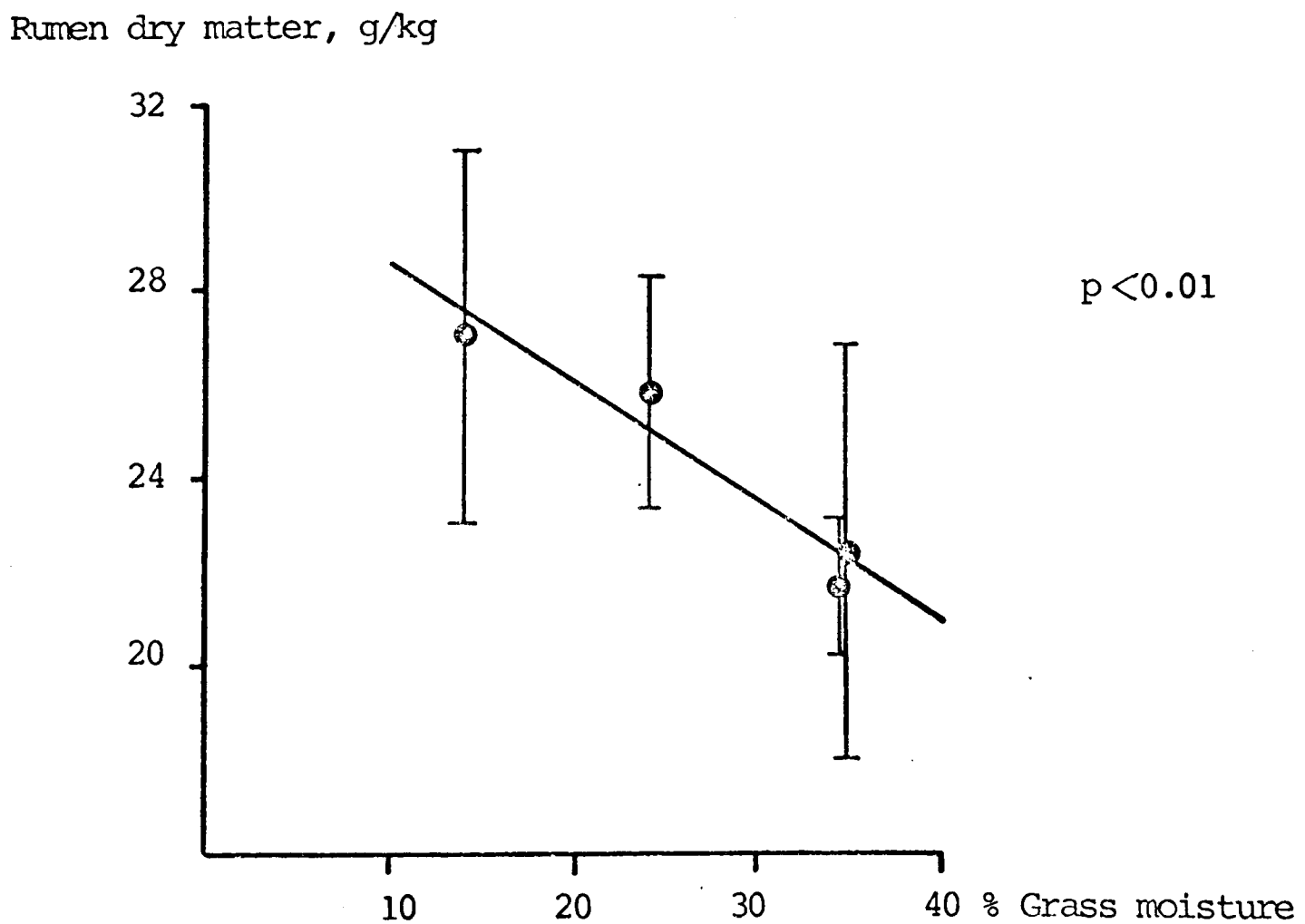


Fig.9.3b. The moisture content of grass (%); and the weight of dry matter in the rumen (g/kg dead weight) in 4 months.

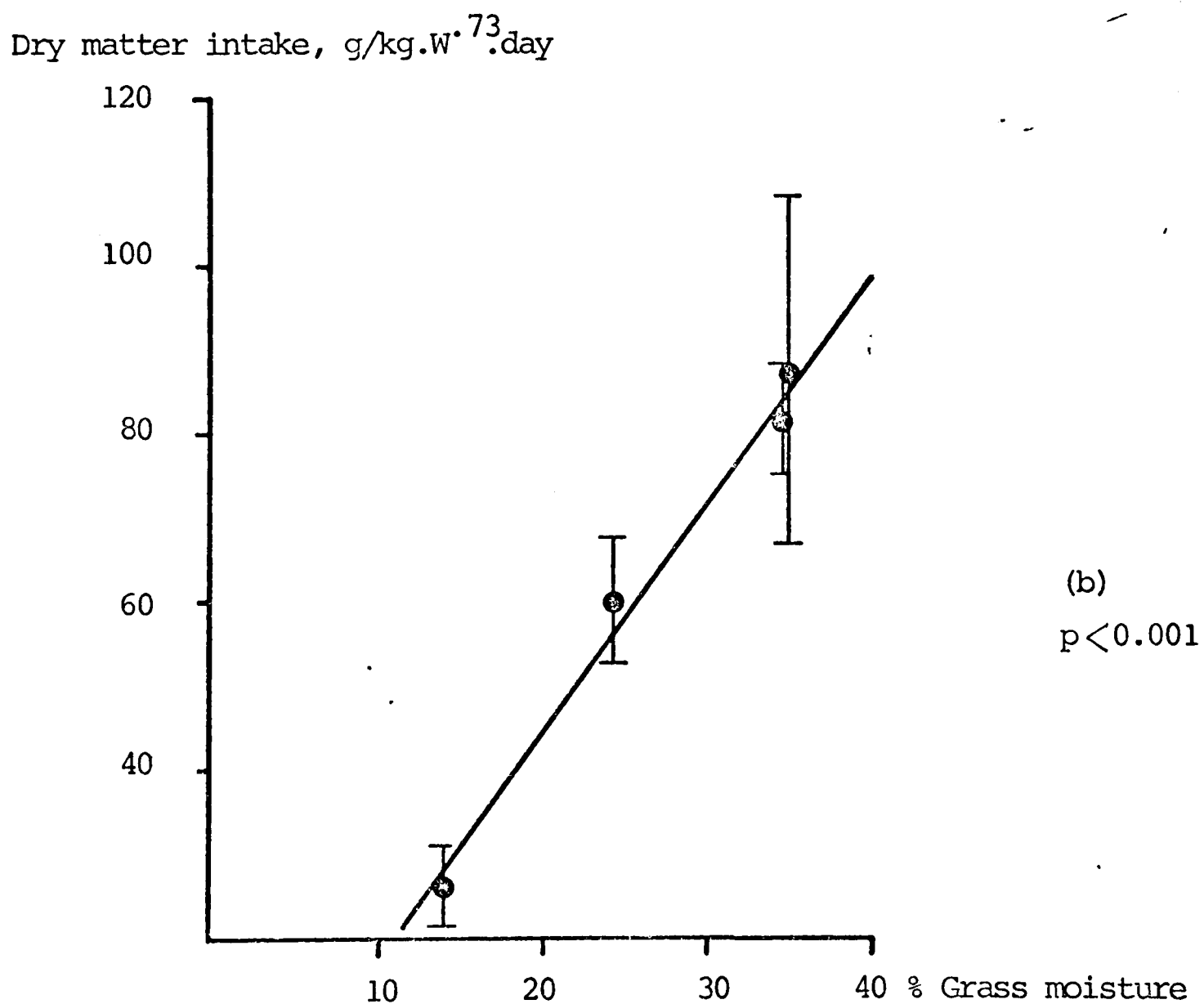
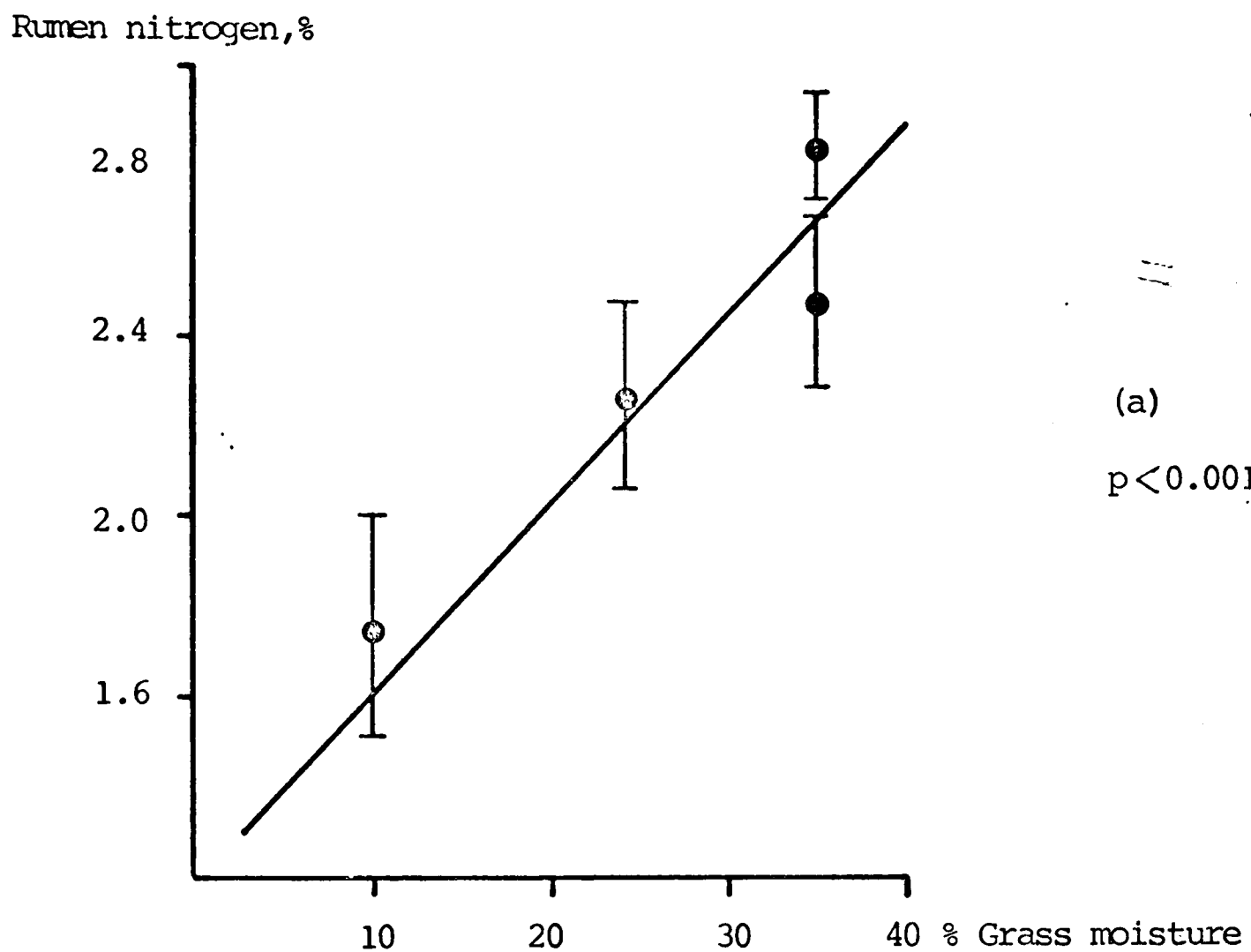


Fig.9.4. The moisture content of the grass (%) and (a) the rumen nitrogen concentration (%), and (b) the dry matter intake ($\text{g/kg.W}^{.73}.\text{day}$) in 4 months.

Environmental factors

The effective rainfall (P/E_t) for the month in which each sample was taken and, cumulatively, for the preceding 2,3 and 4 months, are shown below, with the measured water content of the grass at the same time:

No. of months	P/E_t in			
	January	April	July	September
current	.05	0	0	0
last 2	.84	.33	.03	0
last 3	.69	.46	.42	0
last 4	.54	.35	.31	.01

grass moisture, %	34.9	24.3	35.0	13.9

It is clear from Fig 9.3.a that during this period the water content of the grass varied with the rainfall over the previous 3 or 4 months. As the relationship with the 4-month rainfall is no better than with the 3-month total, grass moisture (GM) is considered here as a function of the rainfall over the preceding 3 months.

RDM and GM are negatively correlated ($r = -.524$, $p < 0.01$, d.f.29), showing in Fig 9.3.b that the weight of the rumen contents is less in the wet season. The correlation is not high because of the relative constancy of RDM between months (above). This contrasts with the high correlation between rumen nitrogen (RN) and grass moisture ($r = .833$, $p < 0.001$, d.f.29) in Fig 9.4.a. The correlation with the rainfall over the previous 3 months is as high ($r = .850$, $p < 0.001$, d.f.29). Thus, when the water content of the sward is high after rain, the ruminal N concentration is high. Since RN and intake (DMI) are related (p.175), GM can be used to predict DMI: (Fig 9.4.b.).

$$DMI = 2.733GM - 10.91 \quad (r = .892, p < 0.001, d.f.29)$$

The validity of this correlation is open to the criticism that these two parameters are not strictly independent, because GM was used to determine RT (Appendix 12), which with RDM was used to estimate DMI

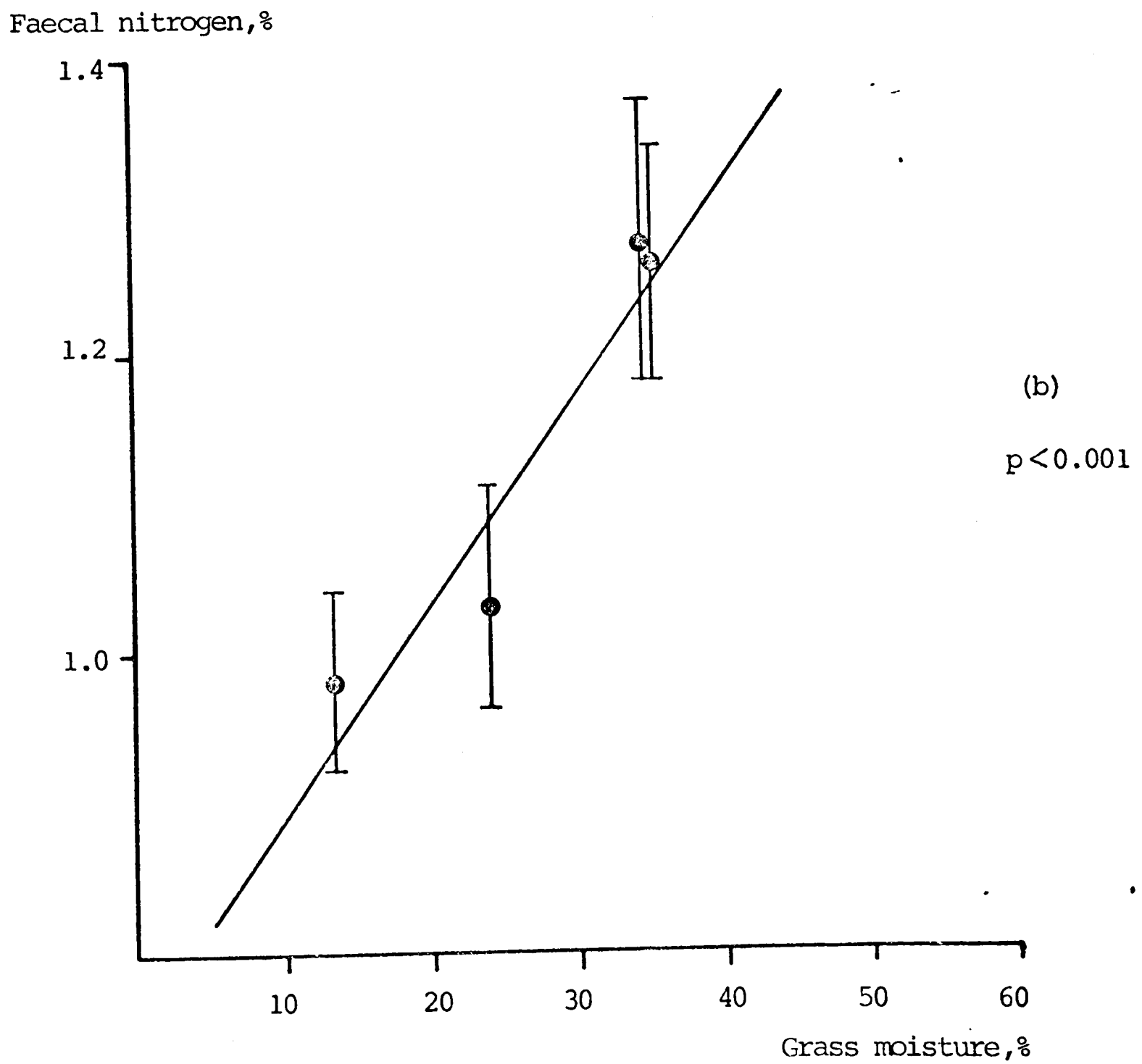
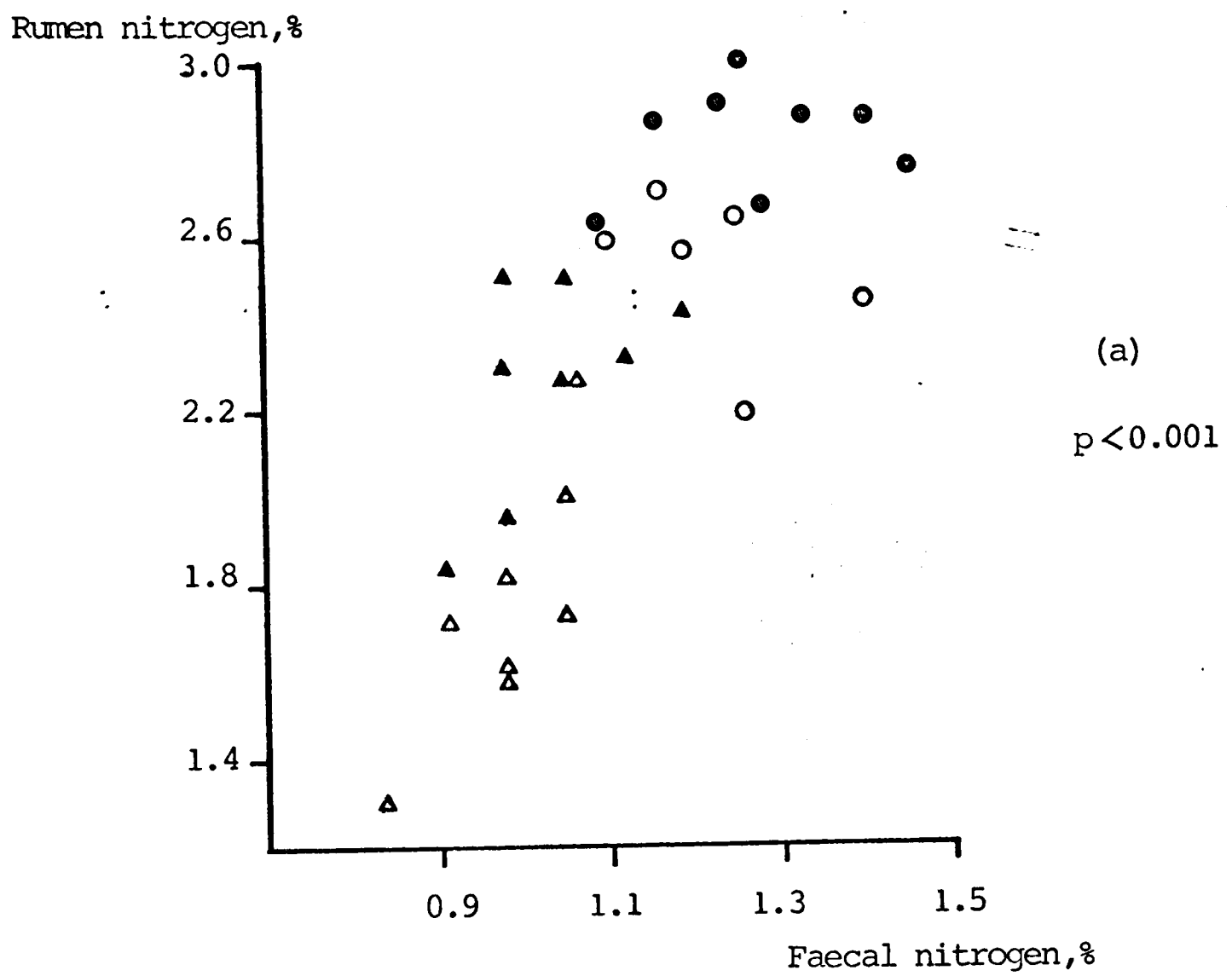


Fig.9.5. The rumen and faecal nitrogen concentrations (a), and the grass moisture content and faecal nitrogen concentration in 4 months. (b).

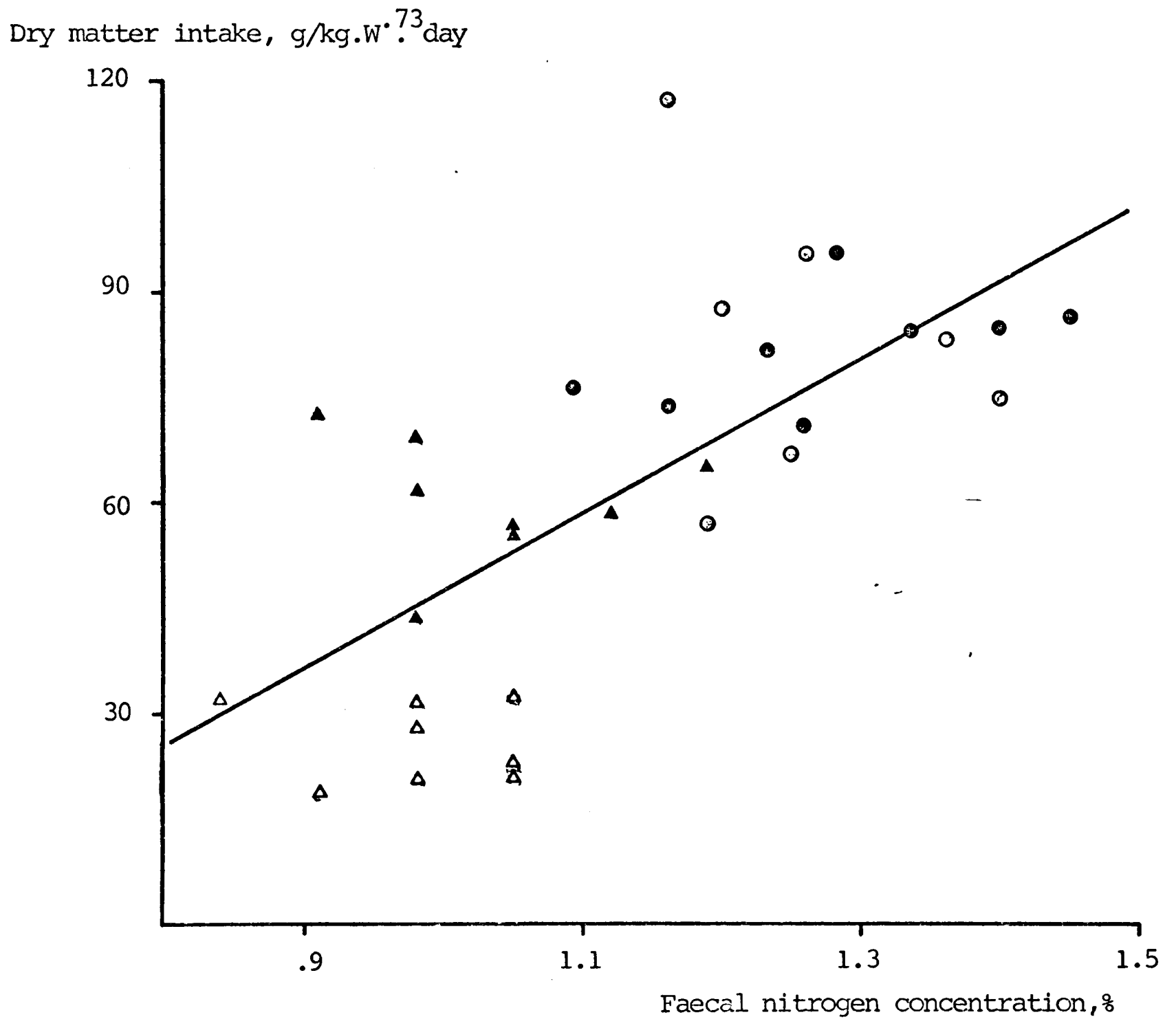


Fig.9.6. The faecal nitrogen concentration,%, and estimated dry matter intake, g/kg.W^{0.73}.day, in 4 months. Month symbols as for Fig.9.1.

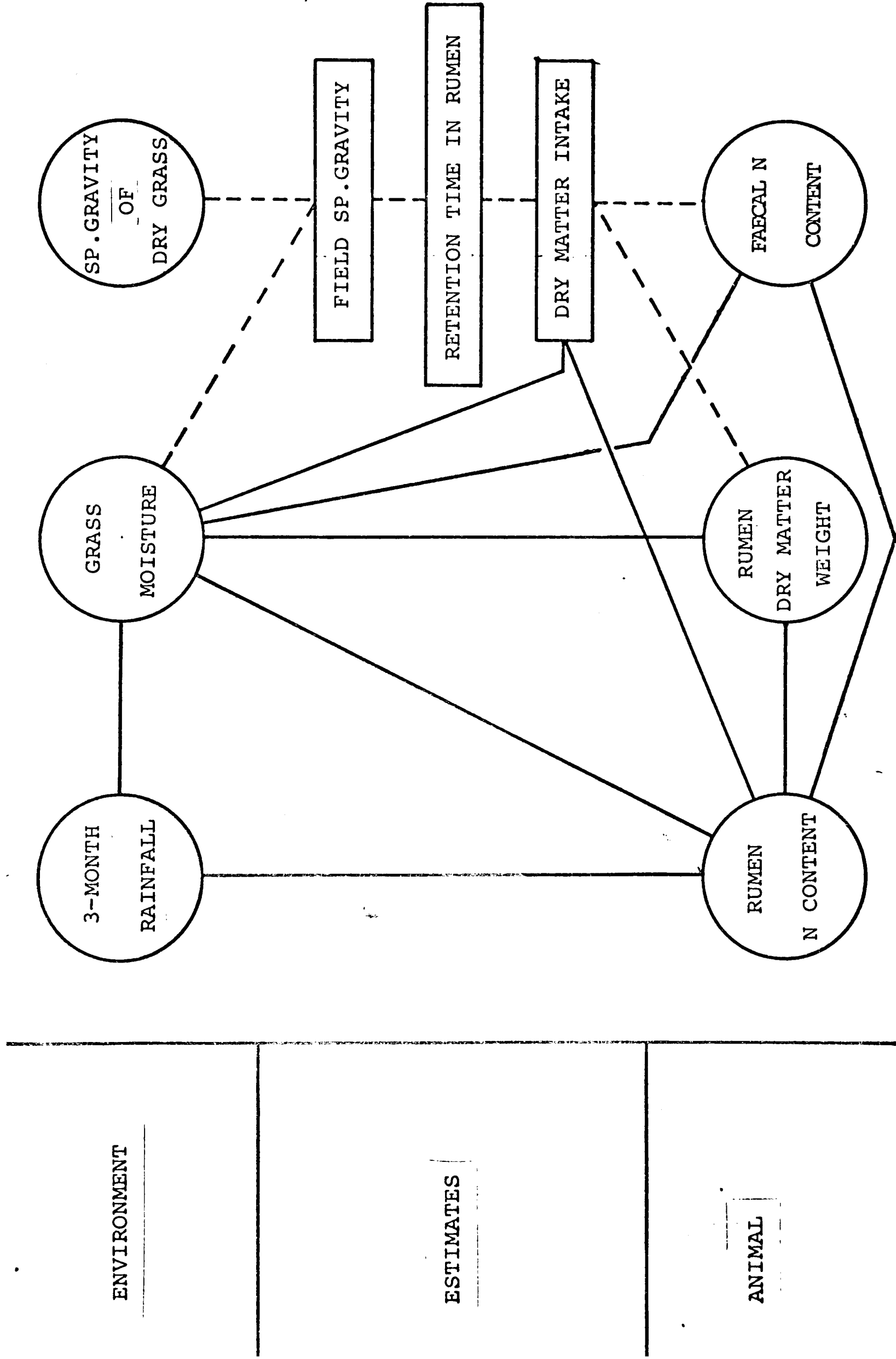


Fig.9.7. A model of some of the environmental influences on the hartebeest's nutrition and associated parameters

(Table 9.2). As the water content was the main determinant of RT (FigA12.2), such a relationship would be expected. But, the correlation above between the estimated DMI and ruminal N, and between ruminal N and grass moisture, both of which are measured rather than estimated quantities, shows that GM and DMI can be considered independent and can be correlated validly. Thus, grass moisture is an important determinant of the daily intake of the hartebeest under these conditions.

Faecal nitrogen

The concentrations of nitrogen in the rumen and faeces are highly correlated ($r = .771$, $p < 0.001$, d.f.28) (Fig 9.5.a), so that a high concentration in the faeces indicates high ruminal levels. Fig 9.5.b. confirms the expected result that FN and GM are correlated ($r = .794$, $p < 0.001$, d.f.29), and Fig 9.6 shows that the concentration of faecal N can be used to predict the animals dry matter intake:

$$\text{DMI} = 109.46\text{FN} - 61.89 \quad (r = .681, p < 0.001, \text{d.f.}28)$$

9.4 Discussion

The relationships described above are summarised in Fig 9.7 to show the interactions between the environment and the hartebeest digestive tract, and the DMI which is calculated from them. The model shows how seasonal differences in DMI arise, and suggest how intake may be controlled.

As the water content of the herbage declines through the dry season, the field specific gravity of the diet also decreases because first, the stem particles become filled with air rather than water, and, second, their abundance in the diet increases (p.155). The behaviour of these particles in the rumen results in longer retention times as described in Appendix 12. Although the capacity of the rumen increases slightly at the same time, the main adjustment by the hartebeest is to reduce the amount eaten each day. This reduction occurs at a time when the protein content, and hence nutritive value, of the grass is also declining because of little or no

rain (Braun 1974).

These changes occur together to minimize variation in the rumen environment, enabling it to operate efficiently as a fermentation chamber (Hungate 1966). As the total dry matter in the rumen increases, the N concentration decreases, resulting in relatively small changes in the total N available for microbial activity. In experimental sheep the density of micro-organisms increases proportionately with the crude protein content of the diet, suggesting that a constant proportion of the food protein is incorporated as bacterial protein under a wide range of conditions (Moir and Williams 1950).

Since plant growth in the tropics is usually limited by the availability of water (Kenworthy 1964), and actively growing grass contains the highest protein levels and water content (Armstrong 1960), the growth stage and nutritive value of grasses are largely determined by rainfall. As dry matter intake varies with the moisture content of the sward because of the influence of the latter on retention time in the rumen, it follows that when food quality is high, the hartebeest consume more each day. This suggests that voluntary intake under the conditions of this study is regulated by the hartebeest in the same way as described for domestic ruminants fed roughage diets (e.g. Blaxter 1962, Campling and Freer 1962), in which intake is partly controlled by attributes of the food rather than by the requirements of the animal. One result of this emphasis on the food is the inability to predict DMI from the weight of dry matter in the rumen (p. 175 and Fig 9.2.b). These 2 quantities were not significantly related in other studies using slaughter methods (Makela 1956, Ingalls et al 1966), while in both, DMI was inversely related to retention time, as here.

On poor quality diets, intake is limited by the rumen's finite powers of distension, but it is uncertain whether the critical limit occurs at the end of feeding (Blaxter et al 1961) or before the next meal

(Campling et al 1961). Although the amount of dry matter in the hartebeest's rumen varied between months, this information does little to solve the problem when the period since the end of the previous feeding period is unknown. The distinction is probably not as clear, anyway, in a wild ruminant feeding regularly through the day (Ch. 11) as in an animal with food available for only a few hours a day under experimental conditions.

On the other hand, most "gut distension" theories of intake regulation agree that intake is regulated by (1) the digestibility of the food in the rumen and (2) its retention time in the rumen (Blaxter 1962). In general, these two factors change together so that good quality foods are highly digestible and pass through the rumen quickly, allowing their consumption in greater quantities. In this study, the in vitro digestibilities of the grass components remained almost constant between sampling months (Table A12.3), although the crude protein levels were lower in the dry month of September, while the daily intake varied by relatively more. Low correlations between the intake of poor quality tropical hays and their digestibility have been recorded from elsewhere in East Africa (Phillips et al 1960, Soneji et al 1971), and Milford (1960) claimed that the relatively slight variations in dry matter digestibility through the year were not primarily responsible for the sub-maintenance intake of nutrients by sheep in winter (see below).

As digestibility was unsuitable for predicting rumen retention time and hence intake (Appendix 12), specific gravity was used which, as shown above, varies principally with the water content of the grass. Unfortunately little is known of the effect of intracellular water levels on intake, although in slaughter experiments, Norris (1943) demonstrated the swift passage of succulent foods through the rumen. Experiments such as those where large quantities of water are poured in to the rumen during feeding (Campling and Balch 1961) or are added to hay (Hillman et al 1958)

Table 9.4. The dry matter intakes (g/kg W^{0.73}.day) of cattle, sheep and hartebeest, from a variety of sources and this study.

Species	DMI g/kg.W ^{0.73} .day	Food	Composition	Source
cow	99.0*	chopped hay	4.9% urea and 0.88 kg concentrates added	Karue Evans and Tillman (1973)
cow	87.9	hay	50% of gross energy metabolisable	Rogerson (1970)
cow	64.4	hay	0.5% DCP	Elliott (1967a)
cow	56.0	straw	3.1% CP	Blaxter et al (1966)
sheep	50.8	hay	0.5% DCP	Elliott (1967b)
sheep	48.7	straw	3.1% CP	Blaxter et al (1966)
sheep	50.5	hay	7.5% CP	Blaxter et al (1961)
sheep	33.9	hay	8.9% CP	This study
hartebeest	41.8	hay	10.6% CP	This study
hartebeest	81.8	forage	1.87% CP	This study
hartebeest	60.0	forage	2.37% CP	This study
hartebeest	95.2	forage	2.01% CP	This study
hartebeest	27.4	forage	0.85% CP	This study

* g/kg.W^{0.75}.day

without affecting dry matter intake do not provide critical evidence of the relationship between the water content of food and its intake. Reductions in the intake of grazing sheep as the pasture matures are well known under temperate conditions (Spahr et al 1961, Minson et al 1964), and these are usually ascribed to declining digestibility, although the water content follows a parallel course (Waite and Sastry 1949). However, a drop in intake which cannot be attributed to changes in digestibility alone (Spahr et al loc. cit, Milford loc. cit) may also be due to the increasing dryness of the grass. Under East African conditions, where the water content of the grass varies between 5 and 70% (Ch. 14), and digestibility changes little, intake may be controlled in this way.

The relationship between food quality and intake is apparently contradicted by the results of the feeding trials, in which the consumption of medium quality hay by both the hartebeest and the sheep was less than the estimated intakes of lower quality forage by the shot animals in 3 out of the 4 months. Although this is treated further in the next chapter (p.198), the nutrient requirements of the penned animals were almost those necessary for maintenance only because of the restrictions upon their activity. The lower intake of penned as opposed to grazing animals is a common finding (Arnold & Dudzinski 1967),^{and,} as the weights of the animals did not increase during the trials, intake may have been regulated under these circumstances in proportion to their energy requirements. This form of regulation is known in ruminants as well as in man (Blaxter 1962).

The observed and calculated intakes by hartebeest and sheep compare closely with those from other studies, as Table 9.4 shows. In general, these figures show the daily intake of sheep to be rather less than that of cattle, which experiments with a single foodstuff confirm (Blaxter

et al 1966). The hartebeest intake in the feeding trial was 23% higher than the sheep's, while the estimated field consumptions are similar to those of cattle on the poorest feeds. The range in hartebeest intakes of 71.2% (the difference between the highest and the lowest values as a percentage of the highest value) are close to those of 73.5% and 72.7% recorded for sheep grazing sub-tropical pastures over two years (Milford 1960).

The rumen dry matter as a percentage of the hartebeest live-weight varies between sample means of 2.15 and 2.74%, while the same figure for Zebu cattle fed a 6% crude protein diet is about 2.5% (Phillips et al 1960). This similarity in RDM and intake of low quality hays by hartebeest and cattle support the conclusion from other evidence that both species have very similar feeding ecologies. Contrasted with the hartebeest, the wet rumen contents of Thomson's gazelle, which feeds on more nutritious dicotyledonous material (p. 145), contribute 11% of the live weight (Robinette and Archer 1971), while those of the hartebeest, using the moisture contents on p.174, are between 13-16% of the live-weight. In making these comparisons, though, interspecific differences in the rate of fermentation in the rumen (Hungate et al 1959) must be considered.

With the non-experimental approach to the food intake of free-living animals used here, perfect correlations between intake, retention times and food quality would be surprising. There are probably 2 main sources of error. The first is associated with the time of which the animal was shot in relation to its last feeding period. An attempt was made to reduce this source of variation by shooting animals only in the morning when feeding had stopped and, of the Series 2 animals, 20/32 were shot between 0900 and 1100 h, 5 between 1100 and 1300, and the remaining 7 between 1300 and 1435. This time effect is most likely to have affected the ruminal N levels which increase rapidly after feeding in sheep fed

twice a day (Blackburn and Hobson 1960). The amount of dry matter in the rumen is probably relatively independent of the period since feeding ceased because small particles leave the rumen during eating, as fresh material is added (Evans et al 1974). Again, there is the possibility that diurnal variations in rumen volume are not as great in wild ruminants as in experimental animals given one or two meals per day. Therefore, differences in the calculated intakes probably reflect seasonal rather than diurnal effects.

The other, potentially more serious, error, is the assumption that food intake and conditions in the digestive tract are the same for animals of all ages and physiological states. The fact the the analysis of variance failed to show any significant differences in the calculated intakes of various groupings of the animals does not vindicate this assumption. The low apparent intakes of the 3 pregnant females shot in September (Table 9.2) may be underestimates because of faster passage times which occur in pregnant ewes (Graham and Williams 1962). Table 9.2 also suggest that the intakes of lactating females may be higher, as in sheep (Arnold and Dudzinski 1967), but the sample is too small to test this.

Although the drop in food intake by the males of deer species with pronounced rutting seasons may be dramatic (Nordan, Cowan and Wood, 1968) no such effect is apparent in the hartebeest data, nor is it as likely because breeding occurs through the year (Ch. 13). The intakes of both territorial and non-territorial males are the same.

There is no consistent difference in the intake of immature animals mainly because their RDM/live - weight values are the same as those of the adults (Table 9.2). This is slightly surprising in view of the extra energy cost of growth over maintenance. The size of the rumen + reticulum relative to that of the omasum + abomasum increases after birth (Church,

Jessup and Bogart 1962), and in deer reaches its adult proportions after 4 months (Short 1964). As the youngest shot hartebeest was 8-12 months old, the calculated intakes are unlikely to have been affected by such changes.

The levels of ruminal nitrogen are more difficult to interpret in relation to the animal's nutrition. This is due to continuously changing conditions in the rumen and to the fact that the measured N may be derived from the ingested food, the saliva, the microbial population or urea which has been secreted in to the rumen from the blood system (Kay 1963). Blackburn and Hobson (loc. cit) showed that in sheep fed twice a day, the total rumen N concentration nearly doubled within an hour of feeding, then steadily decreased to the basal level over the next 7 hours, when the next meal was given.

Despite these fluctuations, high ruminal N levels have been attributed to the ingestion of good quality i.e. N-rich, food (Moen 1973). Klein (1962) came to a similar conclusion in his study of two island populations of deer, although there were no significant differences between the chemical analyses of similar forage plants from the two islands. Differences in rumen N were therefore said to be due to differences in the length of the growing season and forage availability between islands. Klein and Schonheyder (1970) distinguish "animal-derived" and "vegetative" nitrogen in the liquid and washed, solid fractions of the rumen contents of 3 species of deer, and show that these are inversely related. Although this relationship is taken to indicate an ability to compensate for variations in the N level of the food, there are great differences at a given vegetative N concentration in the animal-derived levels for summer and autumn or early spring. This suggests that the total rumen N concentration must be partly independent of the N of the food.

In the model of intake regulation (Fig 9.7), the ruminal N concentration was correlated with DMI and grass moisture, with the conclusion that the N levels are high in animals eating herbage with short retention times. As intake and forage digestibility were not related, the rumen N concentration may be more dependent upon DMI than the protein content of the food. This was also the experience of Ullrey et al (1969) who found that the ruminal N level in 3 groups of deer fed different quantities of a uniform pelleted diet was proportional to their intake. It therefore appears unwarranted to equate high nitrogen concentrations in the rumen with the ingestion of good quality food, assessed solely in terms of its protein content.

Use of faecal nitrogen concentration avoids the need to know the total faecal output of free-living herbivores to predict their intake. Although the regression applies only to hartebeest under certain conditions, the relationship probably holds for other herbivores. The hartebeest is a suitable species for this approach because it is a year - round grazer (p.153). One can only guess at the physiological changes associated with the switch in diet from grass and herbs to browse in the dry season shown by impala or eland (p.142). Differences in the packing ability in the rumen of grass and legumes entails the calculation of separate regression equations for intake (Thornton and Minson 1973), and the ingestion of woody browse would make prediction even more complex.

Grass moisture is an important determinant of intake, but the water content of the grass varied only between 13.9% and 35.0% in the sampling months, even though extreme values of 5% and 70% are encountered (Ch. 14). Intake is unlikely to continue increasing linearly as the water content rises to these high levels, and under these circumstances other mechanisms, similar to those in animals fed concentrate diets (Blaxter 1962), may regulate intake. Here, also, experiments with wild herbivores are needed.

Chapter 10

NUTRITION AND METABOLISM

10.1 Introduction

In the last chapter I considered the daily intake of dry matter and its seasonal variation. With the results of chemical analyses of herbage samples and hays fed to experimental animals, these intakes can be translated in to intakes of nutrients, notably protein and energy. These form the basis of this chapter.

The hartebeest are capable of feeding selectively (p.158), and the nutritional gain from doing so is due to two factors. The first results from the favoured leaf fraction having a higher crude protein content than stem (Table A12.2). In addition, as the occurrence of leaf in the diet increases, intake is greater because of the relatively short retention time of leaf in the rumen (Fig. A12.3), so that, overall, the protein intake is greater than if the grass components were eaten in their natural proportions. The advantage of being selective is measured by calculating for each month the crude protein content of the average diet of the shot animals and of a hypothetical diet which would result from consuming the sward unselectively.

A proportion of the ingested nutrients is lost to the animal through not being assimilated. This proportion can be determined by combining the amounts eaten with the apparent digestibility coefficients obtained from the feeding trial. The proportion of digestible energy available to the animal's metabolism can be calculated from this by subtracting the energy lost in the urine and methane formation in the rumen (Blaxter et al 1966). This metabolisable energy then exceeds the net energy available to the animal by an amount due to the heat increment of fermentation in the rumen, and correction factors again derived for domestic stock are used.

The net quantities of nutrients obtained by the animal are used first for its maintenance (basal or fasting requirements), and any surpluses are then available for processes such as activity, growth or reproduction. The experiments necessary to measure the minimum essential quantities of nutrients were beyond the scope of this study, but have been adequately established for cattle and sheep in the tropics to allow comparison with the data presented here.

Extrapolation of the energy requirements of domestic ruminants to the hartebeest may be less worth-while for there is considerable deviation from the interspecific mean fasting metabolic rate (FMR) of $70 \text{ kcal/kg W}^{.73}$ day (Brody 1945). The mean FMR of cattle is 15% greater than this value while that of sheep is 15% lower (Blaxter 1962). In this chapter the results of measurements of oxygen consumption, and hence heat production, of a tame hartebeest are presented, and the maintenance energy requirement is also calculated from the results of the feeding trials. The latter method, in addition, enables a direct comparison of the requirements of hartebeest and sheep under the same conditions, and the sheep result can be compared with published values.

From these approaches, deductions can be made about the nutritional status of the hartebeest population through the year, and these are pertinent to the discussion of their physical condition (Ch. 12) and reproductive strategy (Ch. 13).

10.2 Methods

The gain from selective grazing.

The amount of digestible crude protein (DCP) is a unit weight of hartebeest food or sward is :

$$(\% \text{ leaf} \times \text{CP}_l \times \text{OMD}_l)/100 + (\% \text{ sheath} \times \text{CP}_{sh} \times \text{OMD}_{sh})/100 + (\% \text{ stem} \times \text{CP}_{st} \times \text{OMD}_{st})/100$$

where CP is the crude protein content of leaf (l), sheath (sh) and stem (st), and OMD is the organic matter digestibility of each.

The retention times of each grass component in the rumen in each month are shown in Table A 12.3. Similarly, the overall retention time (RT_o) of a unit weight of food or sward in the rumen is:

$$(\% \text{ leaf} \times RT_l)/100 + (\% \text{ sheath} \times RT_{sh})/100 + (\% \text{ stem} \times RT_{st})/100$$

Using the mean weight of dry matter in the rumens of the adult hartebeest in each month (Table 9.2), two mean dry matter intakes can be calculated. One intake is the actual intake of the hartebeest, and the other is the hypothetical intake if they ate the sward unselectively, and its calculated retention time then determined the level of intake as described in the last chapter (p.175). As the DCP content of the diet and sward is known (above), its actual and hypothetical intakes can be calculated and the difference between them is the gain to the hartebeest from grazing selectively.

Digestive efficiency

Details of the feeding trials were given in the last chapter (p.170), and the resulting daily intakes of dry matter by the hartebeest and sheep have been discussed (p.173). Here, the digestive ability of the two species is compared by calculating the digestibility of any constituent is calculated as:

$$\frac{(\text{weight of } x \text{ in food}) - (\text{weight of } x \text{ in faeces})}{\text{weight of } x \text{ in food}}$$

Coefficients for dry matter, organic matter, crude protein, crude fibre ether extractives, nitrogen-free extract and gross energy have been calculated.

Intakes of metabolisable energy, digestible crude protein and total digestible nutrients

The daily intake of gross energy for the experimental hartebeest and sheep, and a mean figure for the shot adults, is obtained as the product of the daily DMI and the gross energy of the diet. For the shot animals the latter is calculated in the same way as the DCP content of the diet but the energy contents of the grass parts are used instead. The value for the apparent digestibility of energy from the feeding trial is used to calculate the daily intake of digestible energy (DE). The fraction of DE lost to the animal through urine and methane production is assessed according to the method of Blaxter, Clapperton and Martin (1966). The remaining energy is metabolisable energy (ME). To remove the effects of body size, the daily intake of ME is expressed per kg metabolic weight (p.172) as $\text{kcal ME/kg.W}^{.73} \cdot \text{day}$.

The measured digestibility coefficients are used with the chemical composition of the hartebeest and sheep hays to calculate their TDN contents. This is defined as :

$$\text{TDN} = \% \text{DCP} + \% \text{DCF} + \% \text{DNFE} + 2.25 (\% \text{DEE}) \quad (\text{McDonald et al 1973})$$

where DCP = digestible crude protein

DCF = digestible crude fibre

DNFE = digestible N-free extractive

DEE = digestible ether extract

Using the daily dry matter intake, the daily intake of TDN is obtained.

The incomplete data on sward/^{chemical}composition when the hartebeest were shot (Table A.12.2) meant that TDN content had to be calculated using the conversion factor that 3.56 cal ME are equivalent to 1 g. TDN (McDonald et al loc. cit). TDN intake was then calculated using daily DMI, as above.

Weight changes

As both hartebeest and sheep were weighed at the beginning and end of the feeding trials, any increase or decrease in weight would suggest nutrient intakes either above or below those necessary for maintenance.

Maintenance standards of DCP and TDN for domestic ruminants were stated by Brody (1945) as 3.65 g DCP/kg.W^{.73}.day and 36.5 gTDN/kg.W^{.73}.day, but subsequent work in Africa (Elliott and Topps 1963, 1964) has shown that under some conditions, at least, these requirements are inflated. Maintenance requirements for cattle have been formulated from long-term feeding trials, allowing weight changes to be predicted when intake of these nutrients is some percentage of Brody's standards.

The measured intakes of DCP and TDN by hartebeest and sheep enable the observed weight changes to be compared with the predicted ones. Agreement between these values means that the hartebeests requirements for these nutrients are similar to those of the domestic species. The calculated intakes of the shot animals can then be used to suggest the pattern of weight change through the year under field conditions.

Measurement of metabolic rate

Two methods were used to measure metabolic rate. One was direct, the other indirect.

In conjunction with Dr. V.A. Finch the fasting metabolic rate of a 100 kg tame hartebeest was measured using the methods of Finch (1972). The animal was trained to stand in an outdoor crush and to wear a face mask, which did not affect the respiratory rate below rates of 60 expirations per minute. A two-way valve allowed the expired air to pass through flexible tubes in to Douglas bags. The oxygen tension in the expired air samples was analysed on an oxygen electrode (Cambridge blood gas analyser, Model 48C, Electronic Instrument Ltd.,). As preliminary

experiments had established the relationship between respiratory rate and the minute volume of air, the minute value of oxygen consumed could be calculated and converted to standard conditions of temperature and pressure.

The hartebeest was deprived for food for 16 h before each measurement in an attempt to attain the post-absorptive state. The metabolic rate measured under these conditions approximates to the fasting metabolic rate, which is almost equal to the basal metabolic rate of ruminants (Blaxter 1962).

Calculation of metabolisable energy intake during the trial allows the metabolic rate to be calculated indirectly. If there are no weight changes and the animals are not fasted, the maintenance energy requirement is measured, from which the FMR can be calculated because ruminants need 1.36 kcal ME for every 1 kcal expended during fasting (Blaxter 1962). The FMR of sheep obtained by this method is compared with published figures.

Water consumption

Water intake was measured during the feeding trial by replenishing a graduated bucket each day (p.170). As consumption was measured only to the nearest 0.5 l, the loss from evaporation was considered insignificant. The mean daily intake has been calculated in terms of the metabolic weight of the animal.

Gross energy values

Sward samples collected when the hartebeest were shot were burnt in an adiabatic bomb calorimeter. Separate values for the leaf, sheath and stem components were obtained.

10.3 Results

Selective feeding

The mean daily intake of DCP by adult hartebeest in each month is shown in Table 10.1, calculated by the methods above, The last

Table 10.2. The digestibility coefficients of hartebeest and sheep fed medium-quality hays.

	Digestibility coefficients, %	
	Hartebeest	Sheep
Dry matter	49.7	56.6
Organic matter	56.0	58.4
Crude protein	59.0	61.9
Crude fibre	56.8	60.4
Ether extractives	50.9	65.4
N-free extract	54.8	55.1
Gross energy	50.4	55.0

column shows the percentage increase in DCP intake due to grazing selectively, rather than consuming the grass components in their natural proportions.

The most notable result is the virtual constancy of daily DCP intake in the first 3 months, with its reduction by about 80% in September. By comparison, the hypothetical intake increases through the first 3 months, so the gain to the hartebeest declines from 77% through 51% and 11% to 9%. Because of the doubtful value of comparing the January sward sample with the mean diet of that month (p.157), the 77% increase is almost certainly an overestimate. Disregarding this month, the hartebeest appear capable of increasing their daily DCP intake by one and a half times by feeding selectively, although when, as in September, the amount of available protein is very low, the protein content of their diet is almost that of the sward. This situation obviously coincides with their observed failure to eat significantly more leaf than that on offer (p. 158).

Digestive efficiency

The composition of the hays fed to the hartebeest and sheep are included in Table 9.1, which shows them to be very similar. The similarity in composition of the hay eaten and refused by the former shows that it was not feeding selectively. This hay contained slightly more CP and carbohydrate (NFE), and less crude fibre than the hay fed to the sheep. However, the apparent digestibility coefficients (Table ¹⁰9.2) of the hartebeest are in each case almost the same or several units lower than those of the sheep. The latter is more efficient by several units at digesting dry matter, crude fibre energy and fat. Although the trials only involved a total of 3 animals, these results suggest that the two species do not differ radically in their ability to digest medium - poor quality hays.

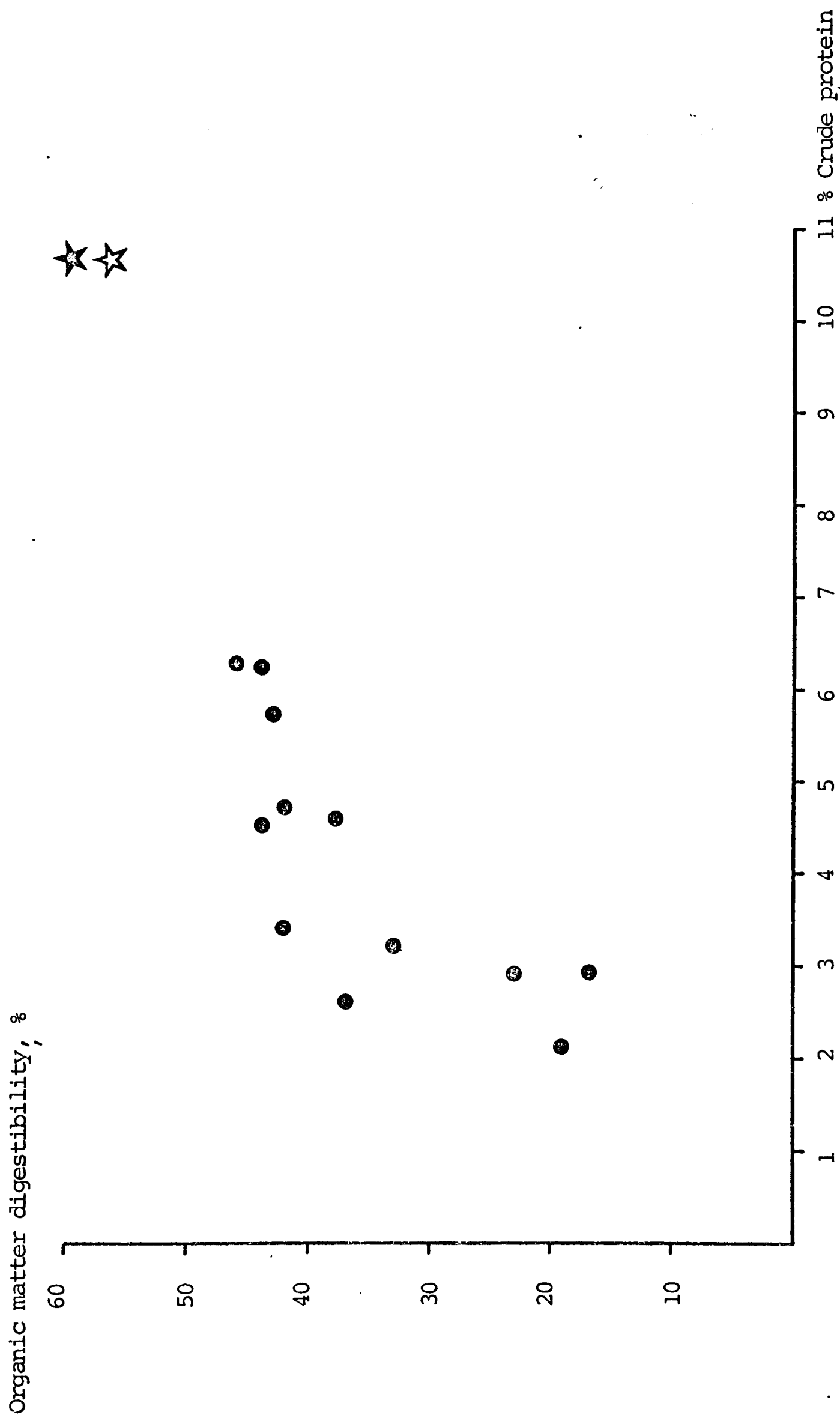


Fig 10.1. The crude protein contents and in vitro digestibilities of grass components, and the hartebeest's organic matter (★) and crude protein (★) digestibilities measured in vivo.

In the last section, the DCP contents of the diets were calculated as the products of the CP content and the in vitro organic matter digestibilities of the grass components. Although there are many expressions relating the CP of feeds to its digestibility (Glover, Duthie and French, 1957, Steenkamp and le Roux 1972), OMD was considered appropriate because of the similarity between measured hartebeest protein and organic matter digestibilities, and their position close to the line relating CP and in vitro OMD values of the grass samples (Fig 10.1).

Intakes of DCP, ME, and TDN.

Table 10.3 shows the mean DMI and DCP content of the diet of the shot adults (from Table 10.1), and the experimental hartebeest and sheep (columns, A, B). Their product is the total DCP intake (Col.C) which, when divided by the metabolic weight ($\text{kg.W}^{.73}$, col D) is the daily intake of DCP as $\text{g/kg.W}^{.73}.\text{day}$ (col.E).

Column E shows that the DCP intake of January, April, and September remained relatively constant between 1.47 and 1.89 $\text{g/kg.W}^{.73}.\text{day}$, but dropped in September to only 0.23 $\text{g/kg.W}^{.73}.\text{day}$. The intake of the experimental sheep of 1.85 $\text{g/kg.W}^{.73}.\text{day}$ is about that of the hartebeest in the first 3 months, although the CP content of the hay was higher. The intake of the experimental hartebeest was even higher at 2.6 $\text{g/kg.W}^{.73}.\text{day}$.

These intakes are compared first with Brody's (1945) maintenance requirement of 3.65 g DCP/ $\text{kg.W}^{.73}.\text{day}$ (Col.F), and then with the standard of 1.3 $\text{g/kg.W}^{.73}.\text{day}$ (Elliott and Topps 1963) in Column G. The higher intake by the experimental hartebeest is only 71% of Brody's maintenance requirement, while all the other values are about 45% of this standard, except for that of September which is only 6%. On the other hand, except for this latter month, intake by the hartebeest in the field and by the experimental animals exceeds the requirement of 1.3 $\text{g/kg.W}^{.73}.\text{day}$ (Col.G). The experimental hartebeest was obtaining exactly twice this amount each day.

Table 10.4

The estimated daily intakes of metabolisable energy by shot hartebeest, and measured intakes by experimental hartebeest and sheep.

Month of sample or experimental animal.	A		B		C		D		E		F		G		H		I	
	Gross energy of diet cal/g	DMI kg/day	GE intake kcal/day	GE digestibility %	Digestible energy intake kcal/day	Metabolisable energy (ME) as % of DE	ME intake kcal/day	ME intake kcal/kg W ^{.73}	ME intake kcal/kg W ^{.73} .day									
January	4039	2.68	10824	50.4	5455	80.8	4408	32.8	134.4									
April	4002	2.08	8324	50.4	4195	80.8	3389	33.6	100.9									
July	3995	3.25	12984	50.4	6544	80.8	5287	34.5	153.2									
September	4033	0.96	3872	50.4	1951	80.8	1576	35.4	44.5									
Hartebeest	4135	1.27	5251	50.4	2646	80.8	2138	30.5	70.1									
Sheep	4038	0.67	2705	55.0	1488	82.0	1220	19.9	61.3									

Table 10.5 The estimated daily intakes of total digestible nutrients of the shot hartebeest, and measured intakes of the experimental hartebeest and sheep.

Month of sample or experimental animal.	A			B		C		D		E		F		G	
	TDN in diet g/100 g	DMI kg/day	TDN intake g/day	W ^{.73} kg	ME intake kcal/kg W ^{.73} .day	TDN intake g/kg W ^{.73} .day	TDN intake as % of 35.2 g TDN/kg W ^{.73} .day								
Hartebeest	51.2	1.27	650.2	30.5	- (70.1)	21.3 (19.7)	61								
Sheep	54.1	0.67	362.5	19.9	- (61.3)	18.2 (17.2)	52								
January					134.4	37.7	107								
April					100.9	28.3	80								
July					153.2	43.0	122								
September					44.5	12.5	35								

Table 10.4 shows the energy intakes calculated in the same way. Column A contains the gross energy content of the diet, and column B the daily DMI. Their product (Col.C) is the gross energy intake per day. The apparent digestibility coefficients of gross energy of 50.4% for the hartebeest and 55.0% for the sheep (Col.D), obtained from the feeding trials, are used to calculate the digestible energy (DE) intake (Col.E). The fraction of DE lost through urine and methane is proportional to the apparent digestibility, and from these coefficients, 80.8% of the hartebeest's DE is metabolisable energy, and the value for the sheep is 82.0% (Blaxter et al 1966) (Col.F). Column G contains the metabolisable energy intake, which when divided by the metabolic weight (Col.H), shows the intake of ME as $\text{kcal/kg.W}^{.73}.\text{day}$.

The intake of ME by the experimental hartebeest is slightly greater than that of the sheep: 70.1 and 61.3 $\text{kcal/kg.W}^{.73}.\text{day}$ respectively. These values are clearly exceeded by the calculated intakes of the hartebeest under field conditions in January, April and July, but the September intake is only 44.5 $\text{kcal/kg.W}^{.73}.\text{day}$.

Table 10.5 shows how the daily intake of TDN is calculated. Column A shows the TDN content of the hays with the digestibility coefficients of CP, CF, NFE and EE, measured for the experimental animals, used in the expression on p. 188. Multiplication by the daily DMI (Col.B) gives the daily intake of TDN (Col.C). Column D shows the metabolic weights, and column F contains the daily intake as $\text{g TDN/kg.W}^{.73}.\text{day}$. The equivalent intakes by the hartebeest under field conditions have been calculated as the product of the daily intake of ME (Col.E, from Table 10.4), using the relationship that 1 g TDN provides 3.56 cal ME. The intakes of the experimental animals calculated in this way are included for comparison. From column F, the TDN intake of the experimental hartebeest is slightly greater than the sheep's (21.3 and 18.2 $\text{g/kg.W}^{.73}.\text{day}$), but is less than the calculated intakes under field conditions in all months except September.

Intake in this month drops to 12.5 g/kg W^{.73}.day from the maximum of 43.0 g/kg W^{.73}.day in July.

Column G shows the TDN intakes as percentages of Brody's maintenance requirement of 35.2 g TDN/kg W^{.73}.day. Compared to this, intake by the experimental hartebeest and sheep fell short by 39 and 48% respectively. Under field conditions, apparently deficient intakes occurred in April and September, while the intakes of 37.7 and 43.0 g/kg W^{.73}.day in January and July were only just adequate.

Water consumption

Over the 10 day trial period the hartebeest drank an average of 3.2 litres/day. With a live-weight of 108 kg, this is equivalent to 9.46 litres/100 kg W^{.75}.day. The total amount available to the hartebeest exceeds this by the quantity of preformed water in the hay and the water formed by oxidation of the food.

Weight changes

During the feeding trials the weight of the hartebeest dropped by 1 kg (Table 9.1), which is no more than the limits of accuracy of the weighing station (p.171). On the other hand, the sheep's weight decreased by an average of 3.8 kg over 17 days, equivalent to a loss of 0.22 kg/day, showing that their nutrient intakes were not meeting their maintenance requirements.

Elliott and Topps (1964) have calculated from experimental results the weight gains or losses to be expected in cattle with intakes of different amounts and proportions of TDN and DCP, relative to Brody's standards of 35.2 g TDN/kg W^{.73}.day and 3.65 g DCP/kg W^{.73}.day. The measured intakes of these nutrients by hartebeest and sheep are shown as percentages of these figures in Tables 10.3 and 10.5. With the sheep's intake of 51% and 52% of the DCP and TDN requirements respectively, a cow would lose 0.25 kg/day, compared to the observed loss of 0.22 kg/day by the sheep. With the hartebeest intake of 71% and 61% of these standards, the weight

loss would be lower at 0.1 kg/day.

These predicted losses cannot be compared too literally to those observed during short-term experiments because:

1. The body sizes of the species differ, so that the significance of a given weight change is not the same for all.
2. Their requirements for these nutrients may differ. The requirements of sheep and cattle for DCP are certainly not the same (Elliott and Topps 1963, 1964).

Despite these limitations, the observed weight changes suggest that the hartebeest's requirements for DCP and TDN are not very different from those of the domestic species. When the calculated intakes of the shot animals are compared in the same way (Tables 10.3 and 10.5), the January intake appears adequate to maintain bodyweight, whereas substantial surpluses for production would exist in July. The intakes of April and September are below these maintenance requirements, indicating weight losses which on this basis would be considerable in the latter month.

Metabolic rate and energy intake

The mean metabolic heat production at midday of the hartebeest at Athi River was $0.113 \text{ cal/cm}^2 \cdot \text{min}$ (Finch 1972). Over a series of 19 determinations covering respiratory rates between 14 and 28 expirations per minute, the mean oxygen uptake and its standard deviation was 0.479 ± 0.087 litres oxygen/minute, equivalent to a mean heat production of $0.117 \text{ cal/cm}^2 \cdot \text{min}$ (Finch pers.comm.1974).

The fasting metabolic rate (FMR) is calculated from the first figure as follows :

$$\begin{aligned} \text{mean } O_2 \text{ uptake} &= 0.479 \text{ litres/min.} \\ &= 2.322 \text{ kcal/min produced, when consumption of} \\ &\quad 1 \text{ litre } O_2 \text{ causes the release of } 4.85 \text{ kcal.} \\ &= 3343 \text{ kcal/day.} \end{aligned}$$

weight of animal (W) = 100 kg. Metabolic weight ($W^{.73}$) = 28.8 kg.

$$\begin{aligned}\text{therefore, FMR} &= 3343/28.8 \\ &= 116.1 \text{ kcal/kg.}W^{.73}.\text{day.}\end{aligned}$$

The intakes of metabolisable energy by the experimental hartebeest and sheep were 70.1 and 61.3 kcal/kg. $W^{.73}$.day respectively (Table 10.4), which divided by 1.36 gives FMR's of 51.5 and 45.1 kcal/kg. $W^{.73}$.day. As the hartebeest's weight stayed constant, this can be regarded as a reasonable estimate of its FMR from this indirect method of measurement, but the FMR of the sheep value must be an underestimate because of the weight loss described above. The mean FMR of 6 year old wether sheep of 52.4 kcal/kg. $W^{.73}$.day (Blaxter 1962) confirms that this value is low, but it is almost exactly that of the hartebeest. On these grounds, the latter also has a lower FMR than the interspecific figure of 70 kcal/kg $W^{.73}$.day.

The difference between these estimates of FMR are discussed later (p.199). The following table compares the intakes of ME by the shot animals with the two estimates of the energy required for maintenance, calculated as 1.36 x FMR.

Month	ME intake kcal/kg. $W^{.73}$.day	ME intakes as % of 70.1 kcal/kg. $W^{.73}$.day	ME intakes as % of 157.9 kcal/kg. $W^{.73}$. day.
January	134.4	192	85
April	100.9	144	64
July	153.2	218	97
September	44.5	63	28

Using the higher metabolic rate the daily intake of ME is apparently below the maintenance level in all four months, although weight losses were surmised for only April and September. On these grounds the lower maintenance requirement of 70.1 kcal/kg $W^{.73}$.day seems more reasonable, in which case energy surpluses would exist in all months except September when daily ME intake dropped to 63% of the maintenance requirement.

10.4 Discussion

The ability of sheep and cattle to feed selectively in a grass sward is well known, and some of the factors affecting this ability were discussed in Chapter 8 (p.164). However, the number of cases in which the total gain to the animal has been measured is small. Bredon, Torrel and Marshall (1967) showed that oesophageal fistula samples from steers in Uganda contained 66.4% more crude protein and 7.7% less crude fibre than clipped samples, but they did not consider the possibility of an enhanced intake from their selection of a more digestible diet. The difference between DCP levels of the diet and the sward is much less in this study, but under some conditions the hartebeest appear capable of increasing their DCP intake by 50% by feeding selectively. The importance of this to the hartebeest is indicated by the fact that, without selection, in January, April and September the calculated intakes of DCP would be below the maintenance standard of $1.3 \text{ g/kg W}^{.73} \text{ .day}$, whereas the actual intake was inadequate on this criterion only in September.

The finding that the digestive efficiency of the hartebeest compares well with that of sheep agrees with Rogerson's (1968) comparison of eland and wildebeest with cattle. There is little difference in the ability of reindeer and sheep to digest high quality, artificial diets (Eriksson and Schmekel 1962) or between sheep and red deer given hay diets (Maloiy and Kay 1970). There is therefore little evidence to suggest that domestic ruminants are superior in this respect.

The low intakes of DCP and TDN compared to Brody's standards for maintenance suggest that some ruminants, at least, can survive on lower amounts. Elliott and Topps (1963) showed that tropical cattle accustomed to feeding on low quality, unimproved pastures had DCP requirements as low as $1.3 \text{ g/kg W}^{.73} \text{ .day}$, although this phenomenon is not confined to the tropics (Robinson and Forbes 1966). Further work showed that this was

due to the efficiency of utilisation of N by cattle, provided the amount of available carbohydrate was adequate. Thus, the inverse relationship between the amount of DCP required and the energy consumed, measured as TDN (Elliott et al 1964), shows that when the energy is adequate, dietary protein is used for tissue maintenance and is not catabolised as a source of energy. The intake of DCP by the experimental hartebeest was twice the minimum requirement of $1.3 \text{ g/kg.W}^{.73} \cdot \text{day}$, suggesting that this enabled it to maintain its weight despite a lower energy intake than that calculated for the shot animals. The sheep's protein intake also exceeded this requirement, but by a smaller margin. The measured intake of $18.2 \text{ g TDN/kg.W}^{.73} \cdot \text{day}$ is less than the maintenance requirement of $22 \text{ g/kg.W}^{.73} \cdot \text{day}$ estimated for Blackhead Persian sheep in Rhodesia (Elliott and Topps loc.cit.) and this combination may have been inadequate to prevent the observed loss of weight.

Applying the same minimum needs to the shot animals, the calculated DCP intakes in January, April and July exceed the figure of $1.3 \text{ g/kg.W}^{.73} \cdot \text{day}$ by smaller margins (Table 10.3). On the other hand, the intakes of TDN are relatively high compared to either Brody's standard or those of the studies quoted above (Table 10.5). This suggests that under field conditions in these months, the intake of dry matter was more than adequate to satisfy the hartebeest's energy requirements. This is due to the high DMI's of the shot animals compared to that of the experimental hartebeest (Table 10.3). Thus, in such months production would be limited by the level of available protein rather than energy. In the dry season, represented here by September, the intakes of both DCP and TDN drop and this might lead to weight losses.

The ability of ruminants to maintain a positive N-balance when the protein content of the food is low is of obvious adaptive significance for survival in the semi-arid tropics where grassland crude protein levels are low compared to the values found in temperate regions (Milford 1960).

The mechanisms of N conservation by recycling it have been studied in the camel (Schmidt-Nielsen et al 1957) and in sheep (Somers 1961). But despite the low requirement due to such mechanisms, the daily intake of DCP by the hartebeest never exceeds the minimum amount of $1.3 \text{ g/kg W}^{.73}$ day by more than 50% (Table 10.3). This small range is partly due to the small variation in the measured CP content of the sward (Table A12.2) although CP levels depend on rainfall (Braun 1974), and the rainfall in this period of 1972 was typical in quantity (p. 156).

The discrepancy between the measured heat production of the hartebeest and the calculated requirement of metabolisable energy is considerable. Part of this difference may result from using a single animal only for each measurement. Silver et al (1969) recorded considerable inter-individual variation in the heat production of white-tailed deer in any season, with values between 80% and 120% of the mean. The hartebeest used in the metabolism measurements had a long history of infestation by gut parasites, and for this reason was not used in the feeding trial. Although one cannot predict the systematic effect of this on his metabolism, his normal diet included quantities of lucerne and concentrates, both of which are rich sources of energy, and would probably provide a normal hartebeest with a diet considerably above the maintenance level. Blaxter (1962) shows that heat production by sheep is 1.88 times greater on a full-feed diet than on a fasting diet, whereas the ratio on a maintenance diet is only 1.47 : 1. Thus, the measured fasting heat production of $116.7 \text{ kcal/kg.W}^{.73}$.day may be an overestimate for these reasons, and also because the animal was almost certainly not in a truly post-absorptive state after a fast of 16 h. This state is reached in sheep on a maintenance diet only after 72 -96 h without food (Harston 1948). Heat production after 16 h fasting might be 25% greater than that of the true fasting state.

Rogerson (1968) observed that although the efficiency of utilisation of food by wildebeest and eland was the same as by cattle, the higher

metabolic rates of the wild species would require larger intakes of food each day. The experimental hartebeest consumed 23% more dry matter per day on a metabolic basis (Table 9.1) than the sheep but a parallel difference in metabolism cannot be presumed because the sheep's intake was below the maintenance level. The hartebeest FMR of $51.5 \text{ kcal/kg.W}^{.73} \cdot \text{day}$ is lower than the value of $80.4 \text{ kcal/kg.W}^{.73} \cdot \text{day}$ for indigenous cattle in East Africa (Rogerson 1970), although the dry matter intakes of both species appear to differ little (Table 9.4). It is reasonable to conclude that the hartebeest FMR is probably rather less than the interspecific mean figure of $70 \text{ kcal/kg.W}^{.73} \cdot \text{day}$, tending, therefore, to be nearer that of sheep than cattle.

Although there are few measurements of the metabolic rates of wild ruminants, the values obtained directly or indirectly tend to be higher than $70 \text{ kcal/kg.W}^{.73} \cdot \text{day}$, for a fasting animal. This applies in temperate regions to white-tailed deer (Silver et al 1969, Ullrey et al 1969), caribou and reindeer (McEwan 1970, McEwan and Whitehead 1970), red deer (Brockway and Maloiy 1967). Fasting metabolic rates reported for tropical ruminants are those of $104.3 \text{ kcal/kg.W}^{.73} \cdot \text{day}$ for wildebeest and $111.2 \text{ kcal/kg.W}^{.73} \cdot \text{day}$ for eland (Rogerson loc.cit), and $141.0 \text{ kcal/kg.W}^{.73} \cdot \text{day}$ for blesbok, recalculated from du Plessis (1972). The first two rates are based on respiratory exchange measurements, the last indirectly from food consumption.

The hartebeest value of $51.5 \text{ kcal/kg.W}^{.73} \cdot \text{day}$ is clearly lower, but meaningful comparison with these other species must take account of the ecological conditions normally experienced by them. The hartebeest inhabits open plains, rarely seeking shade, and is adapted to the heat stress imposed by the extreme insolation found in East Africa (Finch 1972). The Beduin goat is found in even hotter and more arid areas, and at air temperatures of 30°C its minimal metabolic rate is 30% below the interspecific $70 \text{ kcal/kg.W}^{.73} \cdot \text{day}$ (Shkolnik et al 1972). The fasting

Table 10.6 The minimum water requirements of some East African
bovids, at 22 oC.

	litres/100 kg ^{.75} .day
Hereford cow	18.49
Buffalo	12.72
Eland	12.71
Wildebeest	10.53
Hartebeest	9.17
Zebu cow	8.13
Oryx	5.66
Grant's gazelle	4.63
Thomson's gazelle	4.37

The data are from Taylor (1968) except for the hartebeest figure which is calculated from Maloiy and Hopcraft (1971).

metabolic rate of $49.1 \text{ kcal/kg.W}^{.75} \cdot \text{day}$ of the kangaroo, Macropus, (Dawson & Hulbert 1970) which also inhabits semi-arid areas suggests that animals in such environments have relatively low rates of heat production, although the FMR's of all marsupials tend to be slightly lower than those of eutherian mammals (Dawson and Hulbert loc.cit.). In this context, it is unfortunate that there are no measurements of heat production by East African oryx or gazelle. Although found in arid areas, the eland survives through behavioural rather than physiological ~~adaption~~^{adaptation} (Taylor 1968).

Possible differences in metabolic rates within the spectrum of East African ruminants can be surmised because of the positive correlation between basal metabolism and water turnover rates (Macfarlane and Howard 1972). The latter is easier to measure than heat production under semi-natural conditions. Table 10.⁶/₇ shows the minimum water requirements of some East African bovids, taken from Taylor (loc. cit.). Although the hartebeest was not included, its requirement can be calculated as $9.17 \text{ litres/100 kg.W}^{.75} \cdot \text{day}$ from the data of Maloiy and Hopcraft (1971). The rank order shows the water requirements of the hartebeest to be slightly greater than those of the Zebu cow, although under field conditions (Maloiy and Hopcraft loc.cit), the water turnover by Boran cattle was $222 \text{ ml/kg.W}^{.82} \cdot \text{day}$, while that of the hartebeest was only $116 \text{ ml/kg.W}^{.82} \cdot \text{day}$.

Considering the wild ruminants along, at 22°C the eland and wildebeest need 39% and 15% more water daily than the hartebeest, which agrees qualitatively with their higher FMR's of 111.2 and $104.3 \text{ kcal/kg.W}^{.73} \cdot \text{day}$ (Rogerson 1968). Water consumption by the experimental hartebeest amounted to $9.46 \text{ litres/100 kg.W}^{.75} \cdot \text{day}$ which, even with the water of the food and the metabolic water, is close to the figure of $9.17 \text{ litres/100 kg.W}^{.75} \cdot \text{day}$ above. Assuming the general relationship between FMR and water turnover, the hartebeest's water economy is further evidence of a lower metabolic

rate than that of either the wildebeest or eland. Its FMR is closer to that of the cow, although its water requirement is considerably lower.

Although the hartebeest survives on poor quality grasslands, the calculated intakes in the dry season imply weight losses. In chapter 12 seasonal weight changes are shown to be slight and this suggests the operation of mechanisms to reduce the impact of such conditions, which may last for several months of the year. During the dry season, the animals are under stress because environmental temperatures are highest, the moisture content and protein level of the grass are lowest, the grass biomass has been reduced through grazing and water sources are more localized.

Farrell et al (1972) describe how under conditions of malnutrition due to low herbage availability, the fasting heat production of sheep decreases as their weight drops, and similar effects are known in man (Blaxter 1962). Dehydration produced the same effect in the camel (Schmidt-Nielsen et al 1967), whose metabolism dropped by 23.5% when the body weight was only 77.7% of that of the fully hydrated animal. Although a lowered metabolism reduced the amount of heat to be dissipated, thereby saving water, net heat production by the camel during dehydration was greater because its labile body temperature allowed heat to be stored. During outdoor experiments Finch (1972) found that with shade temperatures between 22° and 32°C from 0900 to 1500 h, the body temperature of the hartebeest increased only by 0.6°C, which suggests that, under normal conditions, heat storage is small. Thus any decrease in metabolic rate would reduce the amount of heat, and hence water, to be lost through panting, the hartebeest's main avenue of heat loss (Finch loc.cit).

Silver et al (1969) showed that the FMR of adult male white-tailed deer in summer coat was 49% higher than when in winter coat. The parallel reduction in voluntary intake even with food available ad libitum in captivity suggests an adaptation to the lower quality foods eaten in winter

Table 10.7. The dry matter content of hartebeest faeces and the urinary loss of water by hartebeest.

Conditions	% dry matter - S.D.	urinary loss litres/100 kg.day	Source
<u>Wild population</u>			
Jan.	40.0 [±] 8.3	-	this study, shot animals
April	42.1 [±] 6.2	-	"
July	41.4 [±] 4.6	-	"
Sept.	46.6 [±] 4.3	-	"
<u>Experimental</u>			
22°C, water <u>ad lib.</u>	41.7	1.87	Maloiy & Hop- craft (1971)
22°C, minimum water	43.9	0.70	"
22-40°C, water <u>ad lib.</u>	42.0	0.71	"
22-40°C, minimum water	48.1	0.42	"
Approx. 22°C, water <u>ad lib.</u>	42.7	-	this study, feeding trial

under natural conditions. There is no direct evidence, that heat production by the hartebeest is lower in the hot and dry months when diet quality is lower (Table 10.3), but adjustments in the water economy are suggested by the dry matter contents of the faeces of the shot animals (Table 10.7). The faeces in the dry month of September clearly contain less water. Comparable figures for various treatments can be calculated from the data of Maloiy and Hopcraft (loc.cit), obtained in an indoor environment, and these are included in Table 10.7. The data on urinary output also show the water-conserving consequences of high temperatures and restricted water intake.

In this same study food consumption by the hartebeest dropped by 15% when water was limited at 22°C, and at 22-40°C it decreased by 24%. As these conditions partially simulate those of a dry season, it is interesting that the calculated DMI's of the shot animals (p.174) also declined drastically when food quality was low in the dry month of September because of the limits of rumen distension. A lowered intake would reduce the loss of water through the faeces, but if energy intake is below the maintenance level, weight losses can be minimized only by reducing either the basal metabolic rate or the time spent each day in energy-requiring and heat-producing activities such as walking and running, or both. The difference in activity patterns between the wet and dry seasons is examined in the next chapter.

Finally, if the hartebeest's energy intake and requirements decline concomitantly in the dry season, weight losses might also be due to an inadequate protein intake as the field data suggested (p.198). The ability of ruminants to retain N by recycling urea back to the rumen rather than losing it in the urine has already been mentioned (p.199). N retention is most necessary when urine production is low anyway (above), and as urea excretion in cattle drops first as the dietary protein decreases and is then more pronounced when water is withheld (Livingston et al 1962), the

ruminant is least dependent on exogenous N supplies under the typical dry season conditions experienced by the hartebeest. Moreover, under conditions of prolonged under-feeding, cattle show appreciable weight losses only in the first few weeks, showing an apparent "adaptation" to low intakes of energy and protein (Elliott, Reed and Topps 1964). Again, in an environment where climatic conditions and food quality reach extreme levels in two dry season every year, the hartebeest may possess mechanisms to mitigate their severity, thereby reducing the need to catabolize body tissues.

Chapter 11.

HARTEBEEST DAILY ACTIVITY AND ENERGY EXPENDITURE

11.1 Introduction

In the last three chapters I have described the diet and food selection of the hartebeest in different seasons, and have calculated the resultant gain to the animals in terms of protein and energy. The fraction of the ingested energy used for maintenance has been estimated, and from the animal's point of view, this is an inescapable expenditure. In the next three chapters, the fate of the remaining energy is followed, first as fuel for muscular work and then for the productive processes of growth, fattening and reproduction. Assessment of the total daily cost of muscular work to an animal requires information on its activity patterns, and those of the hartebeest in wet and dry seasons are described in this chapter.

The ways in which observations of activity are made depend on what is required of the information. The behaviour of the hartebeest was classified in to broad categories on the basis of the known energy costs of the activities in domestic species. Preliminary observation on the daytime activity of individual animals showed considerable variation between consecutive days. Under these circumstances the detection of any seasonal variation in activity patterns would have required an unwarranted number of days of observation. Moreover, it would have been impossible to follow the movements of a single, unmarked animal at night. For these two reasons, the recording of the activity of the majority of animals in a herd was preferred. Construction of a picture of the daily pattern of energy expenditure has inevitably meant failing to take account of many aspects of the social behaviour of the hartebeest, covered by Gosling (1969, 1974).

11.2 Methods

Activity patterns

Observations were confined to herds of females with their offspring, but included any associated male or males. Before any observation period, a herd of about 15 adult animals was sought in the Nairobi Park study area in the vegetation types most used in that season (Ch. 14). The herd was watched from a vehicle at a distance of 50-100 m, and was followed at the latter distance wherever it went. Greater separation was maintained when the hartebeest were approaching a river course to drink because of their extreme nervousness in these circumstances, and the rougher terrain of the lower valley slopes. If the herd was added to by other hartebeest, the newcomers were included in subsequent observations. If an observed herd split through, for example, some animals moving off to water while the remainder continued feeding, observation was continued on the larger fraction of the herd.

For the reasons discussed above, the hartebeest's activity was classified into one of four categories - feeding, walking, standing and lying. These were mutually exclusive so that, for example, any movement by a feeding herd would be scored as feeding. "Minor" activities such as defaecation, urination, maternal or sexual behaviour were classed appropriately as walking or standing. The occurrence of rumination when performed by the majority of individuals was also recorded, and this could occur simultaneously with either walking, standing or lying. However, observations of rumination could not be made at night.

Although a 4-minute interval for recording the activity of cattle is satisfactorily accurate (Harker, Taylor and Rollinson, 1954), and has also been used for wild species (Spinage 1968, Jarman and Jarman 1973), the activity of the hartebeest herd was recorded every 3 minutes in this study. With a herd of about 15 adults, this interval allowed the changes in individual behaviour to be monitored so that the most common activity was easily

assessed on the exact 3-minute mark. Observation was confined to adults of both sexes to reduce the influence of any age - specific variability in activity patterns.

The results are based upon two 12-hour periods of day and night observation in each of the wet and dry seasons. The dates of the observations were chosen to maximise any seasonal differences. The night observations were made only on nights of full moon and the following night to minimize the period when both sun and moon were below the horizon. As only one observer was available, the daytime observations were made on two days close to the full moon:

Observation period	wet season	dry season
Day 1	5.7.72	25.10.71
Day 2	10.7.72	8.11.71
Night 1	26.6.72	2.11.71
Night 2	27.6.72	3.11.71

Day observations covered the period 0630-1830 h. To see whether the data from four 12-hour periods in one season could be combined in to an overall picture, night observations started at 1630 and continued until 0830 on the next morning. As the activity seen in the periods 1630-1830 h and 0630-0830 h was the same as in these periods during the comparable day observations, pooling of the data seemed valid.

During the day observations, shade temperature and wet and dry bulb temperatures (for estimation of the relative humidity) were recorded at every hour and half-hour.

The frequency of visiting a water source in the dry season

Total counts of hartebeest in the Nairobi Park showed that at its extreme east end, the Athi Basin supported a fairly constant number of hartebeest at relatively low densities. The topography of this area was such that the only free water in the vicinity during the dry season was

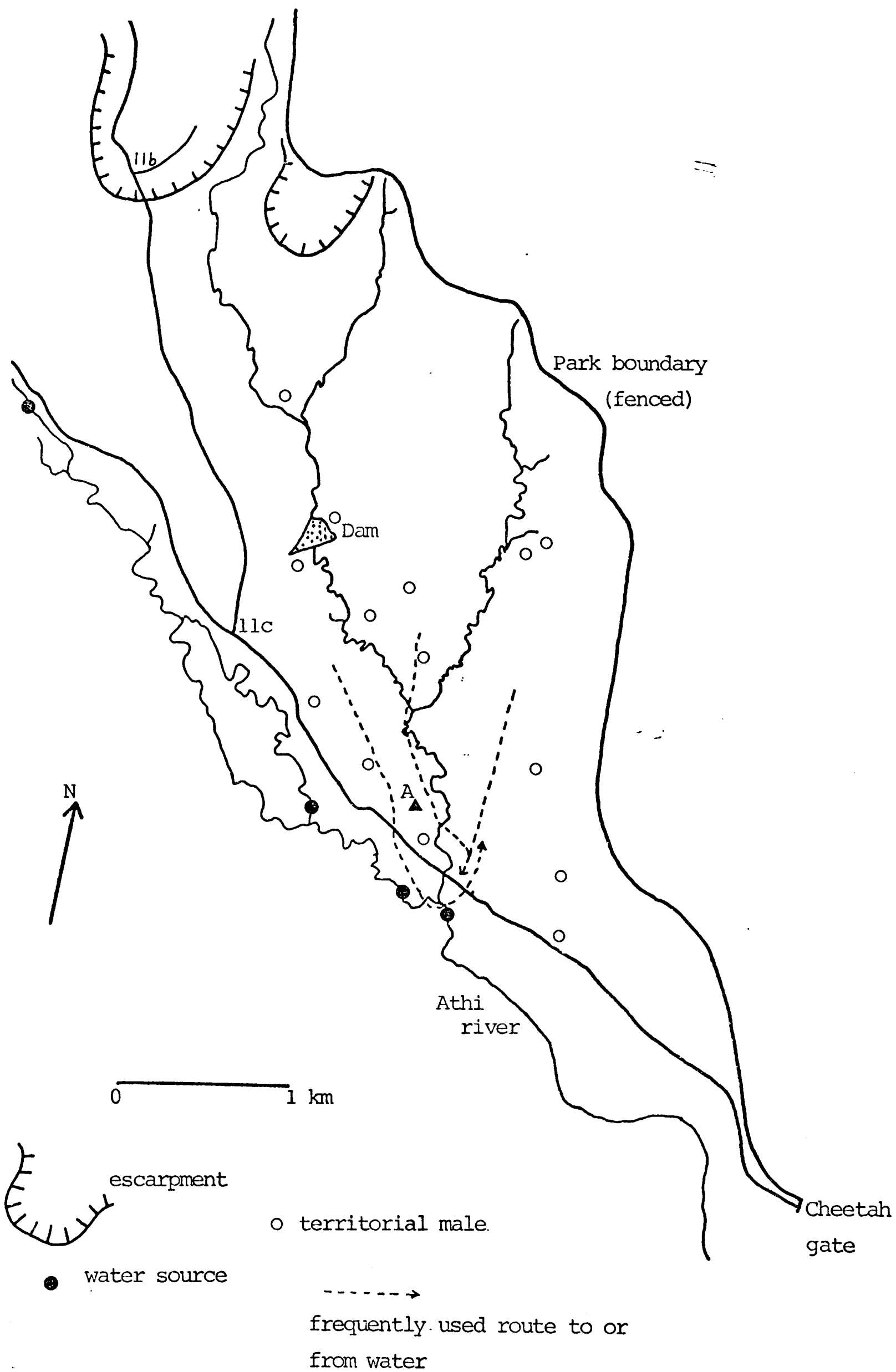


Fig.11.1. The area in which the frequency with which hartebeest visited water was measured.

in the Athi River, which also forms the boundary between the park and an area occupied by Maasai and their stock (Fig. 3.1). These conditions seemed ideal for observing within the park the number of hartebeest visiting known water sources each day and comparing this number with the size of the population of the same area. From the mean percentage of the population visiting water on any day, the frequency of visiting and, by implication, drinking, could be calculated.

For this purpose a study area in the Athi Basin was defined (Fig. 11.1), bounded by the road between signposts 11c and 11b, the escarpment along the northern end of the basin, the park fence between the escarpment and the Cheetah Gate, and the Athi River between the gate and signpost 11c. The animals in this area were reasonably enclosed by the escarpment, the fence and the riverine woodland, but movement in to and out of the western end of the basin was possible. However, observation showed that exchange was slight perhaps because of the gap of several kilometres without drinking sites at the river. During the relevant period the dam in the study area was dry. Before observations began, the locations of all river pools were mapped, and are shown as drinking sites in Fig. 11.1. The single site west of signpost 11c was used by hartebeest from the western part of the basin. No hartebeest moved to it from the study area.

Observations in the form of timed records of all hartebeest arrivals at and departures from the water sources were made on 5 consecutive days (Oct. 6-10, 1972) at the height of the dry season. Observations started at 0630 h and continued until 1230 h. After this time hartebeest had rarely ever been seen drinking in the park. By watching from a vehicle at point A in Fig. 11.1, all the drinking sites were in view and almost all the study areas could be monitored for animals moving towards or away from the river or within the area. Because this point was about 500 m from the river, the hartebeest's extremely cautious approach to water appeared unaffected by the vehicle's presence. On the other hand, because

the river pools were between deep earth banks and trees prevented a clear view, actual drinking could not be seen. If animals were seen to approach the river and subsequently leave undisturbed, they were assumed to have drunk. This could usually be confirmed by their muddy hocks and the freshly-plastered mud on the flanks of the males.

At 1230 h on each day a total count of hartebeest was made in the study area and all animals classified in to the usual sex and age classes (p. 15), but juveniles and newly-born calves were combined. Over 5 days a picture was built up of the number and location of the territorial males and their approximate positions were mapped.

The energy cost of activity and daily expenditure

The total time spent in each activity has been used to calculate the daily energy expenditure of hartebeest living free, using values of the cost of these activities reported for domestic species. The following volumes are used for the cost of each activity above the basal expenditure.

walking	0.59 kcal/kg. body weight.km (horizontal)	(Clapperton 1961)
feeding	0.54 kcal/kg.h	(Graham 1964)
ruminating	0.24 kcal/kg.h	(Graham 1964)
standing	0.08 kcal/kg.h	(A.R.C. 1965)

The expenditure of a lying animal is taken to be the same as that of an animal under basal conditions. No measurement was made of the speed of walking, but considerable following of hartebeest in a vehicle suggests that 3 mph (4.8 kph) is a reasonable figure. The cost of walking for one hour is therefore $0.59 \times 4.8 = 2.83$ kcal/kg. For present purposes all walking is assumed to be on horizontal ground, and as slopes of more than 3° from the horizontal are uncommon in the Nairobi Park study area, this is an acceptable simplification.

Hour Starting	WET SEASON					DRY SEASON				
	Feed	Walk	Stand	Lie	Ruminate	Feed	Walk	Stand	Lie	Ruminate
0530	1.5	4.5	21	33	-	30	7.5	6	16.5	-
0630	60					49.5	10.5			
0730	60					58.5		1.5		
0830	60					13.5	30	16.5		12
0930	27	7.5	25.5		25.5	12	13.5	34.5		2.85
1030	1.5	1.5	39	18	52.5	30		30		7.5
1130	22.5		37.5		34.5	21	3	36		6
1230	3	1.5	55.5		27			57	3	54
1330	6		12	42	12			12	48	9
1430				60	3			21	39	21
1530	18		3	39		13.5	7.5	9	30	4.5
1630	36		6	18		33	7.5	1.5	18	
1730	60					51	7.5	1.5		
1830	54			4.5		36	1.5	16.5	6	
1930	6	6	11.5	36	-	7.5		3	49.5	-
2030	9	18	12	18	-	9		4.5	46.5	-
2130	39	9	12		-	16.5	3	9	31.5	-
2230	48	9	3		-	45	4.5	3	7.5	-
2330	57	3			-	60		9		-
0030	60				-	24	4.5		22.5	-
0130	6	3	24	27	-	4.5	1.5		54	-
0230				60	-				60	-
0330				60	-	1.5			58.5	-
0430				60	-				60	-
Day total	354	10.5	178.5	177	154.5	282	79.5	220.5	138	142.5
Night total	280.5	52.5	88.5	298.5	-	234	22.5	51	412.5	-
24h total	634.5	63	267	475.5	154.5	516	102	271.5	550.5	142.5
min	10.6	1.05	4.4	7.9	2.6	8.6	1.7	4.5	9.2	2.4
h.										

Table 11.1. The mean hourly periods and total time spent (minutes) in each activity in the wet and dry seasons, over 24 h.

Table 11.2. The mean diurnal shade temperature (Temp) and relative humidity (R.H.) at half-hour intervals in the wet and dry seasons.

Wet			Dry	
Time	Temp. °C	R.H. %	Temp. °C	R.H. %
0530	12.5	71.5	13.5	79.5
0700	13.75	77.0	16.0	71.5
0730	15.0	70.5	18.25	73.25
0800	15.5	74.25	20.0	61.5
0830	17.0	70.0	23.5	56.5
0900	19.25	64.5	23.5	54.25
0930	22.0	50.25	24.25	49.75
1000	23.25	50.25	30.0	41.5
1030	25.0	49.0	32.0	43.75
1100	25.25	48.75	33.5	35.5
1130	26.25	44.75	35.0	37.5
1200	27.0	42.75	34.0	38.5
1230	28.75	41.5	32.75	36.0
1300	26.75	36.25	31.5	35.0
1330	25.75	42.75	30.75	33.5
1400	26.25	36.5	32.5	36.0
1430	25.25	41.25	31.25	35.0
1500	25.75	34.75	31.75	35.75
1530	27.0	35.5	30.25	47.75
1600	27.25	40.25	27.0	43.5
1630	27.5	40.75	25.5	47.0
1700	25.75	38.5	24.75	41.5
1730	24.25	50.25	22.0	44.75
1800	22.5	47.0	22.75	42.75
1830	21.0	52.25	22.0	47.5

Fig.11.2. The time spent feeding and walking (shaded) by hartebeest in each hour of the day and night in (a) the dry and (b) the wet seasons, with the diurnal shade temperatures and relative humidities.

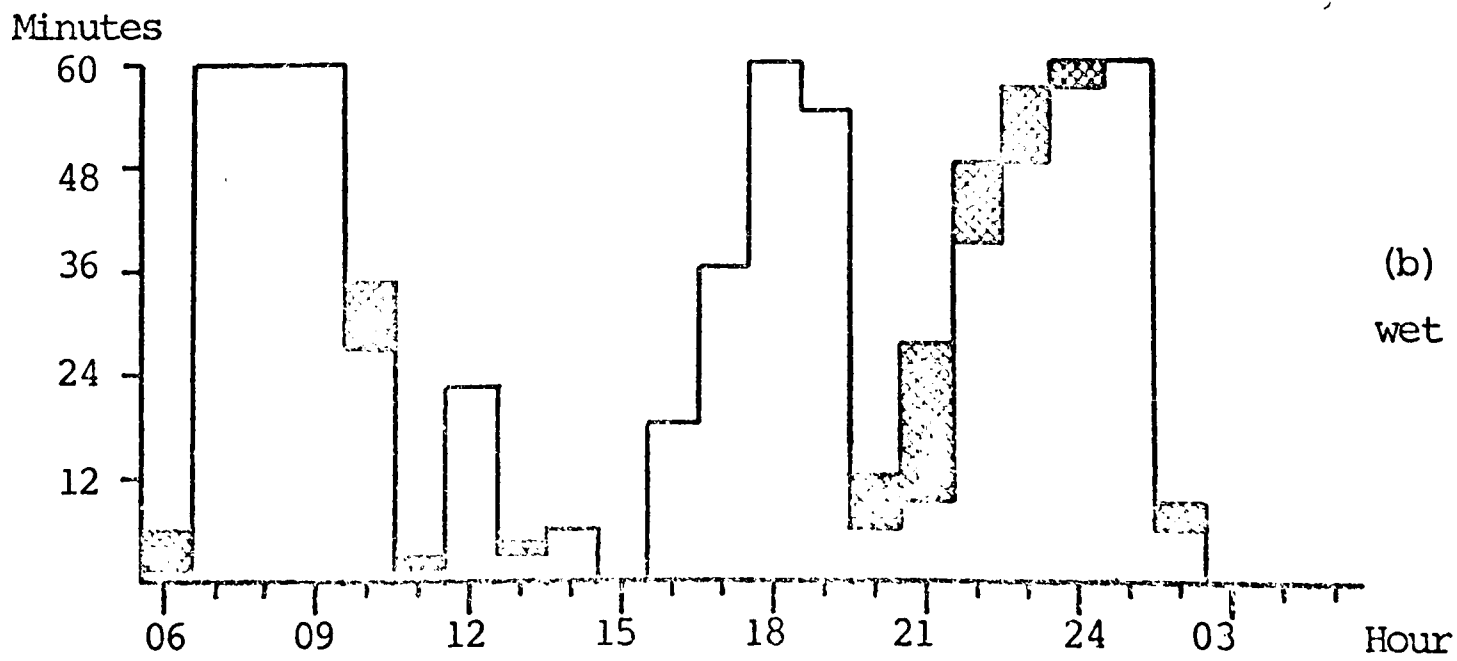
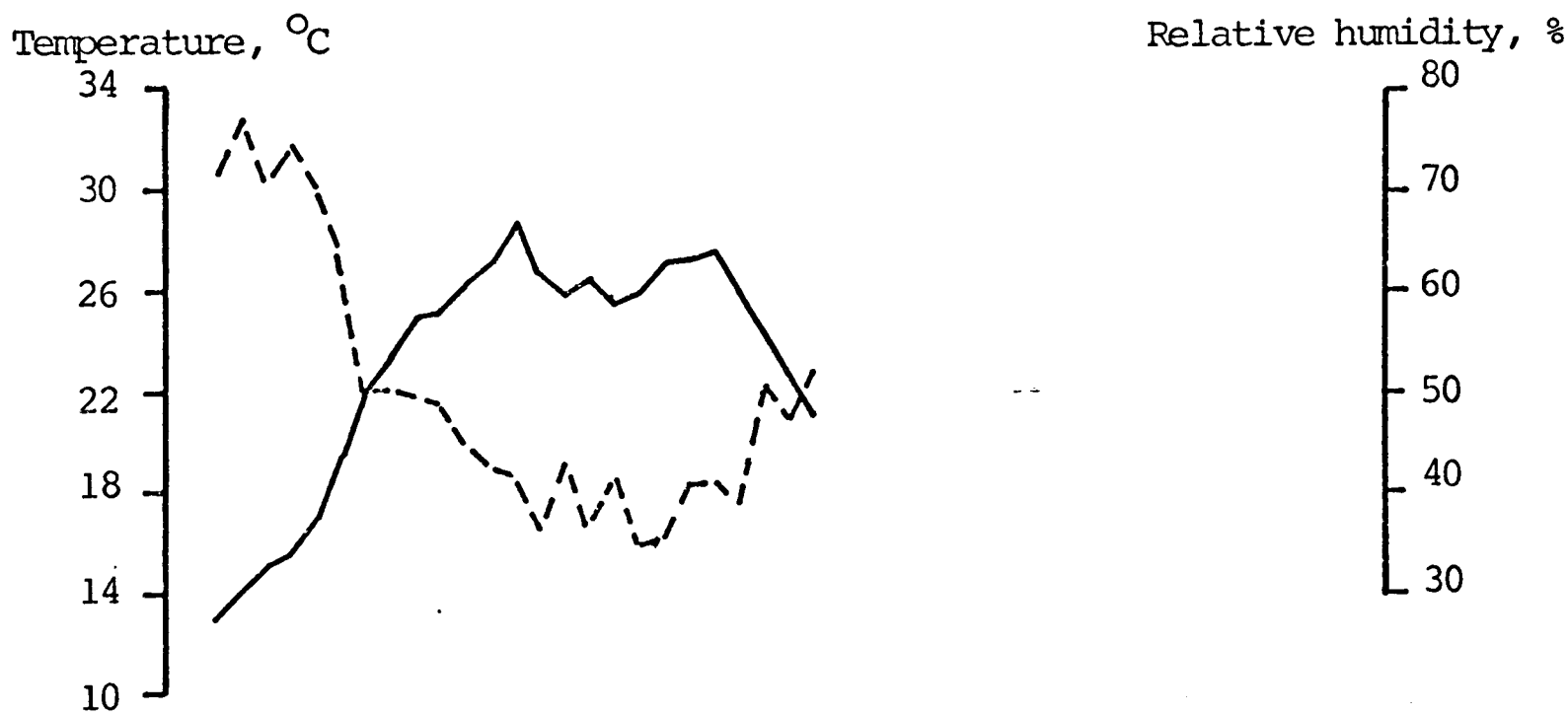
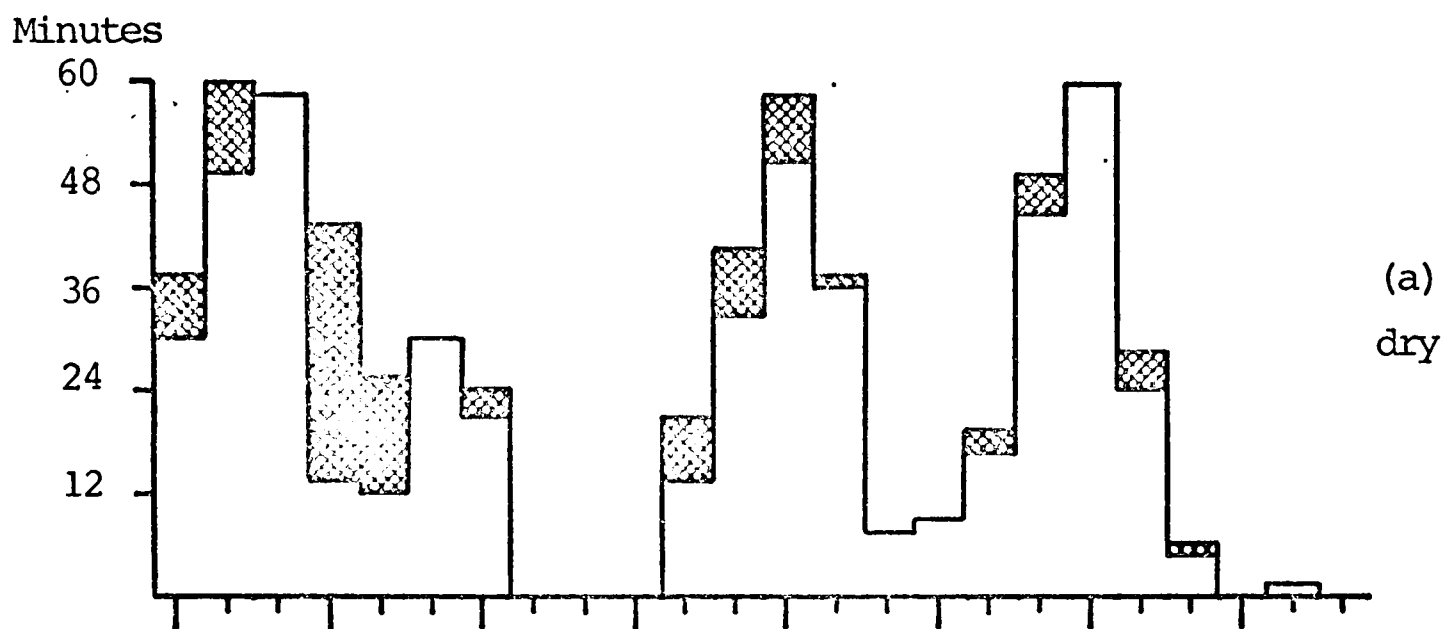
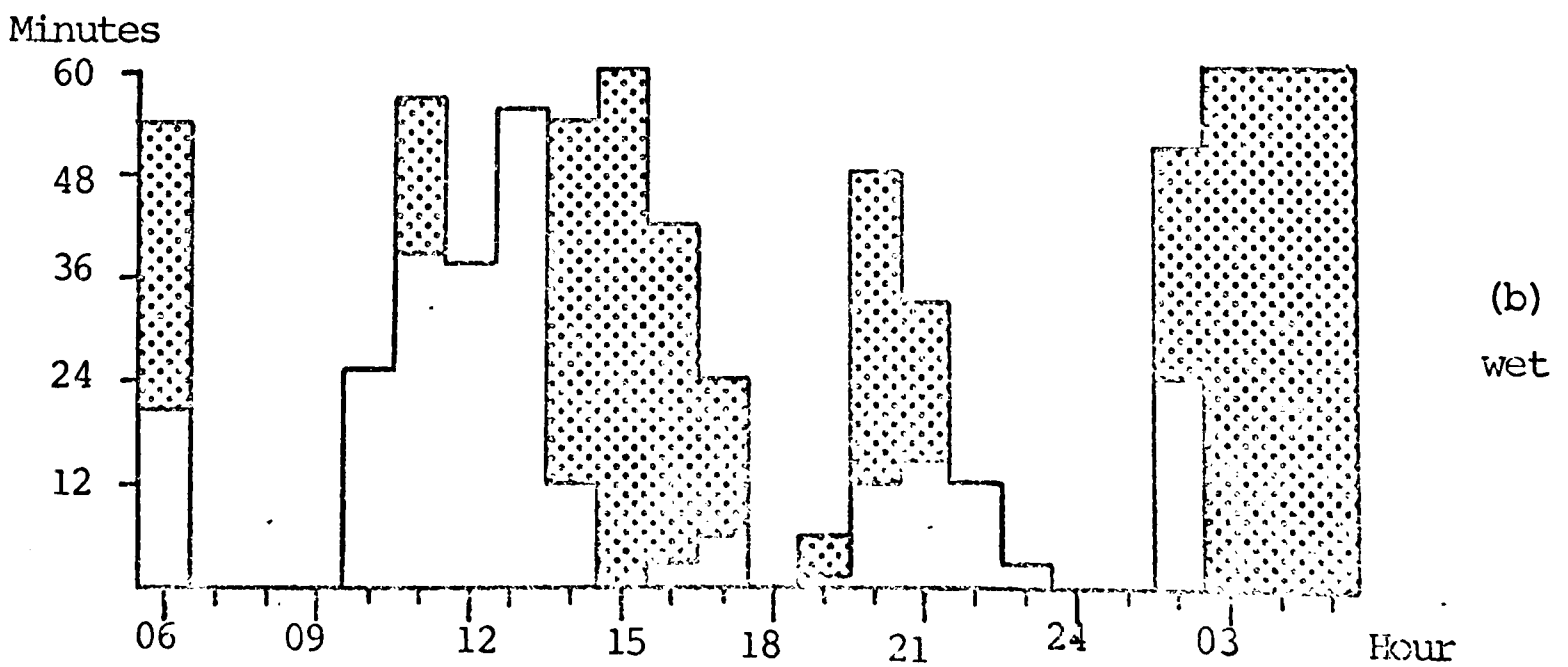
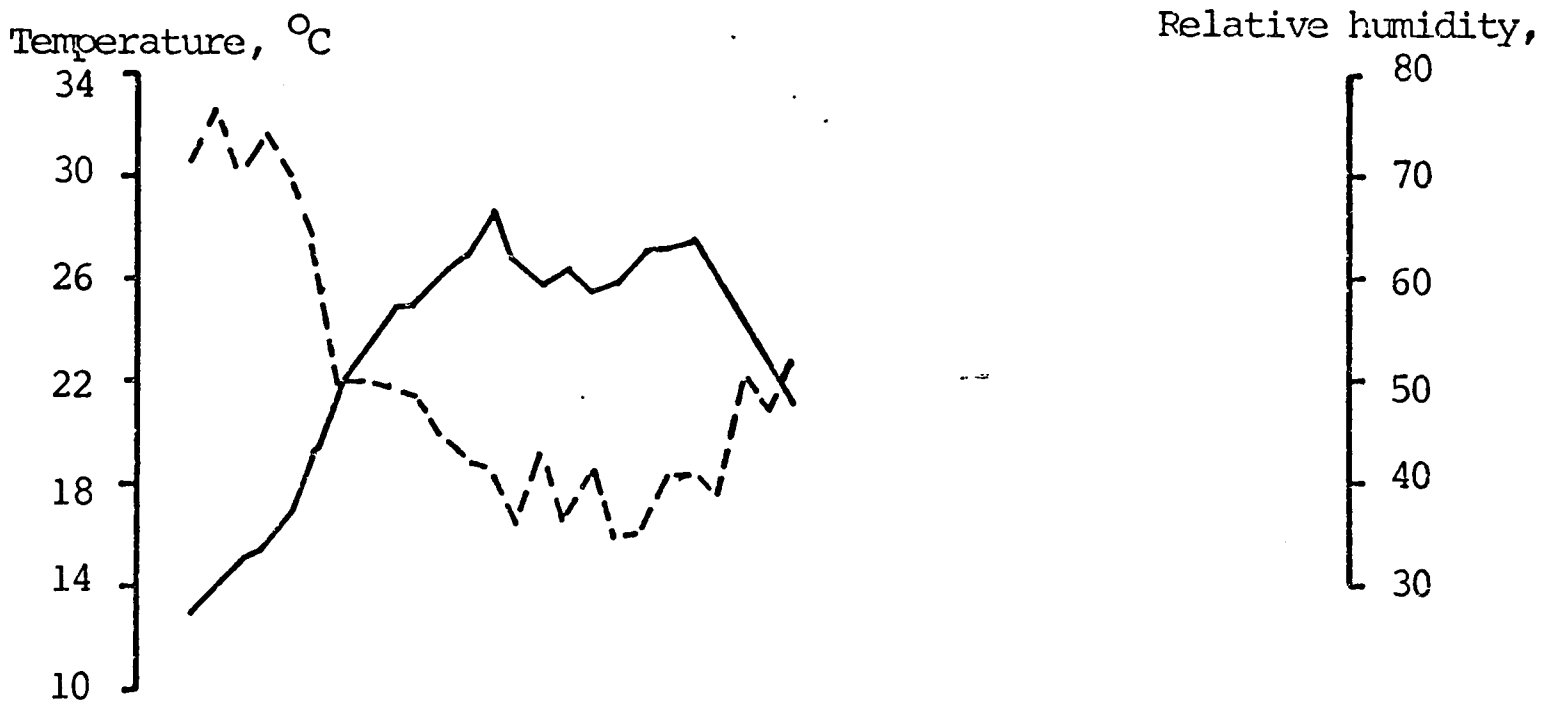
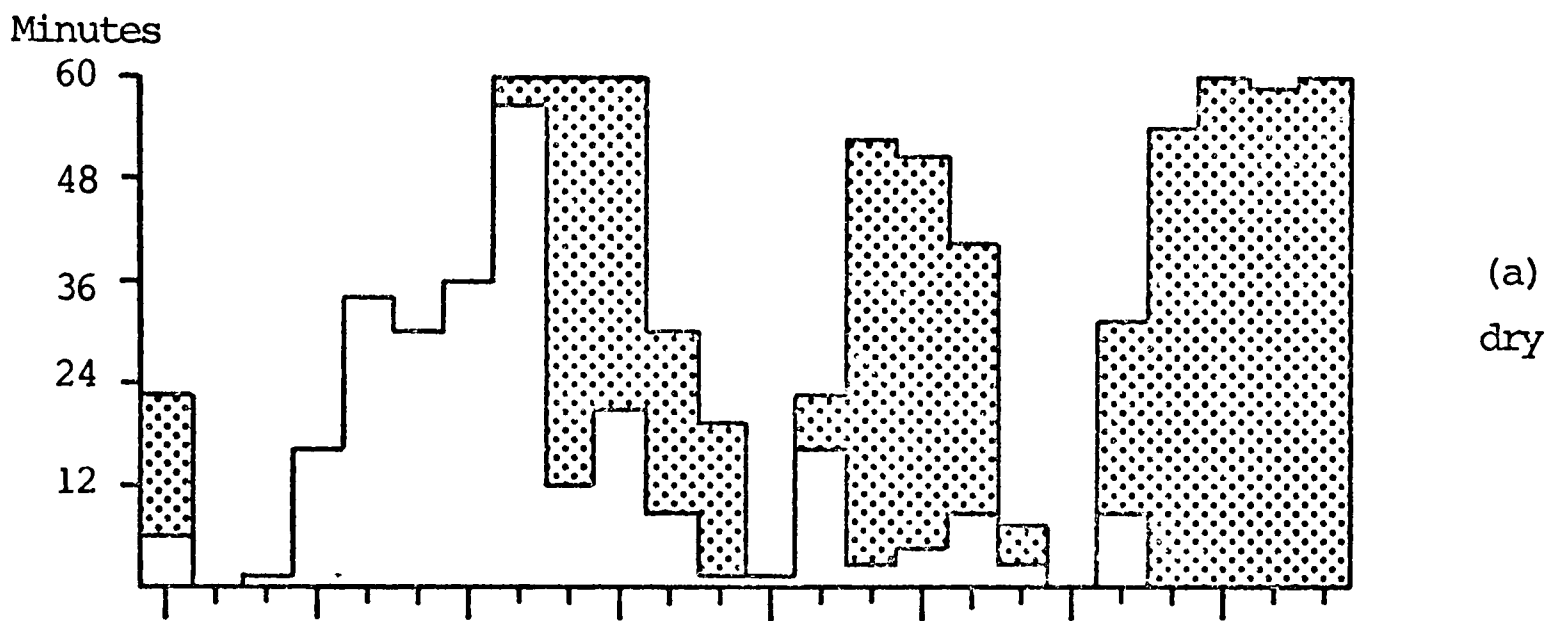
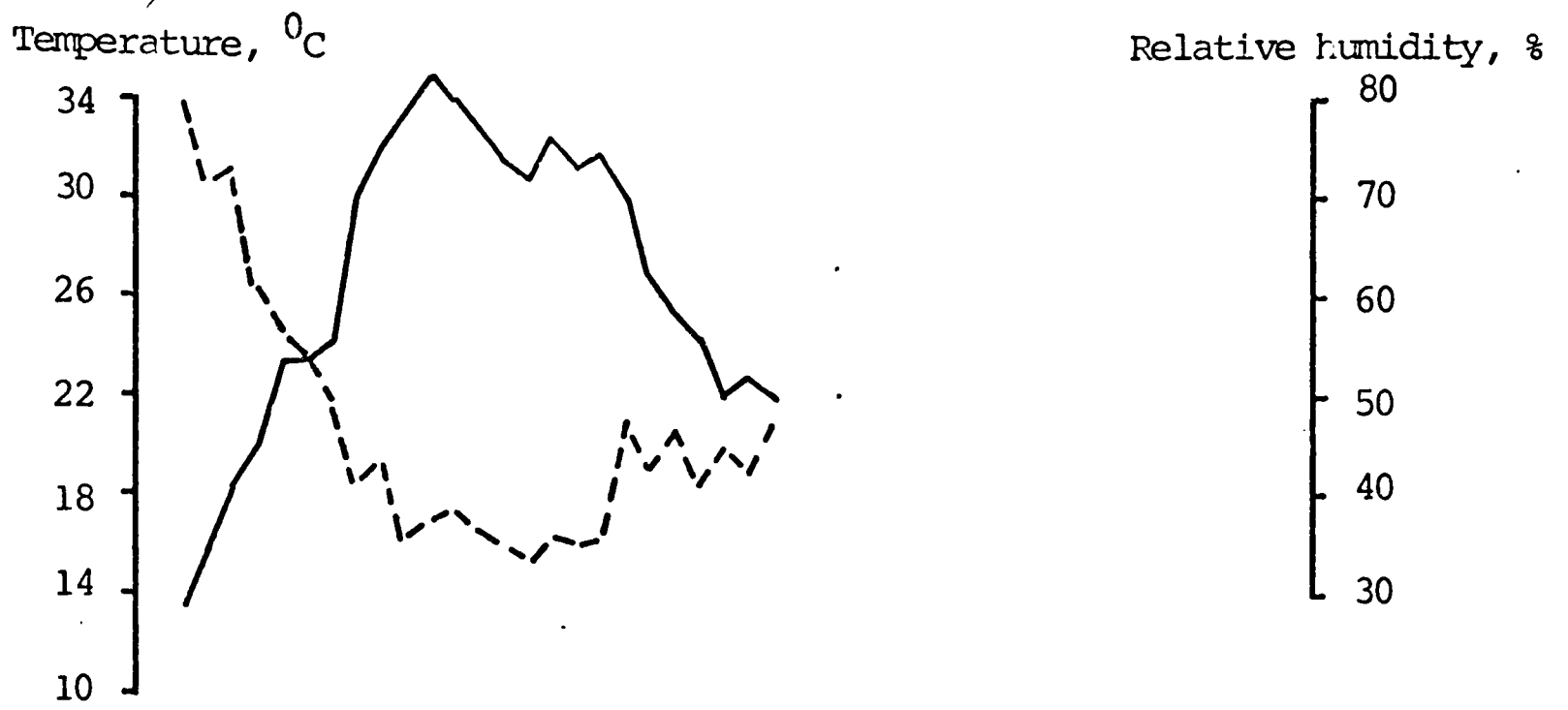


Fig.11.3. The time spent standing and lying (shaded) by hartebeest in each hour of the day and night in (a) the dry and (b) the wet seasons, with the diurnal shade temperatures and relative humidities.



11.3 Results

Table 11.1 contains the mean time spent in each activity in each hour through the two seasons. In Table 11.2 are presented the mean shade temperatures and relative humidities recorded during the day observations.

The basic pattern of activity

Fig. 11.2 shows the time spent each hour in feeding and walking in each season with the climatic measurements, while Fig. 11.3 shows the same for standing and lying. During the second night of wet season observation the herd was attacked by lions. As a result no data could be collected between 2130 and 0230 h, and the data shown for these hours are those of the first night only.

Considering both seasons together, there is a clear pattern in the hartebeest's activity. Feeding occurs as 3 main bouts in roughly the early morning (0630-0930 h), the evening (1530-1930 h) and the middle of the night (2230-0130 h). There is an indication of a smaller peak of feeding at 1130-1230 h. Walking occurs at almost all hours of the day but reaches a minimum between 1130 and 1530 h when air temperatures are highest (Fig. 11.2).

The morning feeding period is followed by a period of standing (0930-1330 h) which is replaced by lying down (1330-1730 h). The proportion of animals lying decreases through late afternoon as more animals start their evening feeding bout, which wanes sharply after dusk (1930 h). The hours 1930-2230 are spent predominantly in lying and standing but these activities decrease in importance as the midnight feeding period builds up. This ends between 0130 and 0230 h, whereupon the animals lie down until dawn, between 0530 and 0630 h. Lying down decreases during this last hour as the animals stand before starting to feed.

Rumination was recorded only between 0930 and 1530, with most occurring before 1330 h. It therefore co-incided with the long period of standing in late morning (Fig. 11.3), although lying animals also ruminate.

Although no quantitative recording was possible at night, hartebeest were seen ruminating in the lying and standing period at dawn, and it seems likely that rumination also occurs during the resting period following the evening feeding bout.

Seasonal changes in weather and activity patterns

The diurnal changes in relative humidity (R.H.) are very similar in both seasons (Fig. 11.2). Values exceed 70% in the early morning, falling rather sooner in the dry season, but in both the lowest R.H.'s of 30-40% occur in the middle of the day, before a slight upward trend in the late afternoon or evening. The fluctuations in air temperature are more extreme. Although the dawn and dusk temperatures are similar in both seasons, the temperature rises more rapidly through the morning in the dry season, reaching a maximum of 35°C at 1130 h, and then staying above 30°C until 1530 h. This is in marked contrast to the wet season in which the highest temperature of only 29°C was reached at 1230 h.

Considering the total time spent in the various activities, feeding occupies 10.6 h (634.5 min) in the wet season but only 8.6h (516 min) in the dry season (Table 11.1). The total reduction of 18.7% in feeding time is spread almost equally between daytime (20.3% reduction) and nighttime feeding (16.6% reduction). These reductions are partly accounted for by an increase in the time spent lying and standing ("resting") from 742.5 to 822 minutes over 24 hours. Although 355.5 and 358.5 minutes are spent in diurnal resting during the wet and dry seasons respectively, the proportion spent standing increases in the latter from 50.2% to 61.5%. The main dry season increase in resting occurs at night when the time spent standing changes little (88.5 and 51 minutes), but the period of lying increases from 298.5 to 412.5 minutes. The shorter diurnal feeding time in the dry season is also accompanied by an increase in the time spent walking, from 10.5 to 79.5 minutes.

Rumination occupied 154.5 and 142.5 minutes during the wet and dry seasons respectively. These figures represent daytime feeding to ruminating ratios of 2.29:1 and 1.98:1. The difference between ratios is the same if the feeding time over 24 hours is used. Therefore, unless proportionately more rumination occurs at night in the dry season, the hartebeest spend 16% longer ruminating per unit period of feeding in the dry season.

Although the general patterns of activity and the time spent on them are not radically different in wet and dry seasons, the timing of certain activities or bouts varies between seasons. The greater proportion of the hour 0530-0630 spent feeding in the dry season was due to feeding starting almost at dawn. In this season feeding was first recorded as the predominant activity at 0554 and 0606 on the 2 days of observation. In the wet season the same observations were made at 0630 and 0648. Temperatures as low as 7°C at dawn in the wet season may have been partly responsible for the delay in the start of feeding. However, as the total length of the morning feeding period varied little between seasons (Fig. 11.2), feeding had declined markedly by 0830 in the dry season whereas nearly half of the hour 0930-1030 was spent feeding in the wet season. In each case the reduction in feeding co-incided with the rising temperature reaching approximately 24°C (Fig. 11.2). The minor mid-day feeding period also occurred earlier and was more sharply defined in the dry season (between 1030 and 1230 h) than in the wet season (1130-1430 h).

As the timing of the evening and the midnight feeding periods are the same in both seasons, the earlier dry season feeding in the morning suggests the avoidance of feeding in the hottest part of the day. In the dry season the hartebeest spent the whole period 1230-1530 h lying or standing, and feeding only started again between 1530 and 1630 as the ambient temperature dropped below 30°C. The earlier morning feeding is also associated with observations of the hartebeest drinking free water

Table 11.3 The number of hartebeest (a) in the study area each day,
(b) visiting water each day, and (c) the mean interval
between visits to water for each sex/age class.

(a)

Day	Males	females	sub adults	juveniles
1	39	49	9	27
2	42	49	10	27
3	39	47	12	31
4	43	52	12	28
5	51	49	9	32
Mean	42.8	49.2	10.4	29.0
(b)				
1	21	30	5	13
2	6	18	10	6
3	22	16	4	11
4	8	30	10	11
5	20	29	6	20
Mean	15.4	24.6	7.0	12.2
(c)	<u>Males</u>	<u>females</u>	<u>sub adults</u>	<u>juveniles</u>
Percentage drinking on any one day	15.4/42.8 = 36.0	24.6/49.2 = 50.0	7.0/10.4 = 67.3	12.2/29.0 = 42.1
Interval between drinking, days	3	2	1 - 2	2 - 3

in the drier months. Drinking was observed only in the morning, with most activity at water sources at the end of the morning feeding period. This is one cause of the longer time spent walking between 0830 and 1030 h in the dry season. Walking also occurs at the end of the morning feeding period as the hartebeest move away from the steep, lower valley slopes, their dry season feeding areas (Ch. 14), to more open and level resting areas higher up the slopes. The walking associated with the evening feeding period is the reverse of this movement. The observed herd did not use the lower slopes during their midnight feeding. In the wet season the hartebeest were feeding in the Acacia drepanolobium grassland and on the open plains at the top of the catena. During the day they rested in the bush grassland but moved on to the plains to rest at night, producing the movement associated with the midnight feeding period.

Frequency of visiting water

A maximum of 14 territorial males were present in the study area, and their approximate positions are shown in Fig. 11.1. Also marked are the most frequently used routes to and from water, all of which could be watched from point A.

Table 11.3 contains the daily and mean numbers of hartebeest of each class in the study area, and the numbers drinking each day. Also shown is the calculated frequency of drinking of the adult males, females, subadults and juveniles. The mean of 36% of the mean number of males drinking on one day shows that they drink once every 3 days. As the numbers of females visiting water daily is equivalent to 50% of their mean population, they drink every 2 days under these conditions. The subadults appear to drink every 1-2 days, but this is probably the result of the few animals of this age class in the area (Table 11.3). The juveniles are calculated to drink every 3 days, compared with every 2 days for their mothers. This interval is certainly an over-estimate because no calf considered less than 3 months old by its horn development was actually seen

Table 11. 4 The energy cost of activity above the basal level for a hartebeest weighing 121.3 kg. under natural conditions in wet and dry seasons.

Activity	Cost kcal/kg.day	Wet Season		Dry Season	
		time spent h	total cost kcal/day	time spent h	total cost kcal/day
Walk	67.9	1.05	360.7	1.7	584.0
Feed	0.54	10.6	694.3	8.6	563.3
Stand	0.08	4.45	45.0	4.5	45.5
Ruminate	0.24	2.6	74.8	2.4	69.8
Lie	-	7.92	-	9.1	-
		TOTAL	1174.8	TOTAL	1262.6

to move in to the river bottom. Exclusion of such unweaned calves from the calculation would result in the juvenile interval approaching the 2 day interval of the females.

Total energy cost of activity

Table 11.4 shows the cost of each activity, the time spent on each and the total energy expenditure above the basal level. The total time adds up to more than 24 h because rumination occurs concurrently with standing and lying.

The energy expended in the two seasons is very similar, with the dry season figure exceeding the wet season one by 7%. Although the hartebeest feed for two hours less in the dry season, the energy saved is more than offset by the added cost of walking for an additional 0.65 h/day. The times of day at which the walking occurs suggests that it is a consequence of having to visit water rather than moving between feeding and resting areas which also occurs in the wet season (Fig. 11.2).

The average weight of adult hartebeest of both sexes is 121.3 kg (p. 229). The basal energy requirement of such an animal with a fasting metabolic rate (FMR) of $51.5 \text{ kcal/kg.W}^{.73} \text{ day}$ (p. 196) would be 1730 kcal/day. The activity patterns of the wet and dry seasons therefore represent energy requirements of 67.9% and 73.0% over and above this basal requirement. A metabolisable energy intake of $70.1 \text{ kcal/kg.W}^{.73} \text{ day}$ maintained the penned hartebeest. This is equivalent to a maintenance need of 2327 kcal/day for an adult of average weight. On this basis a free-living animal of the same weight would need 50.5% more energy in the wet season and 54.2% more in the dry season (Table 11.4).

11.4 Discussion

The hourly and daily totals of the predominant activity show how adult hartebeest apportion their time. This method avoids the need to assume that a single observed animal is representative of the population, and if herds of approximately the same size are watched on different

occasions, the degree of synchronization of the activities of its members can be measured. This was attempted, but the continuously changing herd size and the high density of hartebeest in the park meant that, on a presence or absence basis, the probability of seeing activities other than the predominant one fluctuated too much for this to be worthwhile. Subjectively, however, the hartebeest's daytime activity was more synchronised during the hot, dry season than the wet season. This was demonstrably the case in impala (Jarman and Jarman 1973).

The necessity of making nocturnal observations on moonlit nights may have introduced biases, most notably in the proportion of time spent feeding. This could be investigated by comparing the time spent feeding on days with nights of full moon and no moon, but at least, as the nocturnal observations were made on the same nights of the lunar cycle in both seasons, any bias may have been consistent.

The pattern of three major feeding periods through 24 hours in the hartebeest is similar to those of the waterbuck (Spinage 1968) and impala (Jarman and Jarman loc. cit.), and is therefore not necessarily restricted to "herd-forming, medium-sized antelope species living in savanna or light woodland (but not in open plains country)" (Jarman and Jarman, loc. cit.). The periods spent feeding, recorded as the occurrence of head movements in the herb layer, in different months do not necessarily reflect differences in the amount of food eaten because of the intervening effect of food selection. The effect of the sward structure on the food intake has been discussed (p.164), and it was subsequently shown that the dry season intake of hartebeest in the Athi Plains is only $\frac{1}{3}$ that of the wet season (p.174). This agrees qualitatively with the shorter feeding time in the park in the dry season. An exactly equal difference in feeding time and intake would be unlikely because of the possible differences in the sward structure and the extent of food selection in the different vegetation types of the two areas.

The decrease in feeding time of the exclusively grazing hartebeest in the dry season is the reverse of that reported for impala (Jarman and Jarman, loc. cit.), though the two situations may not be strictly comparable as the latter species is known to increase the proportion of herbs and shrubs in its diet in dry months (Jarman 1973, Azavedo and Agnew 1968, Ables and Ables 1969). In the same study, the ratio of feeding to ruminating times increased in the dry season, whereas the hartebeest spent proportionately more time ruminating in this season. As the time spent chewing reflects the fibrousness of the diet (Balch 1971), this change would be expected to accompany the increase of fibrous, stemmy material in their dry season diet (p. 155).

Finch (1972 a, b) has described the physiological methods employed by the hartebeest to remain in thermodynamic equilibrium with a thermal environment of intense radiation. This work was done approximately 15 km from the Nairobi Park study area, so large differences in climate between the two sites are unlikely. The hartebeest's dense coat of brown fur with white tips reflects 42% of the incoming short-wave radiation. 80% of the absorbed and metabolic heat is dissipated by panting. The rate of panting varied with the radiant heat load, which peaked at 1300 h and not with the ambient temperature which continued to rise until 1500 h. In the hot, dry season covered by these observations, the hartebeest were least active between 1230 and 1530 h (Fig. 11.2). Although this period also included the days' highest air temperatures, the inactivity was probably a response to the high radiant heat load rather than air temperature per se. This would explain why a mid-day feeding period is possible in both seasons when air temperatures are highest, but solar radiation is still increasing.

The influences of four factors are detectable in the daily pattern of activity. One is common to all ruminants, and the other 3 may be specific to the hartebeest in the Nairobi Park. The first influence, stemming from a consideration of the way in which material passes through

the ruminant digestive system (Appendix 12), suggests that such animals should have several evenly-spaced feeding periods through the day. Fig. 11.2 shows that the hartebeest's three main feeding bouts are evenly-spaced except for the longer break in the middle of the day. Feeding starts at dawn to replenish the rumen after the long period since the midnight feeding. By starting this bout at first light, feeding and drinking, and the walking associated with the latter, are accomplished before the heat load reaches unacceptable levels for these activities. The lesser mid-day feeding period may be an opportunity for "topping-up" the rumen before the enforced period of inactivity. The climatic conditions and their consequent heat load on the hartebeest are the second influence on its activity patterns. This influence is apparent in the seasonal differences in activity. The third influence is the necessity to visit water every 2-3 days, involving an energy expenditure and possibly some sacrifice of feeding time. The fourth influence is the possible anti-predator behaviour of moving away from the bush-covered lower valley slopes and out of the bush grassland before resting. The importance of this behaviour, though, is unclear without knowing, at least, what proportion of the population perform these movements. The over-riding influence appears to be the one causing the spacing of the feeding periods, judging by the very slight difference only in activity patterns between months with high and low heat loads. Finch (1972b) concluded that the hartebeest was admirably adapted to the conditions of intense radiation judging by the near constancy of its core temperature through the day. The low and inconsistent occurrence of shade-seeking behaviour, which would immediately reduce the heat load, bears this out.

Calculation of the interval between visiting water sources in the dry season assumes that the water requirements of all males or all females are the same, irrespective of their physiological state. Further information on possible differences must await a study using a larger population

with a number of marked animals. The data obtained also give no clue as to the point at which the hartebeest have to start drinking free water as conditions become drier after rain.

In estimating the energy expenditure of the hartebeest, there is the recurrent doubt about extrapolating from domestic to wild ruminants. In this case, however, the nearly identical cost of horizontal locomotion in man, the dog and sheep (Clapperton 1961) suggests that a single inter-specific cost for each activity can be assumed for ruminants. The energy needs of the wild hartebeest were about 70% greater than their basal energy expenditure (p. 214) which falls in the range of increments calculated by Moen (1973) for deer on different activity regimes. Coop and Hill (1962) found that in 3 trials the maintenance intakes of digestible organic matter by grazing sheep were 48-70% higher than the comparable intakes of penned sheep. These increases bracket the estimated 52% higher requirement for energy of the free-living hartebeest compared to the penned animals (p. 214).

In general, the estimated maintenance needs of grazing animals are far higher than those determined in the laboratory by calorimetric methods (Blaxter 1965). Blaxter ascribed this difference to the effect of adverse environmental conditions in raising the metabolic rate, rather than through any significant cost of walking and collecting food. Although possibly an adequate explanation in temperate regions, this is unlikely to be the case in the tropics where conditions which are most commonly adverse to the hartebeest require heat to be lost (Finch, loc. cit). This suggests that the cost of grazing and walking is a sizeable proportion of a large herbivore's daily energy expenditure. The cost of walking to water is high (p. 214), which may explain why the hartebeest concentrate around water sources in the dry season (Gosling 1974, and p. 263) even though they drink only every 2-3 days. Although drinking with this frequency could allow more distant grazing areas to be used, the gain from

Table 11.5. The calculated energy available for production in 4 months from the estimated intakes of metabolisable energy (ME) by shot hartebeest.

Month	ME intake, 73 day kcal/kg.W ^{0.73} .day	ME intake above maintenance cost ₃ of 70.1 kcal/kg.W ^{0.73} .day	ME cost of activity, 73 day kcal/kg.W ^{0.73} .day	ME available for production, kcal/ kg.W ^{0.73} .day
January	134.4	64.3	36.7	27.6
April	100.9	30.8	36.7	-5.9
July	153.2	83.1	36.7	46.4
September	44.5	-25.6	36.7	-62.3

using them has to be offset against the cost of getting there and back to water. The distribution of hartebeest in the park and the plains in the dry season suggests that the energy saved by staying in the vicinity of water is the more important factor.

The intakes of metabolizable energy were calculated in Chapter 10 (p.193) for hartebeest under field conditions in 4 months. Subtraction of the calculated maintenance requirements of $70.1 \text{ kcal/kg.W}^{.73} \text{ day}$ leaves the energy available for muscular work and productive processes. The average amount of energy expended by a 121.3 kg hartebeest in its daily activity is 1218.7 kcal (Table 11.4), or $36.7 \text{ kcal/kg.W}^{.73} \text{ day}$. This is used in Table 11.5 to calculate the amount of energy available for production in each of these 4 months. These calculations apply the activity costs of the park hartebeest to the animals shot in the plains, but this is unlikely to alter the picture substantially. Energy surpluses exist for production in January and July. The slight energy deficit of April indicates zero production. The larger deficit in September, when intake would have been inadequate to meet even the cost of daily activity suggests weight losses in the dry season through the catabolism of body reserves. This last aspect is considered further in the next chapter.

Chapter 12.

GROWTH AND CONDITION OF THE HARTEBEEEST

12.1 Introduction.

The metabolisable energy of food must satisfy an animal's maintenance requirements before any surplus can be used for growth, the deposition of energy reserves, or reproduction. The last chapter showed that the hartebeest's energy requirements, including those of their activity under natural conditions, was constant in different seasons. Their energy intake varied between months, which presumes a parallel variation in their production. The latter variation and its implications are considered in this chapter.

In a comparative study of several populations of red deer in New Zealand, Caughley (1971) distinguished between the effects on the animals of their long-term and short-term nutritional history. The first is reflected in the final body size and the second in the "condition" of the animal, although the first phenomenon, in the context of isolated populations, may be largely due to genetic differences. Within a single population, more may be learnt of the long-term nutritional status of the population by looking at the growth rates of individuals for comparison with other populations or species. This assumes that animals grow as fast as they can within the limitations of their food resources. Without the facility of rearing animals in captivity, the hartebeest growth rate has been inferred from the age-weight relationships in a series of shot animals.

The significance of short-term changes are more difficult to assess because of the imprecision concerning the concept of "condition". As a term used by practical livestock managers, it is used loosely as a measure of general bodily well-being, based upon external characteristics. In assessing an animal, a stockman is summing the results of many criteria, which may not be amenable to quantification or objective application.

Research on wild ungulates has borrowed the term "condition", and as a concept it has been invoked to cover a profusion of changes observed in animals in different places or at different times in the same place. In general, observations on condition fall in to one of three types. The first is the assessment of external appearance against prescribed standards (Riney 1960, Albl 1971). The second and most frequent, is the measurement or estimation of the fat deposits of animals (Riney 1955, Ransom 1965), and the third is the investigation of physiological parameters, notably of the blood (Bandy et al, 1957, Franzmann 1971).

Carefully defined and subjectively assessed categories of external appearance in sheep are highly replicable and are correlated with the measured fat content of the carcass (Russel et al. 1969). Rarely, however, are the relationships between different measures of condition, covering a vast range of physiological processes, considered in wild ungulates. It is easy to detect differences in a series of animals collected periodically through the year. It is extremely difficult to say why these differences have occurred and what they mean. Animals are often assessed as in either "good" or "bad" condition, with the implication that this gauges their chances of survival (Caughley loc. cit.). But the weight of kidney fat, for example, varies between individuals according to their sex and age (Monson et al. 1974). Current ignorance of the causes of this variation means that the range of kidney fat weights through which the animal's chance of dying is not significantly impaired, is not known. Consequently, such assessments may have no biological meaning at all.

Although the amount of kidney fat in lambs depends on their plane of previous nutrition (Palsson and Verges 1952), and the sequence of mobilization of body reserves during pregnancy is known in sheep (Russel et al. 1968) and for deer in winter (Harris 1945), experimental work on wild ungulates is needed. Only then will it be possible to resolve problems such as whether in a sample of red deer taken over a short period, the

kidney fat of hinds in later pregnancy is greater because those hinds in "good" condition were able to conceive earlier (Mitchell and Lincoln 1973) or because fat is continually laid down through early pregnancy. The latter could also explain the observations, and has been seen in other deer species (Bear 1971, Caughley 1970). There may also be a danger in assuming that condition reflects current or recently past nutritional quality because of the unsynchronised cycles of changing condition in the males and females of ungulate species which breed seasonally and have pronounced rutting seasons (Sinclair and Duncan 1972, Caughley loc. cit.). Fat deposits are heaviest in males at the start of the rut, while the peak occurs in females in late pregnancy 6-8 months later.

The use of kidney fat, especially, as an index of condition has developed from the study of temperate ungulates. Although it is the most convenient measure to take from tropical species as well (Smith 1970), the carcass fat contents of tropical wild ruminants are far lower than those of domestic stock in the same environment (Ledger 1968) or in their temperate counterparts (Smith loc. cit.). The range of values is, therefore, narrower and measurement may be more difficult. The main body reserve of tropical ungulates seems to be the protein of their muscles (Smith loc. cit.) and, perhaps because of this, seasonal fluctuations in their body weight are far less striking (Talbot and McCulloch 1965). These considerations must be borne in mind when interpreting changes in the condition of the hartebeest.

12.2 Methods

Visual condition of living animals

This method depended upon the fact that adult male hartebeest could be recognised individually by features such as horn shape and ridging, tears in the ears, and scars. This method was used on a large scale by Gosling (1974). At the beginning of the study, standard photographic

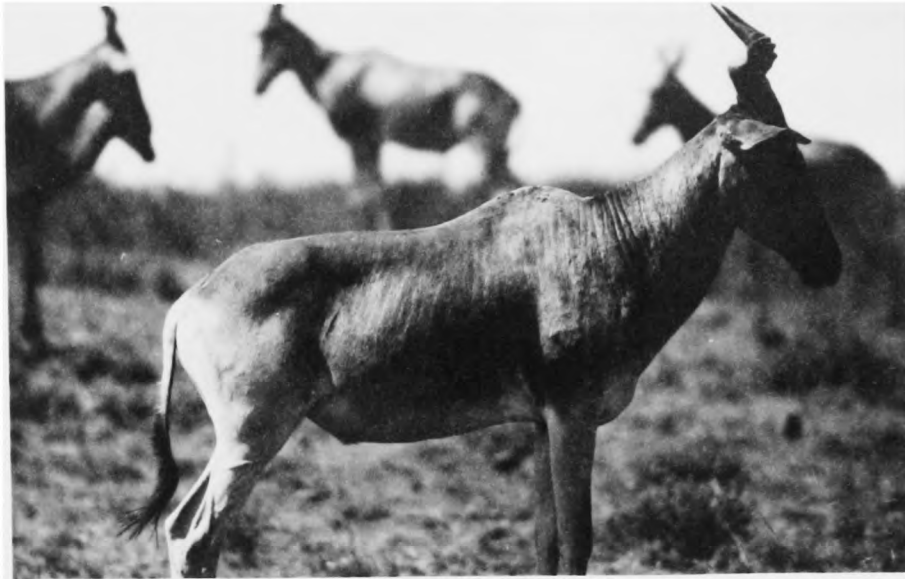
portraits were taken of territorial males in two contrasting areas of the Nairobi Park study area. These were the grassland A. drepanolobium scrub ecotone at the north-west side of the area and the open grasslands and bush grasslands in the southern third of the study area (Fig. 5.3.). At any one time 30-35 males were known, but new animals were continuously incorporated in to the file because of the constant turnover through presumed death, loss of territory or temporary absence on sampling days. There was an inevitable wastage of animals which were photographed and put on file after taking up territories but occupying them for only a few weeks or days.

In the first 3 days of each month, the study area was searched to find and identify positively as many of the known animals as possible. If absent from their territories, males were sought in the herds of non-territorial males which they may join for variable periods before returning to their territories (Gosling 1974). A male found in such a herd was photographed in the same way. The location of all males, and the size and composition of any accompanying herd were recorded, and a standard photograph of the male was taken. This was taken with the animal in a standing position, looking straight ahead and presenting a full flank profile to the photographer at a distance up to 30 m. Fulfilling these conditions was not difficult after practice, mainly because the males, with a few notable exceptions, were approachable to within this range. As animals were photographed at whatever time of day they were found, variations in lighting, which might affect the interpretation of the pictures, were unavoidable. In general, though, photographs were taken with an Asahi Pentax camera and 300 mm lens with F4 film rated at 150 ASA, and were printed at enprint size (80 x 56 mm).

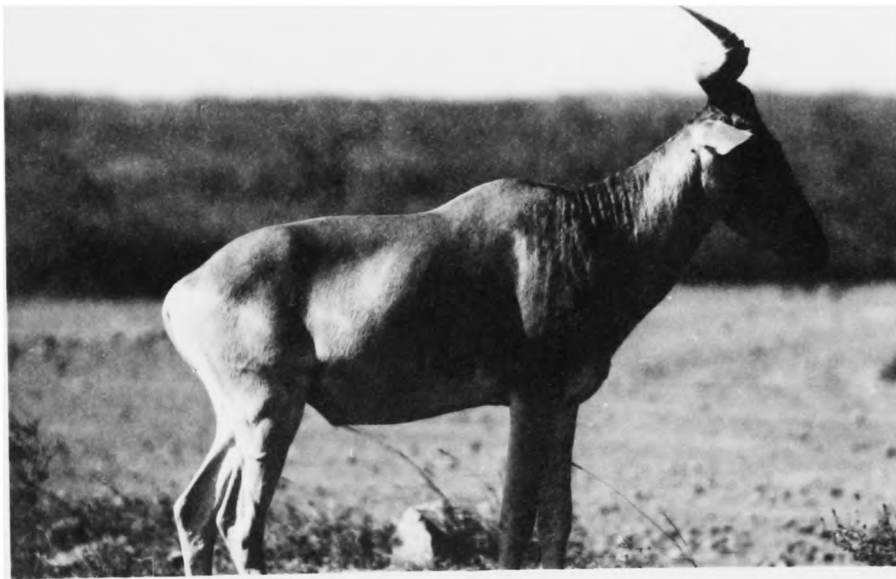
This procedure was followed for 21 months between November 1970 and July 1972, with the exception of January 1971. The number of animals photographed in each month varied, particularly through being low at the



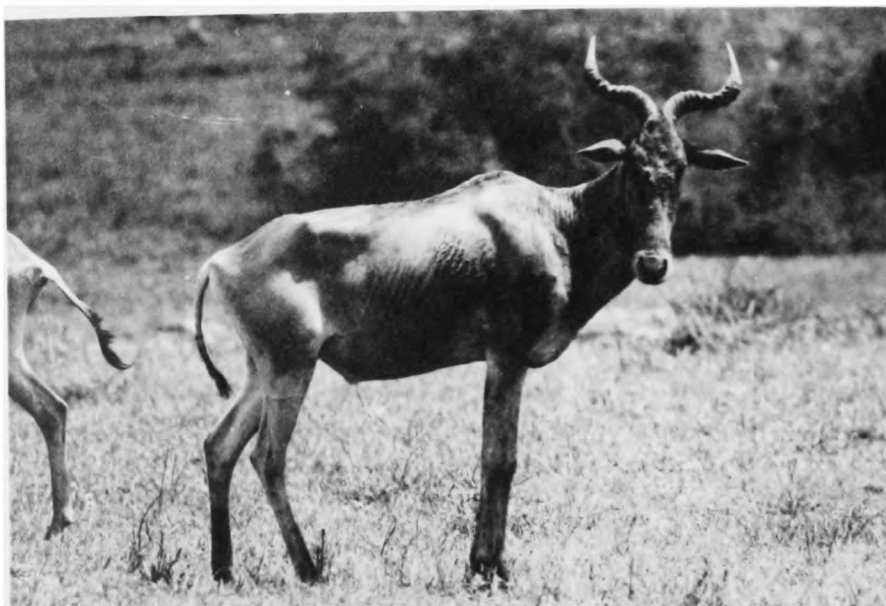
1. "Excellent" condition



2. "Good" condition



3. "Medium" condition



4. "Poor" condition

Plate 1.
Condition
Classes.

beginning, but attempts were made always to find at least 20 males in each month within the time available for this exercise. The results are based on a sample of 375 photographs from this period.

In the final 8 months, 12 non-territorial males, selected randomly from herds, were photographed each month for comparison. Selection was made by driving in to the middle of such a herd and photographing the nearest male to a previously chosen random compass bearing from that point. If the study area contained one male herd, all 12 photographs were taken in it; if there were 2 herds, 6 photographs were taken in each, etc. Thus, 96 photographs were available for comparison.

At the end of data collection, the complete set of photographs was laid out in a 2-way array by months and individuals. Examination showed the general trends of changes in external appearance and the sequence in which they occurred. From this, 4 categories of external appearance were defined (Plate 1):

1. "Excellent" condition. In profile, a completely round or nearly round outline between the withers and the base of the tail. The sacral vertebrae do not appear as a distinct ridge. The outline above the iliac process of the pelvic girdle is smooth, but there may be a faint shadow on its underside, posterior to the abdominal cavity. There is never a sharp line from the iliac process to the sacral ridge.
2. "Good" condition. The sacral vertebrae are distinct. The iliac process only just shows, but has a distinct depression to its anterior.
3. "Medium" condition. The iliac process is now obvious and the vertebral column posterior to the withers is now in three distinct sections. The whole body may have a drawn look, and the top surface of the scapula may show. The ribs may be visible in outline, but this is very dependent on the lighting conditions in the photograph.

4. "Poor" condition. Severe emaciation. The ribs and scapula are all obvious. The outlines of the bones between the tuberosities of the ischium and ilium are visible.

Photographs which exemplified each of these classes were kept as standards for comparison while the photographic record of each animal was scored for each month. The complete set of scores provided a frequency distribution of the condition categories, describing the "mean appearance" of the territorial and non-territorial males of the area.

The changes in appearance were examined in relation to the most obvious seasonal parameter, rainfall. The monthly rainfall totals from Embakasi were used as effective rainfall, P/E_t (p.22), calculated cumulatively for preceding months. Because the condition classes were only ordinal groupings, non-parametric tests were used to relate the condition frequency distributions to the rainfall. As the photos were taken in the first few days of each month, the rainfall of the previous month was used as that of the first month.

The condition of dead hartebeest

Three measures of the condition of the shot hartebeest were taken. The results of only the Series 2 animals are presented. In these measures, the absolute size of the animals has been removed by converting all measurements in to indices. The denominator throughout is the length of the hind foot (HF). As a skeletal measurement, this has the advantage of not varying over short periods of time and, in deer, its adult size is independent of the plane of nutrition of the growing animal (Bandy et al. 1956). Variation in the indices therefore represent genuine changes in the condition parameters.

The more usual denominator in kidney fat indices is the weight of the kidneys (Riney 1955, Ransom 1965). In white-tailed deer, the kidneys continue to grow after the animal's mature body weight has been reached (Hesselton and Sauer 1973), and seasonal variation in kidney weight

due to either growth or stress effects was also observed. Because of this complex of factors affecting kidney weight, and hence its relationship to total body weight, hind foot length was preferred as a denominator in the kidney fat index.

When cows change from being fed hay to grazing at pasture, their weight may alter by 6-8% due to changes in the weight of the rumen contents alone (Balch and Line 1957). As the measured variation of the latter in the hartebeest was similar (p.175), the effect of any variation has been removed by using the eviscerated weight of the animals. This is the fresh dead weight less the weight of the rumen contents.

a. Kidney fat. Both kidneys with their attached fat were removed and weighed separately to the nearest 0.1 g. Delimitation of the margins of the fat was usually obvious, but in individuals with large deposits continuous with the fat around the ureters and the aorta anteriorly, the fat was cut through 5 cm from the kidney edges. The weight of the fat was obtained by difference after weighing the fat-free kidneys. The results are expressed as the ratio :

$$\frac{\text{weight of kidney fat}}{\text{hind foot length}} \quad (\text{KF/HF})$$

b. Muscle weight. From each animal, one quadriceps femoris muscle with its femur was dissected out and weighed to the nearest 1 g. The bone was cleaned and weighed. The resulting muscle weight is also expressed as a fraction of the hind foot length (muscle weight/HF).

c. Marrow dry matter. Sinclair and Duncan (1972) have confirmed for tropical ruminants the finding that in caribou there is a close relationship between the dry matter content of the bone marrow and its fat content (Neiland 1970). As the work of the former authors was partly carried out on hartebeest, fat extraction was not considered necessary.

One femur was taken from each animal and frozen until needed. Then, a sample of about 10 g was taken from the middle of the thawed marrow,

avoiding the haemopoietic portions at the ends. The samples were weighed to the nearest 0.1 g, dried in an oven at 60°C (Neiland loc. cit.) until constant weight was achieved, and reweighed. The dry weights are expressed as percentages of the fresh weight.

Weight and age

The shot hartebeest were weighed whole to the nearest 2 lb (0.9 kg), and were aged according to their tooth replacement up to 3-4 y and on the M3 length of older animals (p. 15). These two sets of information show how body weight changes with age, providing an approximate growth curve.

Condition analysis

The three sets of data on body condition have been investigated for possible effects due to season (measured as the month of collection), the age of the animals, their sex if adult, and the reproductive status of the females. As the 3 measures of kidney fat/HF, muscle weight/HF and the dry matter content of the marrow are all proportions or percentages, arcsine transformations which are appropriate for this type of data in the analysis of variance (Sokal and Rohlf 1968) have been used.

Although the total sample of 32 animals is small, the analysis of their variance (anovar) was facilitated by having 8 animals in each of the monthly samples, consisting of 3 adult males, 3 adult females and 2 immature animals. In a few cases, arrangement of the data in a 2-way matrix produced cells without any value, and these were replaced by the method advised by Kirk (1968), using the following formula:

$$\overline{AB}_{ij} = \overline{A}_i + \overline{B}_j - \overline{ABS}$$

where $\overline{AB}_{ij}$ = estimate of missing cell
mean

$\overline{A}_i$ = mean of observations in
treatment level a_i that
contains missing cell

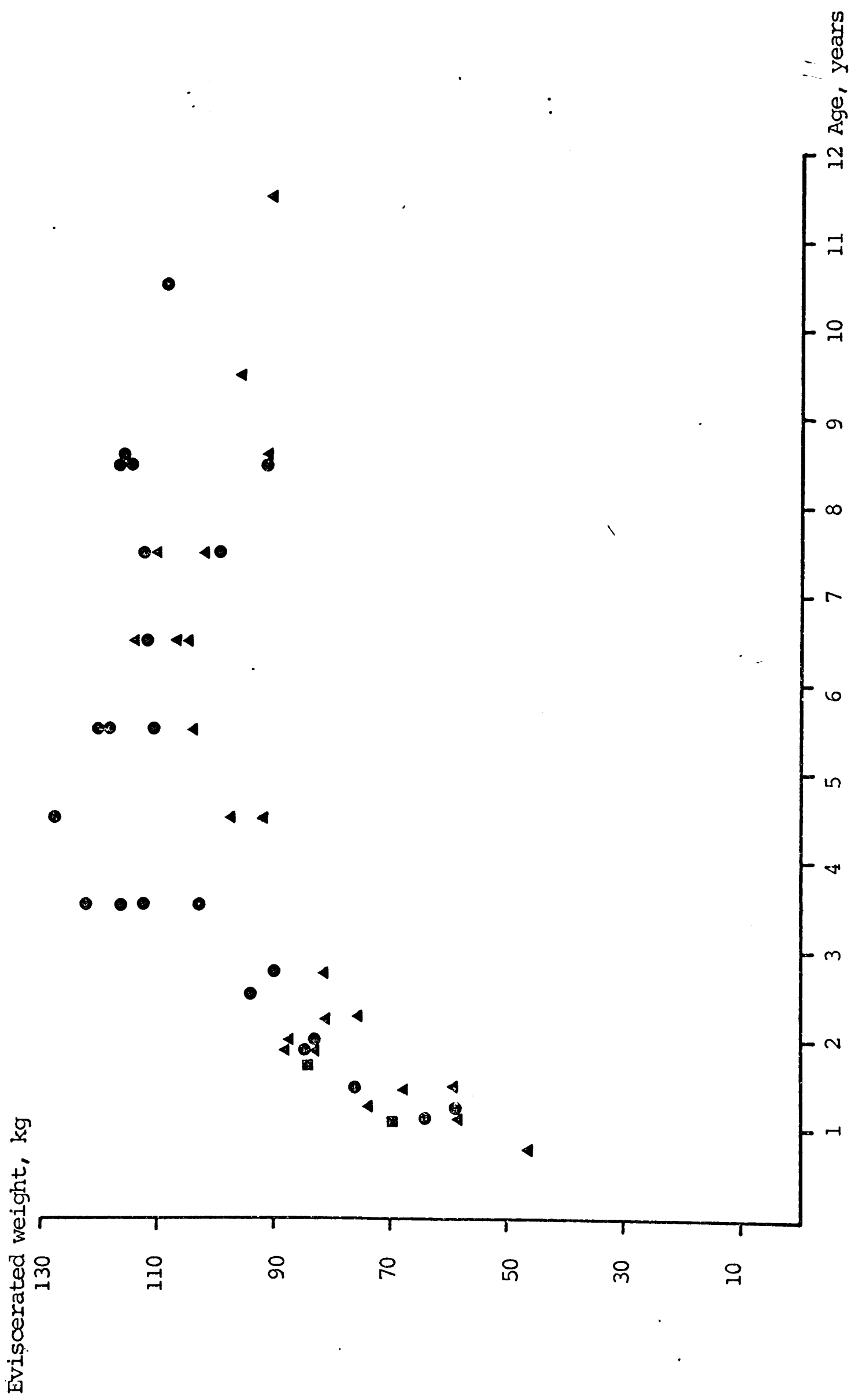


Fig.12.1.1. The age (years) and eviscerated weight (kg) of shot hartebeest. ● males, ▲ females.

$\bar{B}_j$ = mean of observations in
treatment level b_i that
contains the missing cell.
 $\overline{ABS}$ = mean of all available ob-
servations.

When a blank cell has been filled, the subsequent anovar is performed with one less degree of freedom in the error sums of squares (SS) and the total SS (Sokal and Rohlf loc. cit.). In some cases the sample size was too small even for this expedient (e.g. for a 2-way anovar of KF/HF by month between pregnant and non-pregnant females, where the total sample size is 12) and two 1-way anovars were performed, at the expense of being able to detect any interactive effects between the two factors.

12.3 Results

Growth curve

The relationship between the eviscerated weight and age of the shot hartebeest is shown in Fig. 12.1, based on 45 individuals from Series 1 and 2 for which skulls were available for aging (Appendix 13). The median value for each age class has been used to plot the figure.

Although there is only one point below the age of 1 y, the picture is of weight increasing in a curvi-linear fashion to a maximum between the ages of 3 and 4 y. It is clear from this that although hartebeest may have the adult horn conformation at about 2 y old (Gosling 1974), full body weight is not attained until over a year later. This distinction is used below.

At ages greater than 3.5 y, body weight appears to decrease linearly, and the correlation between the two variables was calculated. Using data from 27 animals of 3-4 y or older, the correlation fails by a small margin to be significant ($r = -.370$, d.f. 25, $0.10 < p > 0.05$). Therefore, although suggestive, total body weight does not decline significantly after full adult weight is reached.

The possible effects of age and season on the body weight were examined by dividing the adults into two groups of those 3-7 years old and those more than 7 years old, and running a 2-way analysis of variance of the eviscerated weight/HF index values broken down by month and age group. This index of body weight does not differ significantly between age group ($F = 1.045$, $p > 0.05$), confirming the results of the correlation above, nor between months ($F = 1.669$, $p > 0.05$). There is, however, a small interaction between these parameters ($F = 3.822$, $p = 0.05$), indicating that the weight index of the animals varies, but not systematically, between months or age groups.

Figure 12.1 also shows that the adult males tend to be heavier than the females, with adulthood defined here on horn shape. The mean eviscerated dead weights are 112.5 and 95.5 kg for males and females respectively. The means and standard deviations for the dead weights of intact animals are 131.6 ± 10.9 ($n = 17$) and 110.3 ± 13.8 kg. ($n = 16$) respectively. The latter weights are significantly different ($t = 4.94$, d.f. 31, $p < 0.001$).

Visual condition

The monthly frequency distribution of visual condition classes, expressed as percentages are shown in Table 12.1, with the sample sizes, for both territorial and non-territorial males. The cumulative effective rainfall, P/E_t , over the same period has been calculated from the rainfall data for Embakasi (Appendix 3).

Spearman rank correlations of male condition and P/E_t have been calculated first with the percentage of males in each sample in category 4 of "excellent" condition and, then, for the percentage in the top two categories of "excellent" and "good" condition. These are the results:

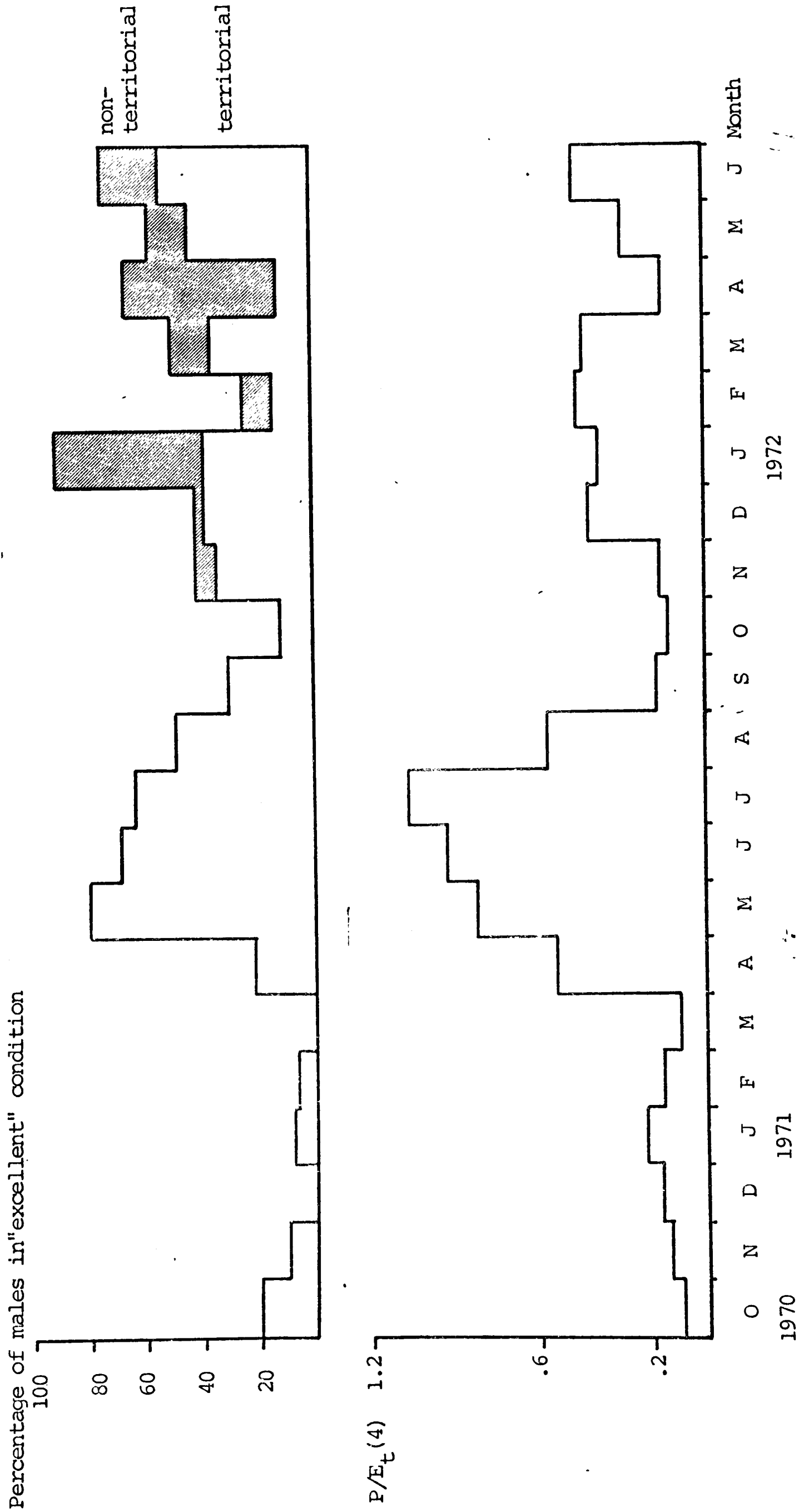


Fig.12.2. The percentage of territorial males over 21 months, and non-territorial males over 8 months, in "excellent" condition, with the effective rainfall over the previous 4 months, $P/E_t(4)$.

Table 12.2. Summary of the results of 2-way analysis of variance on condition variance on condition measures.

1. Adults compared with juveniles = maturity, between months.

		Kidney fat/HF		Muscle wt/HF		Marrow %DM	
A = Maturity	F, d.f.	1.48	1,24	44.44	1,24	4.00	1,24
	prob.	n.s.		.01		n.s.	
B = Month	F, d.f.	1.64	3,24	1.61	3,24	6.66	3,24
	prob.	n.s.		n.s.		.01	
A x B	F, d.f.	1.07	3,29	2.26	3,24	2.02	3,24
	prob.	n.s.		n.s.		n.s.	

2. Adult males compared with adult females = sex, between months.

		Kidney fat/HF		Muscle wt/HF		Marrow %DM	
A = Sex	F, d.f.	1.48	1,16	2.48	1,16	0.03	1,16
	prob.	n.s.		n.s.		n.s.	
B = Month	F, d.f.	2.55	3,16	3.68	3,16	7.84	3,16
	prob.	n.s.		.05		.01	
A x B	F, d.f.	0.52	3,16	1.22	3,16	0.61	3,16
	prob.	n.s.		n.s.		n.s.	

3. Young adults compared with old adults = adult age, between months

		Kidney fat/HF		Muscle wt/HF		Marrow %DM	
A = Adult age	F, d.f.	1.63	1,12	12.12	1,12	4.91	1,12
	prob.	n.s.		.01		.05	
B = Month	F, d.f.	1.55	3,12	7.17	3,12	7.36	3,12
	prob.	n.s.		.01		.01	
A x B	F, d.f.	-0.24	3,12	-1.21	3,12	-0.32	3,12
	prob.	n.s.		n.s.		n.s.	

No. of months cumulative effect- ive rainfall	correlation with percentage of territorial males in			
	r_s	category 4 sig.	category 3 + 4 r_s	sig.
1	.466	< .05	.106	n.s.
2	.580	< .01	.350	n.s.
3	.699	< .01	.430	< .05
4	.785	< .01	.473	< .05
5	.747	< .01	.478	< .05

For each rainfall period the correlation is higher with the proportion of territorial males in category 4 only, and the correlation is significant in each case. The highest coefficient occurs with the cumulative rainfall of the previous 4 months ($r_s = .785$, $p < .01$), showing that the proportion of territorial males classed as in "excellent" condition depends on the effective rainfall over this period. This relationship is demonstrated in the histograms of Fig. 12.2.

The percentage of non-territorial males also in category 4 are included in this figure. The run of data is too short to correlate with the rainfall, but with the exception of January 1972, similar changes in condition as in the territorial males occur. The proportions of the 2 classes of males in category 4 have been compared using a Wilcoxon Matched pairs, signed ranks test (Siegel 1956). As the proportion of non-territorial males in "excellent" condition is always greater, the two distributions are significantly different ($T = 0$, $p = .01$). Thus, in any month, a higher percentage of non-territorial than territorial males are in "excellent" condition.

Condition of shot hartebeest

Appendix 13 contains the relevant data on each of the Series 2 animals, namely its month of collection, sex, age, reproductive status if female, its KF/HF and muscle weight/HF indices, and the percentage dry matter in its femur marrow. Table 12.2 summarises the results of the analyses of variance, showing the F ratios obtained, the degrees of freedom and the significance.

No. of months cumulative effect- ive rainfall	correlation with percentage of territorial males in			
	r_s	category 4 sig.	category 3 + 4 r_s sig.	
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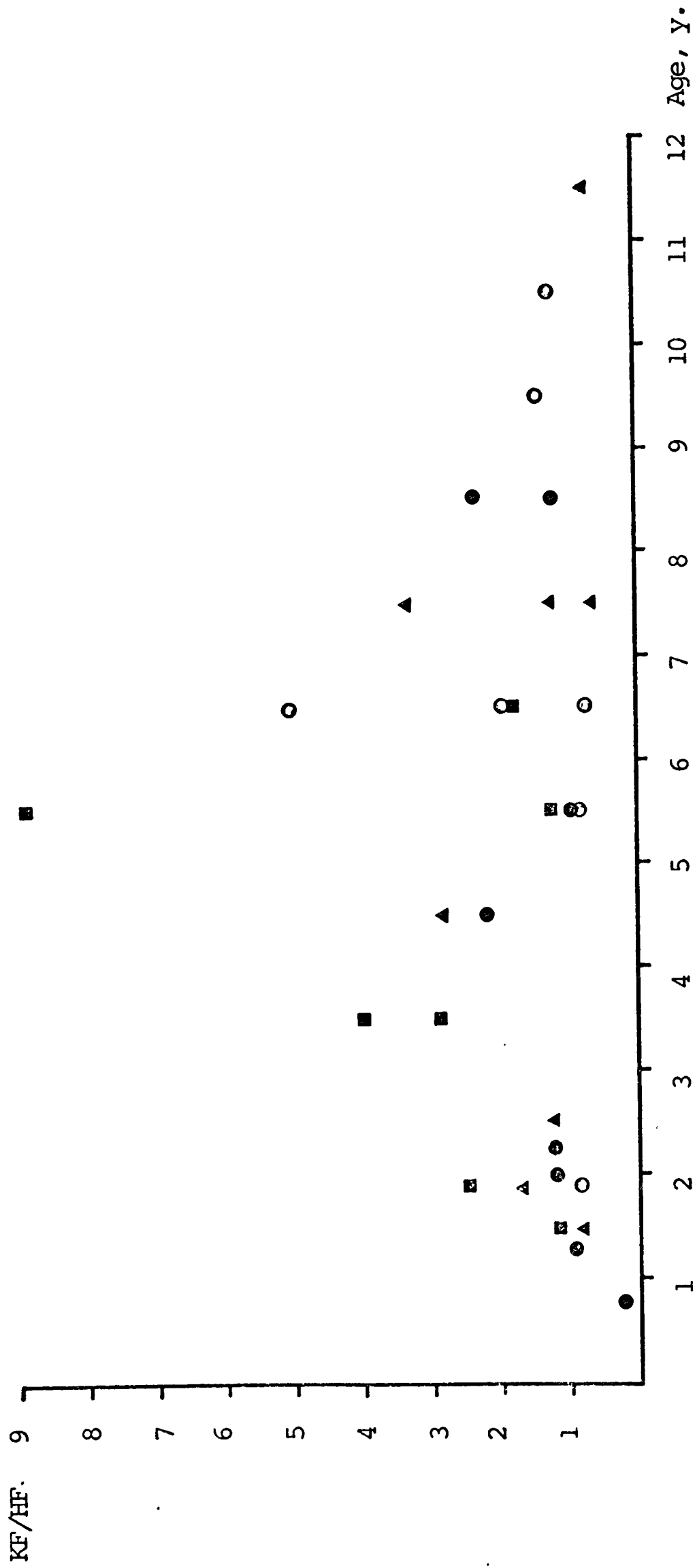


Fig.12.3. The kidney fat weight to hind foot length ratio (KF/HF) and age of hartebeest collected in 4 months: ● January, ▲ April, ■ July, ○ September.

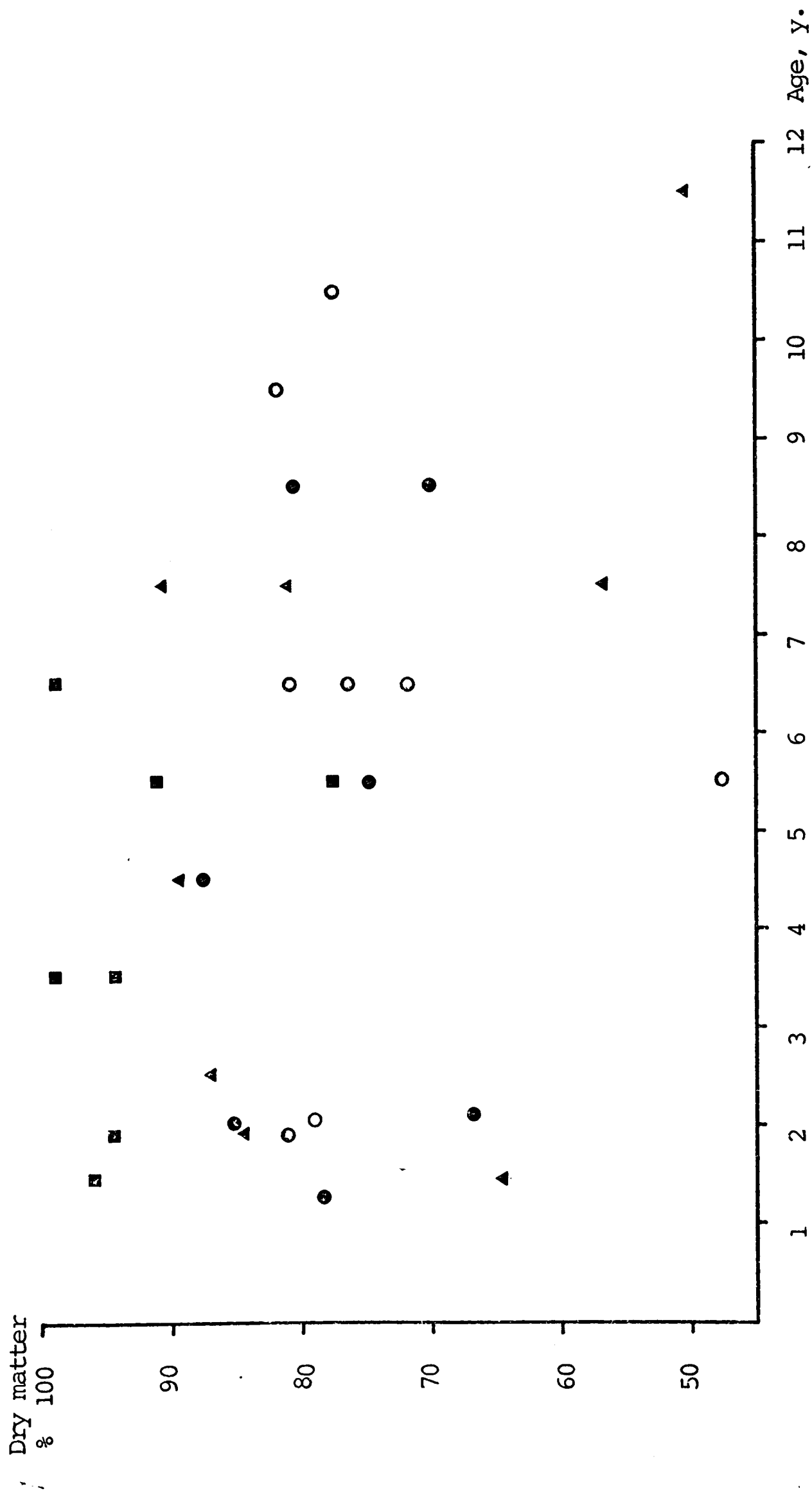


Fig.12.4. The percentage dry matter in the femur marrow, and the age of hartebeest collected in 4 months: $\blacksquare$ January, $\blacktriangle$ April, $\bullet$ July, $\circ$ September.

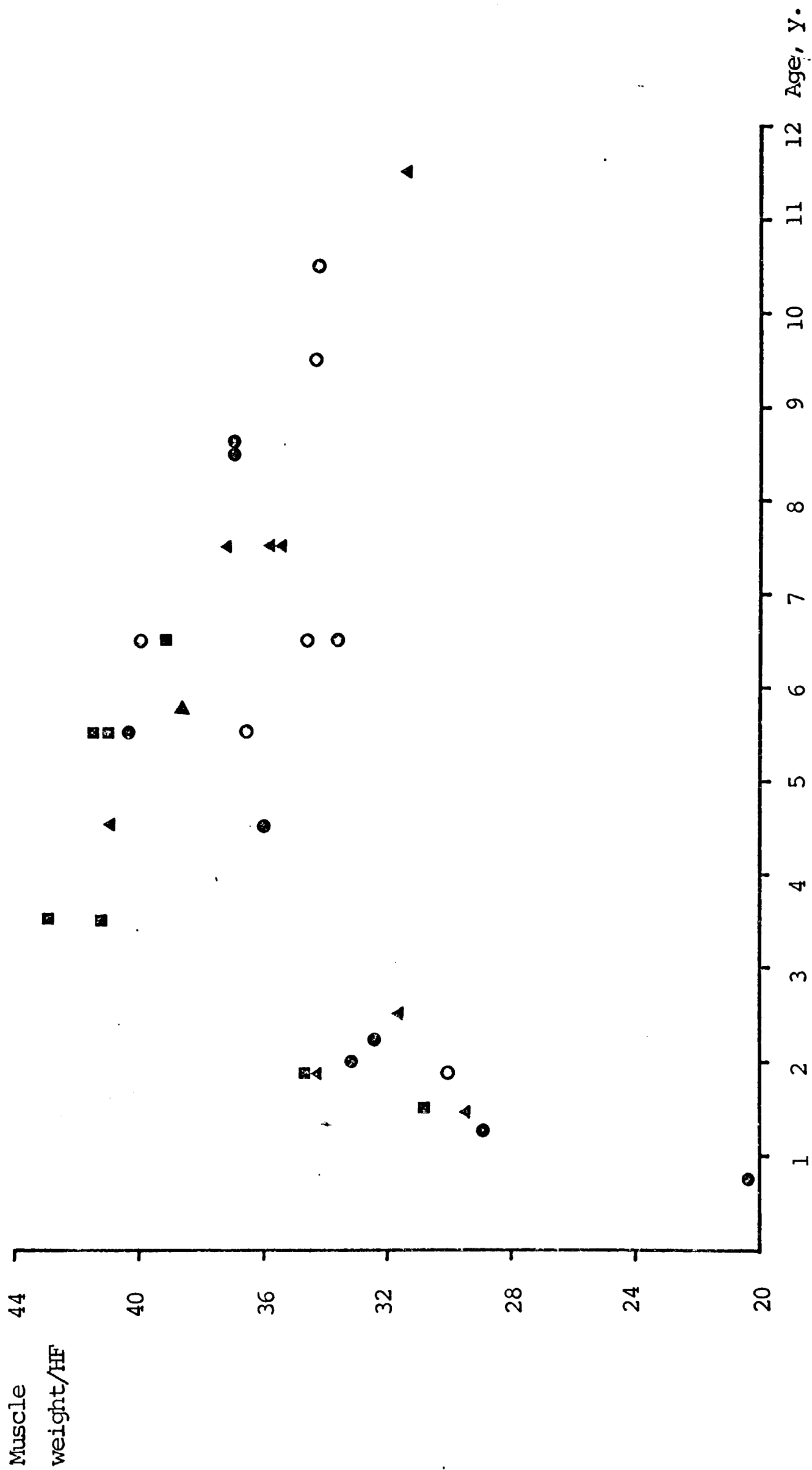


Fig.12.5. The quadriceps femoris muscle weight to hind foot length ratio (muscle weight/HF), and the age of hartebeest collected in 4 months: ● January, ▲ April, ■ July, ○ September.

Fig. 12.3 shows the KF/HF index of all animals plotted against their age. With the animals divided on the basis of horn development in to immature (less than approximately 2 y) and mature (≥ 2 y), there is no significant difference in their quantities of kidney fat. There is also no significant difference between months, although wet and dry seasons are represented. The kidney fat index also does not differ between adult males and females or between adults in their prime (3-7 y) or more than 7 y old. In the last two cases the values are also homogeneous between months. Thus, the amount of kidney fat found in these hartebeest varies little between animals of different physiological status or between different times of the year.

The dry matter percentages in the femur marrow, which are equivalent to their fat contents (p.226), are included in Appendix 13. The fat content in adults does not differ significantly from those of immature animals, nor does it differ between adult males and females. But, in both cases, the values are heterogeneous between months. Fig. 12.4 shows that this is due to the low values in the dry month of September and the relatively high values in July. Comparing prime and old adults, the monthly difference persists, but the fat contents of these two classes are also significantly different, due to the lower amounts of fat in the old adults (Fig. 12.4).

Fig. 12.5 shows the muscle weight/HF indices plotted against the age of the animals. Broken down between young and adult, the data are highly heterogeneous because the immature animals have low indices, but there is no effect of month. Adult males and females do not differ significantly but their values are heterogeneous with respect to month. This effect persists when the indices for adults of both sexes are broken down in to those 3-7 y old and those older than 7 y. These two groups also have highly heterogeneous indices due to the decline in muscle weight/HF ratio with increasing age (Fig. 12.5).

Table 12.3 Summary of results of one way analysis of variance on
condition measures of female hartebeest.

1. All females broken down by month of collection.

	Kidney fat/HF	Muscle wt/HF	Marrow % DM
F - ratio	1.03	1.59	2.49
d.f.	3. 8	3. 8	3. 8
probability	n.s.	n.s.	n.s.

2. Females collected in all months classed as pregnant or non-pregnant

	Kidney fat/HF	Muscle wt/HF	Marrow % DM
F - ratio	0.35	5.08	0.77
d.f.	1.10	1.10	1.10
probability	n.s.	.05	n.s.

To summarise these results, there are effects due to age or growth stage and month within these measures of body condition. Immature animals have lower muscle weight/HF ratios but their marrow fat and kidney fat weights are not significantly different from those of the adults. Overall, adult males and females do not differ significantly according to any of these measurements, but adults of both sexes aged more than 7 y have significantly less marrow fat and lower muscle weights. On a seasonal basis, kidney fat values do not vary significantly. In all 3 comparisons of animal groups, the marrow fat shows highly significant changes, principally due to the high values recorded in July and the low ones in the dry month of September. Highly significant monthly variation in the muscle weight index occurs between young and old adults, and to a lesser extent between the adults of both sexes.

The two-way anovars treat all the individuals of a group as replicates, resulting in the combination of females of very different reproductive states. To look at this in more detail, one-way anovars have been performed on the results of adult females by grouping them first by month, and then by classing them as pregnant or non-pregnant, irrespective of their month of collection. The results are summarised in Table 12.3.

There is no significant difference in the KF/HF indices of adult females between months or between those pregnant and non-pregnant. Similarly, there is no heterogeneity in the marrow fat contents according to month or reproductive state. The muscle weight indices do not vary between months, but there is a significant difference between the pregnant and non-pregnant groups. This means that the muscle weight/HF index of pregnant females (mean 37.67, from Appendix 13) is significantly greater than that of the non-pregnant group (mean 34.13).

12.4 Discussion

The four samples of shot hartebeest are too few to detect any cyclical

changes in condition, but they represent wet and dry seasons. The non-significant difference in KF/HF values between seasons or age classes is in marked contrast to the findings of Caughley (1970) and Bear (1971). The fat content of the marrow shows more seasonal variation and is significantly less in old (>7 y) adults, although this is the last fat reserve to be used (Riney 1955, Ransome 1965, Harris 1945). The slight variation in KF/HF values and the sensitivity of the marrow fat content to seasonal influences suggest that the hartebeest have low fat reserves and that high values rarely occur. Sinclair and Duncan (1972) show the relationship between the kidney fat and marrow dry matter fraction in large series of Serengeti wildebeest, both shot and dying naturally, and both measures of condition span a much greater range than observed here in the hartebeest.

The muscle-weight/HF index varies with the age of hartebeest showing that the low values of immature animals and of old (>7 y) adults are phenomena of growth and senility. Within the adults, the significant differences in muscle weight between months in the two sexes and in the young and old adults suggests that the muscles are used as a mobile reserve of protein, which was drawn upon in the dry season of September 1972. Although the energy value of protein is low compared to that of fat, protein reserves may be drawn upon early in pregnancy rather in the final stages when fat reserves are mobilised (Russel et al. 1968). Clawson and Meyer (1964) found that after restricting the food intake of wether sheep for 42 days by only 16% of the control intake, the fat content of the empty bodies of experimental sheep was no less than that of the control animals, but the protein contents were significantly lower.

With the evidence of no very large fat deposition in the hartebeest, the restoration of the protein reserves may take priority over those of fat when nutrient intake exceeds the animals immediate requirements. The importance of the protein levels in the body is also suggested by the significantly higher muscle weight/HF indices of pregnant than non-pregnant

females, while the two fat measurements showed no difference. The generally low fat content of the indigenous ruminants of East Africa compared to those of cattle (Ledger 1968) indicate that fat is a relatively unimportant reserve in these animals, and in general, far more extreme values are recorded in temperate ungulates (Smith 1970).

These influences of age, season and physiology must be taken in to account when interpreting the changes in the visual condition of the males. The long series of data shows changes in appearance related to the previous rainfall, but presumably mediated through changing food quantity and/or quality, which is discussed below. The changes are not necessarily inconsistent with the lack of seasonal variation in the eviscerated weight of the shot animals as the data refer to two areas supporting very different densities of hartebeest (p.95). Under these conditions the relationship between rainfall, food quality and quantity and physical condition may be different. There is also the possibility that the weight changes associated with the changing appearance might be too slight to be detected, if they occurred, in the shot animals. Again, in marked contrast to temperate ungulates, the variation in adult body weight in tropical species is small (Talbot and McCulloch 1965).

Changes in visual condition are probably due to the same physiological processes as occur in the deposition or mobilisation of any sub-cutaneous fat reserves or changing muscle weight. Changes in the latter were shown above to be partly dependent upon age. However this source of variation was reduced for the territorial males, first, by trying to sample the same animals in each month and secondly because this class of males usually contains those in their prime, aged 4.5-6 y (Gosling 1974). This would tend to maximize the chances that the observed differences are due to variations in nutritional conditions rather than reflecting changes with age. Conversely, this source of variation would be greater with the non-territorial males because their random selection would increase the

inter-individual variation, and because this category contains males within the wide age range of about 2.5 y to extreme old age (approximately 12 y) (Gosling loc. cit.).

Although there are more sources of variance within the non-territorial males, the results clearly show (Fig. 12.2) that these animals are always in significantly better condition than the territorial males. This could be because:

1. the territorial males occupy areas with poorer food or other resources,
2. the food intake by territorial males drops through a reduction in the time spent feeding, or
3. intake is the same but their energy expenditure is greater.

The first possibility seems unlikely because the breeding females in the population occupy the same areas, and drastic difference in food quality within the study area of 20 km² seem unlikely (p. 265). The data on activity patterns do not cover the latter possibilities, but territorial male impala spend a smaller proportion of their day feeding when both with-out and with females (Jarman and Jarman 1973). In the latter case, the time spent in such energy-demanding activities as territorial defence and the herding of females is also greater, and males holding territories "lose condition" in an unspecified way (Jarman and Jarman loc. cit.). Although the pattern of territoriality differs in hartebeest and impala (Jarman 1974), territorial hartebeest perform these same activities (Gosling 1974) which probably accounts for their poorer external appearance.

The age-weight relationship of Fig. 12.1 is not strictly a growth curve because it does not follow the changes in weight of a number of known-age animals. Rather, it is a population mean growth curve reflecting genetic and environmental influences. The growth curves of individual deer under controlled conditions of ad libitum feeding on a high nutritional plane show great seasonal periodicities (Wood et al. 1962). Under these conditions development may be precocial and such complications may

mean that mammalian growth cannot be adequately with a single mathematical expression (Caughley 1971).

The attainment of maximum adult body weight at the age of 3-4 y (Fig. 12.1) suggests that the hartebeest growth rate may be low. As there is abundant evidence that the growth rate of ruminants is largely proportional to their nutritional plane (e.g. Amir, Kali and Volcani 1968), this suggests that the amount of energy which is in excess of the hartebeest's requirements for maintenance and available for tissue production, is relatively small. As a "roughage grazer" (Hofmann 1973), the hartebeest's food is almost certainly of lower quality on a year-round basis than that of the wildebeest, classed as a "fresh grass grazer". This might result in the lower growth rate. An overall low nutritional plane is consistent with the existence of small fat deposits in the hartebeest and the sensitivity of their body protein reserves to the effects of the seasons and age (p. 231).

Use of the age-weight relationship (Fig. 12.1) as a growth curve masks any variations in the growth rate between individuals or over relatively short periods within one animal. In particular, the mean growth rate will be depressed if at any time growth ceases or weight loss occurs. French and Ledger (1957) have observed that frequent periods of subsistence feeding without weight gain are experienced by cattle in East Africa. To select cattle for such conditions according to their performance on high nutritional planes is mistaken for, in general, the fast-growing breeds are those most susceptible to permanent stunting if temporary checks occur (Joubert 1954). Cattle wintered indoors and fed artificially gave consistent weight gains, whereas those grazing outdoors at the same time could only maintain their weight or show slight gains (Pearson-Hughes et al. 1955). However, the summer gains of the outwintered group were much greater than those inwintered, so that the year-round weight gains differed very little. In a review of compensatory growth, Wilson and Osbourn

(1960) conclude that an animal whose intake has been restricted and^{which}/is then realimented is no less efficient at conversion than an animal which has been continuously grown, provided the restricted animal does not actually lose weight and is allowed to express its increased appetite by feeding ad libitum during realimentation.

The hartebeest's energy intake drops in the dry season (p.193), and as it may then be inadequate for even their maintenance (p. 195), growth obviously ceases. Utilisation of the body reserves to compensate for this deficit is suggested by the lower marrow fat contents and muscle weights in the dry season (p. 231). On the other hand, the body weights of these same animals showed no significant variation between months (p. 229), and some of the possible methods by which weight losses might be avoided have been discussed (p.203). If dry season losses are avoided, and the hartebeest can obviously feed ad libitum when the new growth of herbage comes, the conditions for complete compensatory growth are satisfied. Thus, the impact of periodically adverse environmental conditions on the adult body weight are minimized, at the cost of an overall low growth rate.

The trend of progressively declining body weight after maturity (Fig. 12.1) was also observed in wildebeest by Watson (1967) who wondered how widespread the phenomenon was in wild Bovidae.* Human weight increases in males up to 74 y and in females up to 64 y, and subsequently declines (Kleemeier 1959). The hartebeest and wildebeest pattern is unusual in that there is no plateau of nearly constant weight between maturity and the onset of a distinct phase of senescence. As there is no shortening of HF length, which measures skeletal size (p. 225), after maturity, the weight decrease is due to the diminution of soft tissues. This is confirmed by the highly significant difference in the muscle weight/HF indices of young and old adults (p. 231). The extent of weight loss is the same in both sexes, suggesting that it is not due only to the effect of

* It has also been observed in the Serengeti buffalo (Sinclair 1974).

successive pregnancies. I suggest that as this muscle is used largely as a mobile reserve during the dry season, the hartebeest's ability to restore their protein reserves after each period of mobilization declines with increasing age. Nothing can be said of the possible physiological causes of this phenomenon, but the greater reliance of deer on fat reserves (Smith 1970) may explain why this effect has not been noticed in the Cervidae.

Chapter 13.

REPRODUCTION AND THE BREEDING PATTERN OF THE HARTEBEEST

13.1 Introduction

Previous chapters have dealt with the energy expended by the hartebeest in their daily activity and in their growth. The third main avenue of energy use is for reproduction, which is considered in this chapter from the point of view of the female hartebeest only.

The plane of nutrition affects the sexual development and level of reproduction of ruminants in numerous ways. Joubert (1954) found that the age of puberty in cattle, recorded as the first oestrus, is more sensitive to the effects of detrimental nutrition than was the weight at which it occurred, and suggested (Joubert 1963) that first breeding may occur only when some specific size is reached. In view of the small surpluses of energy intake above the field requirements in some months (p. 219) and the hartebeest's slow growth rate, one might predict on this basis that puberty would occur at a relatively late age. Late maturity in tropical Bos indicus breeds of cattle is common (Lamond 1970), with cows not calving for the first time until 4 years old.

In sexually mature animals the level of nutrition markedly affects the onset and cessation of breeding (Sadleir 1969a), but in attributing causation one must distinguish between the ultimate, or evolutionary, and the proximate, or physiological and behavioural, reasons for any observed phenomena (Lack 1954). Nutrition is particularly important in tropical and arid regions where the quantity and quality of food depends largely on a low and possibly erratic rainfall (Sadleir loc. cit.). Consequently, rainfall, the nutritional plane and their effects on the animals could include the main ultimate and proximate factors determining the timing of the breeding season. This could then account for the lack of any clear influence of photoperiodism on the breeding seasons of tropical African ungulates (Spinage 1973) in an environment where temperature fluctuations through the year are also small (p. 47).

If nutrition is implicated as a determinant of the timing of the breeding season, the stage of the reproductive cycle at which its effect is most critical must be identified. The energy cost to the female ruminant of pregnancy and lactation are well established (A.R.C. 1965), but breeding may not necessarily be timed so that the greatest energy demanding stage occurs at the time of best nutrition. Factors such as the quality of food at the time of weaning may also be important, and the advantage of breeding in any particular month or season must be roughly proportional to the fraction of the population exhibiting this pattern. These factors are investigated in this chapter to describe the reproduction of the hartebeest in the context of its ecology.

13.2 Methods

Shot animals.

The reproductive status of all adult females was investigated macroscopically only. The uterus and contents of pregnant females was removed and weighed intact, and the foetus was also weighed. The time since conception was calculated by the method of Huggett and Widdas (1951), using the expression,

$$W^{.33} = a(t - t_0) \quad \text{where } W^{.33} = \text{cube root of the foetal weight in g.}$$

a = specific foetal growth velocity constant.

t = time since conception, days.

t_0 = constant.

For a , the sheep value of 0.147 has been used. The size of the constant t_0 depends on the length of gestation, and for species with gestation periods of 100 - 400 days, t_0 can be regarded as 0.2 x gestation period (Huggett and Widdas loc. cit.). As the hartebeest has a gestation period of approximately 240 days (Gosling 1969, Skinner et al, 1973, Dittrich, 1972), $t_0 = 48$. For comparison, the value of 37 is commonly

used for sheep, and 50 for cattle.

To test whether the monthly distribution of births showed any pattern or non-random fluctuations, auto-correlations were performed on the run of 24 monthly birth frequencies through the study period. The occurrence of any regular patterns is detected by calculating the correlation coefficients between pairs of values of the index. Starting with no lag, perfect correlation of 1.0 is obtained, but with any other lag the correlation will be between -1.0 and 1.0. The sample size progressively decreases as the lag increases. In general, when there are n observations in the data set,

no. of months lag	sample size	correlation coefficient, r
0	n	1.0
1	$n-1$	$-1.0 < r < 1.0$
2	$n-2$	"
3	$n-3$	"
4	$n-4$	"
$\vdots$	$\vdots$	
$n-1$	1	"

Birth rates

On all counts of hartebeest in the park, and in the plains in 1971-72, immature animals were distinguished as subadults, juveniles or newly-born. The latter category was defined as calves whose horns had not erupted (p. 15). As eruption occurs at the age of 4-5 weeks (Gosling 1969), and counts were made at the beginning of each month, the number of newly born represented those born in the previous month. This number is converted in to a parturition index (Gosling, loc. cit.) by expressing the number of newly born calves as a percentage of the number of adult females counted in the same area.

Climate

The distribution of births in the park, are examined in relation to the monthly rainfall at Embakasi, 8 km distant. The totals are expressed

Table 13.1. The ages, foetal weights, estimated foetal ages and female ages when conceiving of Series 1 and 2 hartebeest.

Number	Age, y	Foetal wt. kg.	Foetal age, months	Female age at conception, y
21	4-5	-	-	-
24	8-9	-	-	-
28	4-5	3.5	5.0	3.5
40	4-5	10.9	6.6	3.5
42	21-24 mth	-	-	-
44	2-2.5	-	-	-
48	7-8	-	-	-
50	10-11	-	-	-
53	7-8	-	-	-
56	6-7	0.7	3.6	5.5
57	5-6	1.8	4.4	4.5
62	21-24 mth	-	-	-
67	6-7	3.8	5.1	5.5
68	6-7	1.5	4.2	5.5
69	9-10	3.4	5.0	8.5

Table 13.2. The monthly parturition indices and months of conception in the Nairobi Park and Athi Plains, 1970-1972, with the effective rainfall of each month.

Month of birth	Parturition index			Month of Conception	Effective Rainfall, P/Et
	Total Park Count	Study Area Count	Plains Count		
Dec. 1970	4.5			April 1970	1.54
Jan. 1971	5.3			May	.79
Feb.	8.1			June	.10
Mar.	7.0			July	.10
Apr.	5.3			Aug.	.01
May	3.5			Sept.	.01
June	6.4			Oct.	.22
July	3.5			Nov.	.28
Aug.	2.9			Dec.	.16
Sept.	2.9			Jan.1971	.22
Oct.	2.3			Feb.	.01
Nov.	1.5	4.9		Mar.	.03
Dec.	1.8	2.2		Apr.	2.16
Jan. 1972	14.6	14.2		May	1.50
Feb.	7.4	6.5		June	.12
Mar.	5.1	10.3	5.7	July	.09
Apr.		9.4		Aug.	.40
May		6.6		Sept.	.11
June		2.4	2.1	Oct.	.02
July		1.5		Nov.	.22
Aug.		0.7		Dec.	1.25
Sept.		1.0	0.6	Jan.1972	.08
Oct.		7.3		Feb.	.36
Nov.		14.4		Mar.	.18
				Apr.	.01
				May	.73
				June	1.23
				July	.09
				Aug.	.02
				Sept.	.51
				Oct.	1.24
				Nov.	.80
				Dec.	.19

in terms of effective rainfall, P/E_t (p. 22).

13.3 Results

Age of first breeding

Table 13.1 contains the data on the age and foetal weights of the adult female hartebeest, both pregnant and non-pregnant for which there are age estimates, in Series 1 and 2. Also included are the estimated foetal ages using the method of Huggett and Widdas (1951), and the calculated age of the female at conception. To obtain the latter, the foetal age is subtracted from the lowest value defining the age class of the mother, to produce a minimum estimate for the age at conception.

There are age estimates for 7 pregnant females, ranging between 4 - 5 and 9 - 10 y of age. The minimum ages at conception range between 3.5 and 8.5 y. The ages of the non-pregnant females covered a larger span of between 21 - 24 months and 10 - 11 y. Although this sample size is small, the fact that there were two non-pregnant females between 21 - 24 months old and one between 2 - 2.5 y, and two females were calculated to have conceived at ages between 3.5 and 4 y old, suggests strongly that female hartebeest in the Athi Plains population did not conceive for the first time during the study period until at least their fourth year. As their maximum body weight is also not reached until the fourth year (p. 228), it seems that reproduction commences only with the attainment of adult body size, even though adult horn conformation is reached at about 24 months of age (p. 15).

Annual reproductive rates

Monthly parturition indices are available from the Nairobi Park for 24 months between December 1970 and November 1972 (Table 13.2). For the first 16 months total counts of the whole park were made, while for the last 13 months counts were made in the study area. For an overlap period of 5 months, therefore, results from total and study area counts exist, and both are shown in Table 13.2. In each of these months except November 1971 and March 1972, the two parturition (continued on next page)

indices are similar, but as the discrepancy has little effect on the overall picture, the reproductive rate for the period December 1970 to November 1971 is based on the figures from the total count, and from the study area for the remaining 12 months.

The parturition indices vary considerably between months, and this is discussed below. The mean monthly index, calculated as the total number of newly-born/total number of females, is 4.34 between December 1970 and November 1971, meaning that $4.34 \times 12 = 52.1\%$ of the adult female population calved in this year. The comparable mean for December 1971 to November 1972 is 5.93%, producing an annual calving figure of 71.1%.

Comparable data from the plains exist only for March, June and September 1972, and the overall parturition indices for 6 study areas in the plains are shown in Table 13.2 by the park figures for the appropriate month. Apart from the March figures of 10.3 and 5.7% for the park and plains respectively, the indices in the other months are almost the same: 2.4 and 2.1, 1.0 and 0.6 for June and September. Although these figures show that during these 3 months, 39% less calves were born in the plains, this may be inflated because the park index of 10.3% for the study area is twice that of the whole park in the same month. However, these results show that parallel changes in the timing of calving occur in the two areas. They also suggest that the calving rate in the plains may be slightly lower, but the data are too few to be conclusive.

An approximate comparison with these figures can be made by calculating the pregnancy rate of the shot hartebeest in the 2 years. Appendix 13 shows that between November 1970 and October 1971 (Series 1), 4/12 or 25% of the adult females were pregnant. With 6 pregnant out of 12 females in Series 2, the pregnancy rate was 50%.

This last rate is considerably lower than the parturition index suggested for the plains on the basis that it was almost the same as in the park. From the population point of view, a serious discrepancy arises

because of the choice of the adult horn conformation as the criterion of adulthood and sexual maturity. Female horn development is reached at about 24 months, yet as shown in Ch. 12 (p.228), full body weight and sexual maturity are not reached until the fourth year, perhaps 1.5 y later. Consequently any expression of pregnancy or calving rates using the number of adult females with full horn development as the denominator leads to underestimates because not all such females are in the reproductive pool. These rates should be calculated as

$$\frac{\text{no. of pregnant females}}{\text{no. of females } \geq 3.5 \text{ y old}} \quad \text{rather than} \quad \frac{\text{no. of pregnant females}}{\text{no. of females with adult horns}}$$

The pregnancy rate in the Series 2 animals can be recalculated in this way because the ages of the 12 females are known (Appendix 13). Three were judged to be adult from their horn development, although aged between either 21 - 24 months or 2 - 2.5 y. Excluding these, the proportion pregnant amongst those sexually mature rises to 6/9 or 75%.

A similar correction can be made in the living population to the number of apparently adult females with calves if the proportion of adult females between the ages of 2 and 3.5 y is known. Gosling (1974) gives survivorship tables for female hartebeest during his study period, 1966-68, from which the number of females dying between 2 and 3 y, and 3 and 3.5 y by interpolation between 3 and 4 y, can be calculated. The females in this age group comprises 11.1% of the females assessed as adult on horn criteria. This is, therefore, the amount by which the parturition index is corrected to estimate the number of calves born to sexually mature females. With this adjustment, 57.9% of the reproducing females gave birth between November 1970 and December 1971, while 79.6% calved in the next 12 months.

Monthly calving rates

The monthly parturition indices (Table 13.2) show that births occur in every month of the year, although fluctuations are obvious. The

Table 13.3. The auto-correlation coefficients calculated with lags of 0-12 months, on the sequence of monthly parturition indices (A), and on the same indices in a random order (B).

No. of months lag	A	Correlation	B
0	1.0 ^{***}		1.0 ^{***}
1	.382		-.204
2	.033		.156
3	-.227		.035
4	-.447 [*]		-.323
5	-.612 ^{**}		.079
6	-.362		-.195
7	-.005		-.178
8	-.116		.232
9	.272		-.432
10	.603 [*]		.235
11	.299		.098
12	.069		-.266

* $p < .05$

** $p < .01$

*** $p < .001$

indices are plotted in Fig. 13.1 with the monthly effective rainfall, P/E_t . The latter has been calculated from data in Appendix 3.

The difference in the number of calves born in the first as opposed to the second 12 month period has already been point out (p. 243). In the period December 1970 to November 1971, the incidence of births reached a peak of 8.1/100 adult females in February 1971, but thereafter declined steadily, with the exception of a small increase in June, until the very low value of 1.5/100 females in November 1971. This was followed by a large peak in January 1972, after which the birth rate remained at more than 6% for the following 4 months. Four months (June - September 1972) with low parturition indices then followed before the birth rate increased first to 7.3% in November and then to 14.4% in the last month of the study, December 1972.

Auto-correlation coefficients have been calculated using the 24 parturition indices (Table 13.2) with lags of 0 - 12 months (Table 13.3). This table shows that only with a lag of 10 months is there a significant positive correlation ($r = 0.6034$, $p < 0.05$, 12 d.f.). The high negative correlation with a 5 month lag shows that a high or low number of births in one month is associated with a low or high number 5 months later, and a high or low number again after another 5 months i.e. 10 months after the last month with a high number of births. This is therefore, a cycle with half the periodicity of the positive relationship. The latter is biologically more meaningful. The rather lower negative correlation with a 4 month lag suggests the existence of an 8 - 9 month cycle, which Fig. 13.1 confirms, but it is not statistically significant because data are available at only monthly intervals.

When 12 coefficients are calculated, there is a probability of 0.08 that one correlation will be significant by chance. To test whether the significant result could have been obtained by chance, the same data values were randomly assigned to the 24 months, and the auto-correlations

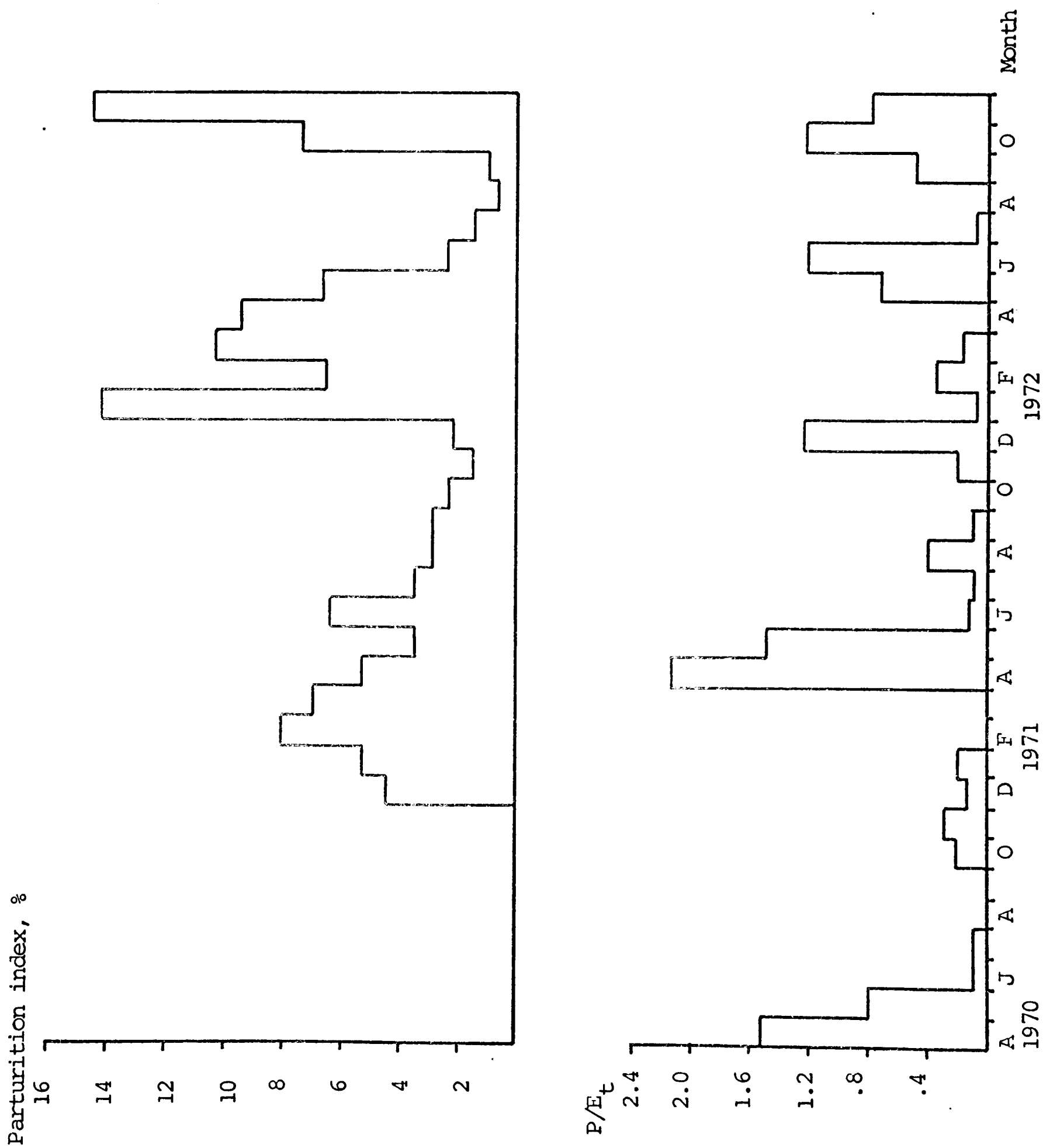


Fig.13.1. The monthly parturition indices and the current month's effective rainfall, P/E_t , in the Nairobi Park.

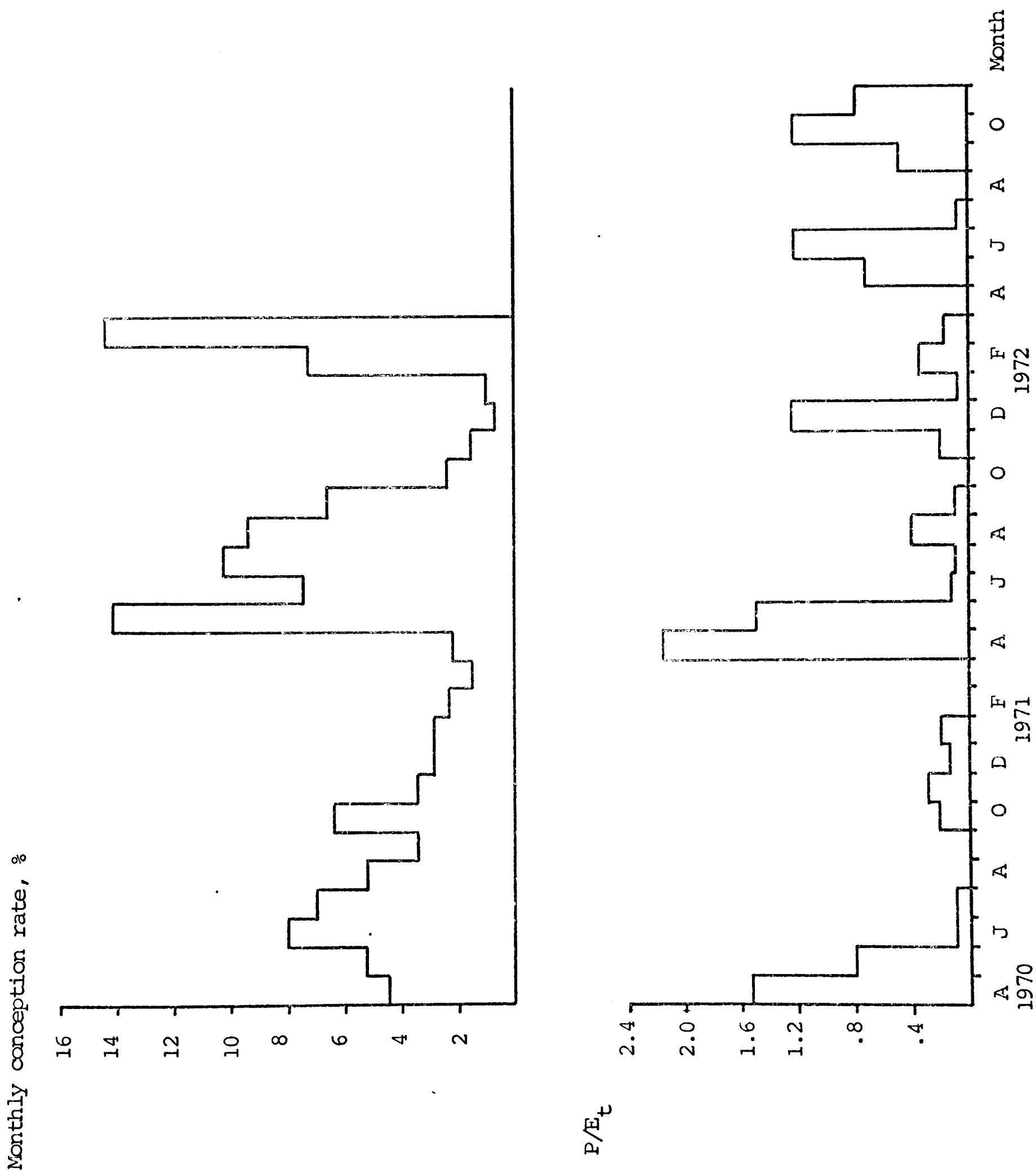


Fig.13.2. The percentage of adult females conceiving and the effective rainfall, P/E_t , in each month in the Nairobi Park.

repeated with the same lags (Table 13.3). The lack of any significant correlation except with no lag, strengthens the conclusion that there was a periodicity in the births, with an interval of 10 months, during the study period.

The monthly rainfall histogram (Fig. 13.1) shows that 5 "wet" months (with $P/E_t \geq 1.0$) occurred during this period. In the first 12 months, the birth rates in the wet months of April and May were above and below the mean birth rate of 4.3%. In the second 12 months the birth rates were below the mean of 5.9% in both wet months of December and June, but above the mean in the last wet month, October 1972. Viewed in this way, there is no consistent relationship of either high or low parturition indices in months of good rainfall.

The monthly conception rates, obtained by offsetting the birth rate histogram by an 8 month gestation period, are shown in Fig. 13.2. Comparison with the rainfall histogram shows that the peak in the frequency of conceptions of 8.1% in the first year occurred two months after the wet month of April 1970. The subsequent decline in conceptions occurred through a period of increasing dryness with little rain. The slight increase in conceptions in October coincides with a light rainfall after 4 nearly rainless months. Fig. 13.2 shows that the short rains of 1970, expected in November - December, failed almost totally, and the conception rate steadily dropped thereafter through a period of great aridity and food shortage. The latter is suggested by the poor visual condition of the territorial males in this period (Fig. 12.2).

The arrival of the long rains in April and May 1971 was associated with a dramatic increase in the number of conceptions, starting in May with a lag of one month after the first rain. The conception rate remained high for 5 months, and during this period 47% of the adult females are calculated as having conceived, with 20.7% conceiving in May and June 1971. By contrast, the next wet month, December 1971, was not associated with a conception peak, and the next peaks occurred in the dry months of February and March 1972.

These results provide evidence of a functional relationship between rainfall and conception for three reasons:

1. The increase in conceptions in October 1970, coinciding with rain in this month, the first after a dry season of normal length. In "normal" years, this rain would mark the beginning of the short rains (p. 41).
2. The decline in the conception rate after October 1970, as the short rains failed. The poor average condition of the territorial males declining until April 1971, bears witness to the nutritional stress caused by this failure.
3. The massive increase in the conception rate one month after the rain of April 1971 ended this long period of near-drought conditions.

However, the relationship between wet months and conception peaks disappeared after the heavy rainfall of April - May 1971, and the frequency of conceptions might then have been controlled by other factors. The small conception peak of 7.3/100 females occurred 9 months after the peak of May 1971. As the hartebeest can reconceive in the first month post-partum (Gosling 1969), a female doing this would produce a second calf after a minimum interval of 9 months. The following table shows the number of females conceiving in May and June 1971 and 9 months later in February and March 1972:

Month of conception	percentage of females conceiving	month of conception	percentage of females conceiving
May 1971	14.2	February 1972	7.3
June "	6.5	March "	14.4
Total	20.7		21.7

The close agreement between the two totals suggests that about 20% of all the females in the population produced two calves with an interval of 9 or 10 months. Although this proportion is so low that the same result could be obtained if 2 sets of females each consisting of 20%

Table 13.4. The numbers and age class distribution in Nairobi Park in September, 1973, with the estimated months of birth and conception of the younger classes.

Age group	Nos.	Age, mths.	Nos. as % of adult females	Month of Birth	Month of Conception
Adult females	258	20	-	-	
VI	52	15-20	20.1	-	
V	19	10-15	7.4		
IV	44)	5-10	28.7	Nov/Dec.72 -Mar/Apr.73	Apr./May -Aug/Sept. 72
III	30)				
II	29	1-5	10.8	May-Aug.73	Oct.72-Jan. 73
I	23	0-1	8.9	Aug-Sept. 73	Jan-Feb.73

of the adult females had one calf each in this period, 3 lines of evidence suggest that this was not the case:

1. If all the females which conceived in the first 2 months of the May - September 1971 peak reconceived after a post-partum interval of only one month, at least some of those conceiving in the last 3 months of the peak might be expected to have done the same. Equivalent information is not available because the study ended in December 1972 when the calves of these later, second conceptions would have been born, but a certain amount can be deduced from the results of a total count done in the same area on September 11, 1973, by L.M. Gosling, who has kindly allowed his data to be used. The relevant numbers and age composition (Gosling 1974) are given in Table 13.4 from which the months of birth and conception have been calculated.

The numbers in age groups III and IV comprised 28.7% of the adult female numbers. Aged between 5 and 10 months, they would have been conceived between April/May and August/September 1972, just after the conception peaks of February and March 1972. If the figure of 28.7% is added to the 21.7% conceptions of these two months, a total of 50.4% of the adult females conceived in the 7 month period between February and August 1972. This figure compares well with the total of 47% of all females conceiving in the 5 month period May to September, beginning 9 months earlier.

The existence of this 9 - 10 month cycle is further corroborated by the high parturition index of 8.9% in September 1973 (see above). These calves would have been conceived in January 1973, 9 months after the middle of the previous peak of conceptions.

2. The number of females conceiving in October - January 1972 following the May - September peak was lower than the number conceiving under the extremely adverse conditions of January - April 1971. The dry season in late 1971 was not unusually severe, and December 1971 was a wet month. This suggests very strongly that the dry conditions,



Plate 2. Adult female hartebeest with 3 successive offspring. From left to right, juvenile, subadult, newly-born calf, adult female.

or some associated effect, were not preventing more females from conceiving. There were either other factors preventing conception in potentially reproducing females, or the number of apparently adult females which were still sexually immature has been underestimated. In the first case, these females might have conceived later, but there is no evidence of a second breeding pattern. It seems more likely that the number of reproductively active females has been overestimated.

3. The count data consist of the total number of females and the number of newly-born calves, juveniles and subadults in each herd. Females were not distinguished on the basis of the number and age of their dependent offspring, but females were frequently seen with two calves classified as juvenile i.e. less than one year old. Plate 2 shows a female with 3 successive offspring, all of which followed her. Without any information on the frequency of such females, one can only conclude that some females demonstrably produce 2 calves in one year, with an inter-calf interval of 8 - 12 months.

13.4 Discussion

Although a 10-month periodicity of births occurs, 26% of all births in the first year of study occurred in the 6 months with parturition indices less than the mean (4.34%). In the year 1971-72 10% occurred in the 5 months with less than average (5.93%) parturition indices. Breeding throughout the year has also been recorded in the Rift Valley, 50 km away (Field and Blankenship 1973). In Nairobi Park in the wetter years of 1966-68, births were more evenly spread through the year with a mean of 45% of all births occurring in 9 "non-peak" months (Gosling 1974). This shows that for the hartebeest, there may be good reasons for not breeding in the peak months, or, at least, the penalty for doing so is not great. In this case the ultimate reason for this pattern may be difficult to identify or distinguish from the proximate cause of conception.

The distribution of births and conceptions during the study period showed that the end of a period of great aridity and food scarcity was followed by a peak in the number of conceptions. Here, rainfall, or an associated effect, determines the onset of reproduction, although most conceptions occurred not in the first month of heavy rain (April 1971, Fig. 13.2), but in the next month. If the response to improved nutrition is the same in both sexes, the parallel lag in the improvement of the territorial males' condition (Fig. 12.2) suggests that breeding depended upon a certain threshold condition being reached by females. This would be the proximate factor causing ovulation or conception. The improved condition would await the fresh growth of grass with higher protein levels (Braun 1974) and its increased intake by the hartebeest (p.177). In these circumstances, rainfall or nutrition would be the ultimate factor initiating reproduction.

The subsequent peaks of conceptions showed that many females were reconceiving in the first and second months post-partum. This indicates that their body reserves and current nutrition were adequate to withstand the demands of another pregnancy despite the drain from suckling the current calf. As the reconceptions were independent of rainfall, and the occurrence of post-partum oestrus in cattle depends largely on the level of energy intake after calving (Wiltbank et al, 1962, 1964), the ultimate factor initiating reproduction appears to be nutrition as a residual effect of rainfall, rather than rainfall itself. From these considerations, I suggest that if rainfall is normal in its timing and average or better in amount, female hartebeest can produce a calf every 9 - 10 months. A prolonged dry period progressively halts breeding which is resynchronised when conditions allow breeding to start again. But, as the period since synchronisation increases, the distribution of births becomes less peaked and more dispersed as the interval between the birth of a calf and the next conception becomes more variable in length. This occurs because births fall independently of rainfall and related changes

in food quality and quantity, and the threshold condition necessary to reconceive may not be reached immediately post-partum. Factors affecting the rate at which adequate condition is regained would include the feeding efficiency of the individual and its age. The latter is indicated as important by the gradual decrease in body protein after maturity and the onset of breeding (p. 231).

In the red deer, which breeds seasonally, hinds lose condition with each pregnancy and lactation, so that old hinds conceive later than those in their prime (Mitchell and Lincoln 1973). Eventually, a conception or ovulation failure occurs and the hind does not breed until the following year. The hartebeest situation is analogous but more complicated because births occur in every month. This produces a more flexible system than the deer one. If a hind has to "rest" from breeding, she must miss a whole year, whereas the female hartebeest will conceive as soon as environmental conditions and her body reserves allow. This system is adaptive in a tropical environment where the changing of seasons is largely determined by unpredictable rainfall.

Although there are dangers in identifying causation from short term studies (Sadleir 1969a), the evidence from 1966-68 is relevant. These years were wetter, and the distribution of births less peaked (p. 249), but the proportion of females producing a calf each year was also higher at 84,79 and 58% respectively (Gosling 1974), calculated using the number of females with adult horns. Conditions were better for the hartebeest in these years, and these facts are consistent with the idea that nutrition and condition are the ultimate and proximate determinants of the rate and timing of reproduction in this population. The functional relationship between the two factors is interesting in the context of reproduction in an unpredictable environment. If reproduction is unseasonal and the ultimate controlling factor is rainfall or nutrition, it would be maladaptive to have an unrelated proximate controlling factor operating

at the same time in each year. Under such conditions, found in the arid tropics, it is not surprising that photoperiodism rarely has the influence claimed for it in temperate regions, reviewed by Sadleir (1969a).

The period 1966-68 was one of great increase in the hartebeest population of the Nairobi Park after the heavy mortality caused by the drought and subsequent floods of 1961-62 (Gosling loc. cit.). By analogy with the less severe situation of 1970-71, the hartebeest's breeding would have been highly synchronised when breeding was able to restart in mid-1962. As years of good rainfall occurred through 1960 - 1968, it seems that this synchronisation was lost, producing the situation described by Gosling (loc. cit.) in 1966-68. He explains the distribution of small peaks of births in terms of females switching between 4 cycles, producing 4 parturition peaks, by adjusting the post-partum interval before the next conception. The best conditions of nutrition then occur at different points in the breeding cycle for different females. This is consistent with the idea of females conceiving when possible. The attainment of the threshold body condition is not closely dependent on the changing seasons in years of average or better rainfall.

This model of the frequency and timing of breeding presumes that the key factor is the nutrition and condition of the female at conception, rather than during pregnancy, at birth, during lactation, or of the calf at weaning. A certain amount of experimental evidence emphasizes the importance of pre-mating nutrition and the animal's condition when mated. The ovulation rate of Scottish Blackface ewes is positively related to their body conditions at mating, and this is dependent on their food intake (Gunn et al 1969). The same work suggests that there is a threshold condition above which the level of food intake has no influence on the ovulation and lambing rates, but below which, food intake is important. In the same breed, embryo mortality in the first 26 days of gestation is higher in ewes in poor condition at mating, but there is no difference in the number of lambs born to ewes kept on high or low nutritional planes for 4 weeks after mating (Gunn et al 1972). These results are consistent with the conclusion of Sadleir (1969b) that

once conception has taken place, the wild female mammal is very resistant to the effects of poor nutrition, the impact of which can be lessened by using the body reserves of energy.

As the level of nutrition immediately after mating seems unimportant for embryo survival, the minimum body condition required by the hartebeest for ovulation and conception might be that in which the body reserves are adequate for the whole reproductive cycle to be completed, even if food quality deteriorates during it. Measured as the time to oestrus, groups of ewes can show the residual effects of various dietary regimes 11 months previously, although all groups subsequently enjoyed the same level of nutrition and differences in body weight had disappeared (Smith 1965). In many ruminants, the accumulation of fat through pregnancy until lactation starts (Sinclair and Duncan 1972, Bear 1971) indicates that if conception has occurred, condition can be maintained or improved by such methods as increased intake (Arnold and Dudzinski 1967) or metabolic adjustments.

The ecological implications of the hartebeest's late first breeding and its breeding pattern are discussed in Chapter 15 where they are compared with the behaviour of other herbivore species. The pattern described here is an adaptation to the conditions of the Athi Plains or perhaps East Africa, for the various species or subspecies of Alcelaphus through Africa show considerable variation in the timing of their birth peaks (Spinage 1973). In South Africa the red hartebeest conceives for the first time at the age of 2y 4 months, and 82.5% of each year's calves are born in October and November, with no births recorded between March and August (Skinner et al 1973). Calving occurs usually just after the first rains have fallen, and, in this more temperate environment, day length appears to be the major factor determining the onset of breeding (Skinner et al, loc. cit.).

Chapter 14.

THE RESOURCES OF THE NAIROBI PARK AND THEIR UTILIZATION

14.1 Introduction

Throughout previous chapters, comparisons have been drawn between the hartebeest living in the Nairobi Park and those of the plains. In some respects, such as the wide variety of vegetation types used their differences are slight (p. 115). In others, notably their population densities, they are very different. This chapter is concerned with the resources of food and water, and their utilization, in the Nairobi Park study area in an attempt to answer the question "Why are there so many hartebeest in the park?" (p. 3). The equivalent data from the plains are less extensive, but are used where possible.

A causal analysis of the hartebeest's movement in the park was attempted using a principal components analysis. This was not very successful, but the methods and approach are described briefly to demonstrate the complexity of the factors on which grazing successions (Bell 1969) or mosaics (Vesey-Fitzgerald 1965) may depend.

14.2 Methods

Animal and habitat parameters.

The data on the hartebeest numbers and their distribution through vegetation types were collected on total counts (p. 17). The habitat parameters (see below) were collected at the same time and were later integrated with the results of the proximate analyses of the grass samples (p. 21). The measurement of the surface area of water is described on p. 24 .

Principal Components Analysis.

Although the data - reducing capacity of PCA is one of its most useful functions (Appendix 14), some pre-selection of variables in the file NNPCOM (p.28), were clearly unlikely to be determinants of the hartebeest's distribution or movements. From the various parameters of grass volume and sward structure, food quality and the availability of water, the following 13 variables were extracted :

1. DOMHTVEG, the dominant height layer of the vegetation.
2. MAXHTVEG, the maximum height layer.
3. MINHTVEG, the lowest height layer.
4. VEGGREEN, the greenness of the grass.
5. CULMHT, the height layer of the grass culms.
6. CROP, the standing crop of grass, dry weight, kg/ha.
7. AQDENS, the density of water.
8. ENERGY, the gross energy content of the grass.
9. DRINK, the distance to the nearest water.
10. MOISTURE, the water content of the grass.
11. PROTEIN, the crude protein content of the grass.
12. FIBRE, the fibre content of the grass.
13. CARBHYD, the carbohydrate content of the grass.

Variable 9 was created to measure the distribution of water. It takes the modal value of the "distance to water" categories of all the sightings of hartebeest in each vegetation type from the appropriate section of the file NNPHART (p. 28). A low value in one month indicates that the hartebeest occupying the vegetation type tended to be near a water source. Unlike the values of variable 7, the hartebeest 's nearest water might not necessarily be in the same vegetation type which they were occupying.

Scattergrams showing the relationships between each pair of variables were made. As no non-linear relationships were obvious, no variables were excluded. Normality was approximated by transforming all data. Logarithmic transformations were applied to variables 1 - 9 above, and arcsine transformations to the plant composition variables, whose values were percentages.

The PCA was performed using the SPSS routine, and the factor scores were calculated as described in Appendix 14. As the dependent variable describing the distribution of hartebeest for the multiple regression, the proportion of the hartebeest in each vegetation type was used. This was considered a better measure than the actual degree of selection shown for each type (see below). Stepwise, additive multiple regressions were run using the factor scores from the whole matrix of data with the proportion of hartebeest in each vegetation type in turn through the 12 months.

14.3 Results

The grazing cycle in the Nairobi Park.

The vegetation of the Nairobi Park study area has been described (p. 56 et seq.), and is shown in Figs 5.3 and 5.11. To recapitulate briefly, the flat ridges are occupied by Acacia drepanolobium bush grassland on Black Cotton grumosols. Within this area, vegetation type 10 comprises those areas whose vegetation was not burnt in November 1970. Type 06 was identical until burnt. Type 35 also covers a burnt area, but its soil and plant species distinguish it from type 06. The more sloping ridges are covered by open grassland on red lateritic soil. Vegetation type 04 includes the area which was not burnt in 1970, while 01 is its burnt counterpart. Type 03 occurs as a narrow band at the edge of the

Table 14.1 The proportions of the hartebeest in the Nairobi Park study area in each of 8 major vegetation types in 12 months.

Vegetation type.	N	D	J	F	M	A	M	J	J	A	S	O
01	.02	.06	.20	.13	.01	.07	.17	.01	.02	.26	.02	.04
02	.46	.15	.10	.20	.28	.18	.01	.03	.03	.15	.28	.59
03	0	.04	0	0	.06	.15	.02	.03	.09	.01	.24	.02
04	.17	0	.22	.27	.24	.05	.04	.03	.01	.31	.21	.09
05	.11	.04	.36	.30	.30	.13	0	.05	.10	.17	.14	.07
06	.01	.52	.04	.01	.01	.12	.42	.45	.61	.03	.03	.10
10	.04	.06	.03	.02	0	.09	.03	.01	.12	.06	.08	.03
35	0	.11	.04	.02	.03	.05	.30	.36	.02	.01	.01	.05
TOTAL	.90	.98	.99	.95	.93	.84	.99	.97	1.0	1.0	1.0	.99

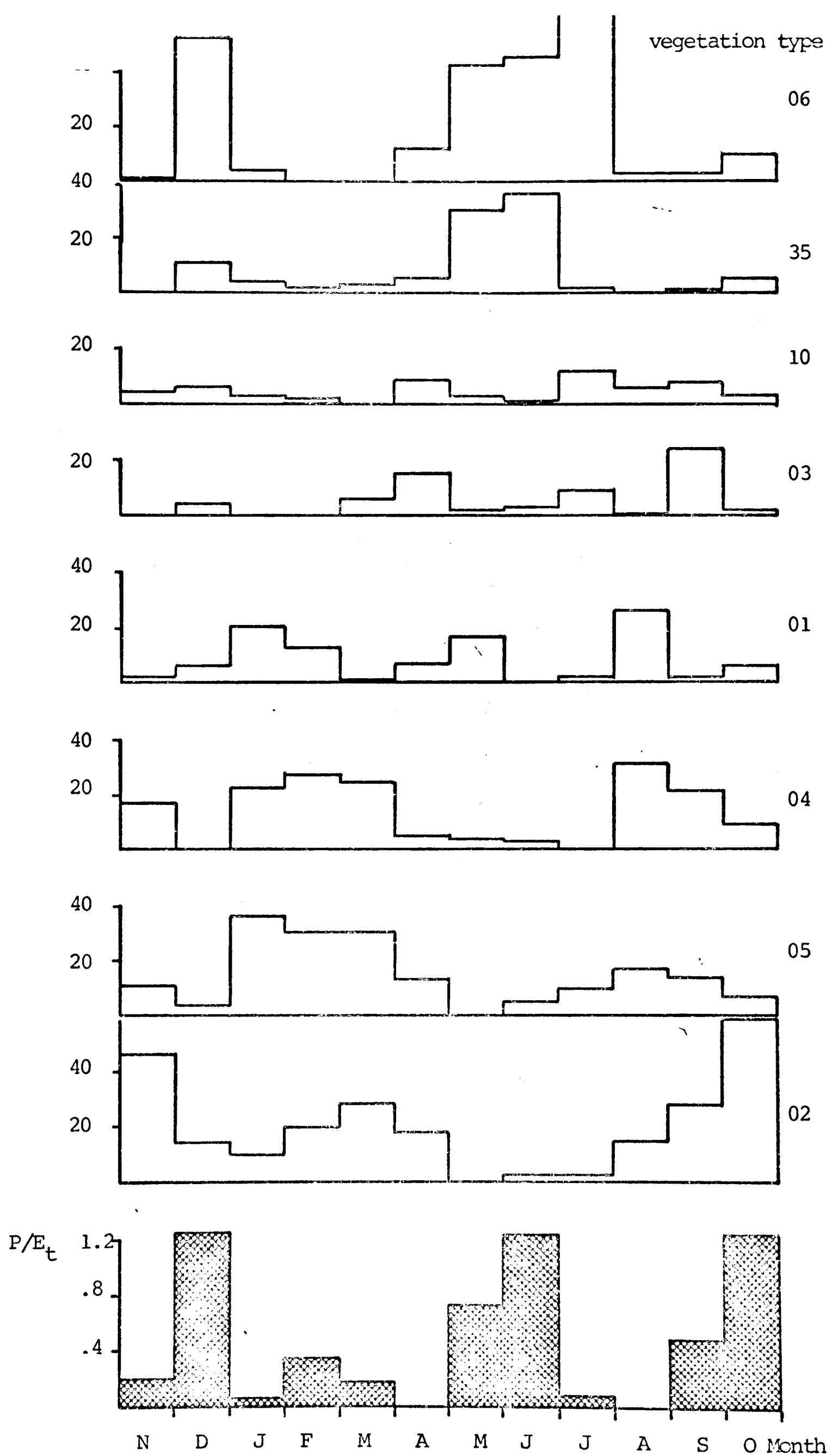


Fig.14.1. The percentage of the hartebeest population of the Nairobi Park study area in each of 8 vegetation types through 12 months with each month's effective rainfall, P/E_t .

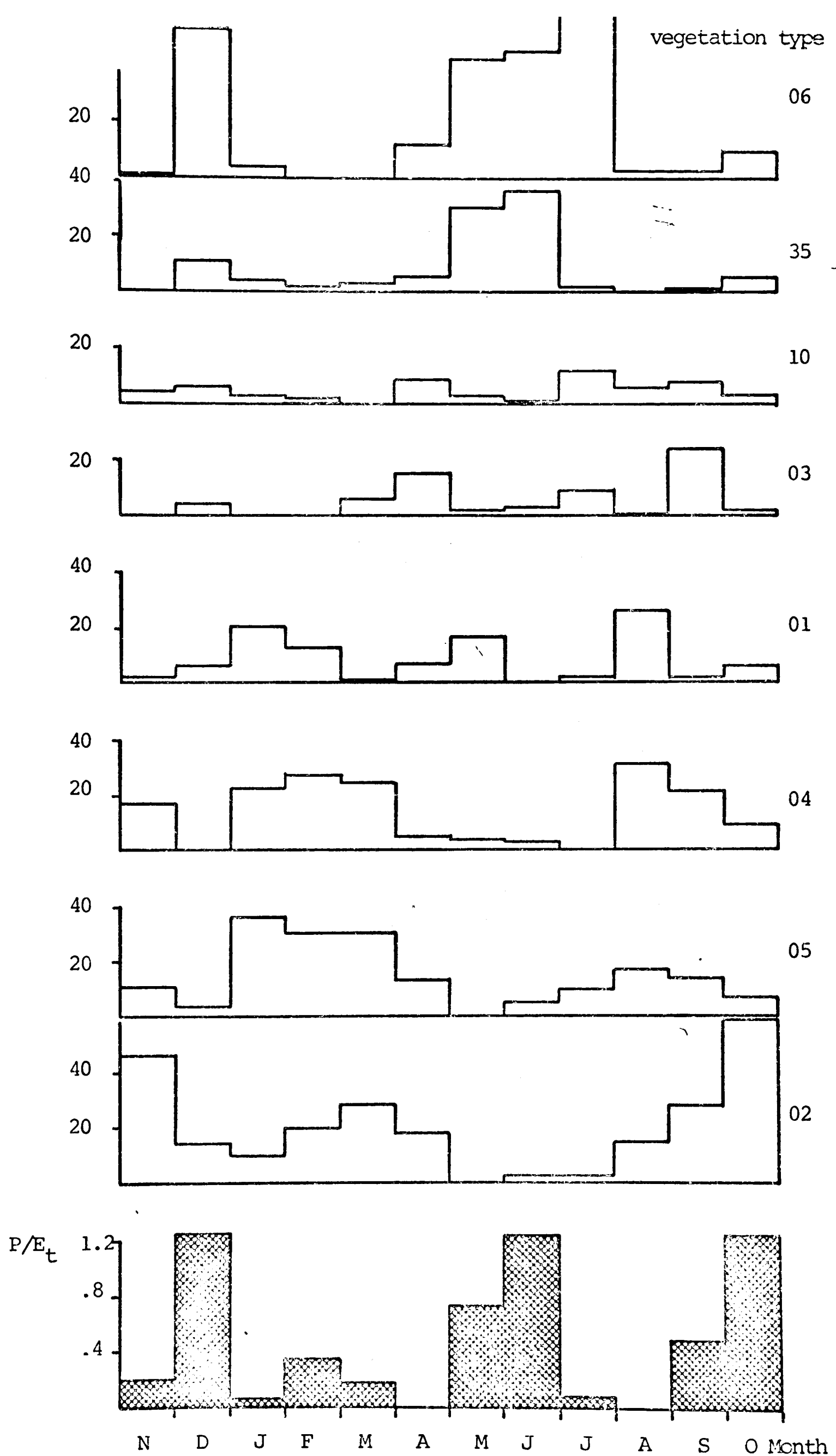


Fig.14.1. The percentage of the hartebeest population of the Nairobi Park study area in each of 8 vegetation types through 12 months with each month's effective rainfall, P/E_t .

A. drepanolobium between 06 and 10, and between 10 and 04. Type 05 forms another ecotonal type between the open plains (04) and the grassland of the steeper, lower slopes, also lying on red soil (type 02). These 8 vegetation types, covering 95% of the study area, are known collectively as the major types.

The use made of these vegetation types by the hartebeest is shown in Table 14.1 as the proportion of the population in each. The equivalent data from the minor types have been omitted, but the summed proportions show that this excludes only a small proportion except in November 1971 and April 1972.

These proportions are shown in Fig 14.1 against the monthly effective rainfall. A distinct pattern of occupancy is apparent. In the wet months of December, May and June the burnt Black Cotton types, 06 and 35, are utilized, with 06 receiving heavier use. September and October appear contradictory in this respect, but the distribution in these months was an after - effect of the atypically high animal biomasses of the previous 3 months (see below) which left the vegetation severely depleted (Appendix 17) despite some rain.

After the rains, they leave the Black Cotton areas and move on to the lateritic soil types open plains on lateritic soil (types 01, 04). The trend of movement is downhill, towards the bottom of the catena (Fig 5.11). Further in to the dry season, the lowest vegetation type of the catena (02) is used by increasingly large numbers of animals as types 01, 04 and 05 are vacated.

The distribution pattern of November 1971 suggests that 02 is used until the rains break, but in April 1972, use of this type was diminishing

Table 14.2 The comparative grazing indices of hartebeest in 8 vegetation types in 12 months, in the Nairobi Park.

Vegetation type	Area, km ²	Month												Mean
		N	D	J	F	M	A	M	J	J	A	S	O	
01	1.9	.19	.69	<u>2.08</u>	<u>1.43</u>	.15	.72	<u>1.77</u>	.09	.21	<u>2.73</u>	.19	.44	.89
02	3.03	<u>3.07</u>	.99	.64	<u>1.32</u>	<u>1.84</u>	<u>1.22</u>	.09	.23	.18	.98	<u>1.85</u>	<u>3.93</u>	1.36
03	0.41	0	<u>2.0</u>	0	0	<u>2.86</u>	<u>7.48</u>	.85	<u>1.32</u>	<u>4.30</u>	.43	<u>11.91</u>	.84	2.66
04	2.18	<u>1.60</u>	.02	<u>2.06</u>	<u>2.49</u>	<u>2.21</u>	.49	.34	.32	.10	<u>2.83</u>	<u>1.93</u>	.84	1.27
05	0.86	<u>2.67</u>	.90	<u>8.4</u>	<u>6.99</u>	<u>7.06</u>	<u>3.02</u>	.08	<u>1.14</u>	<u>2.41</u>	<u>4.06</u>	<u>3.19</u>	<u>1.68</u>	3.46
06	5.04	.03	<u>2.06</u>	.14	.03	.04	.48	<u>1.67</u>	<u>1.82</u>	<u>2.45</u>	.13	.11	.41	.78
10	3.10	.27	.39	.19	.16	.03	.60	.17	.06	.76	.39	.51	.19	.31
35	2.67	.03	.81	.33	.14	.24	.39	<u>2.24</u>	<u>2.68</u>	.15	.08	.05	.37	2.67

although it was a rainless month. In most years the short rains break in March, and this departure from type 02 is seen as a response to the late arrival of rain. This idea is supported by (1) that in April the most equitable distribution of hartebeest between the major vegetation types occurred, and (2) these same types contained only 84% of the total hartebeest of the study area. This is the lowest proportion of any month, showing that the minor vegetation types were being used. With the lack of rain this indicates that the normal dry season food resources has been depleted.

The fraction of the population in each vegetation type is proportional to the extent to which each is used by the hartebeest. And, because the counts were made in the early morning, this is equivalent to showing which vegetation types are exploited most during the morning feeding period (Fig. 11.2). However, because the vegetation types vary in size, their distribution gives no idea of the extent to which the hartebeest are selecting or avoiding these types. For this, comparative grazing indices (c.g.i.) have been calculated for each month and type. This index is calculated as the proportion of the hartebeest population in a vegetation type divided by the proportion of the total area covered by that type (p. 114). The array of c.g.i. 's is shown in Table 14.2. Indices of >1.0 , indicating the selection of a type, are underlined.

On the whole, the vegetation types in which most of the hartebeest were seen have indices of >1.0 , and parallel seasonal changes to those described above occur. The 2 types which have the highest mean c.g.i.'s and are most consistently selected are types 05 (selected in 10/12 months) and 03 (selected in 6/12 months). These two have the common characteristic of being ecotones (p. 59 and Fig 5.11). Not surprisingly, the areas of these types are smaller than those of any other of the major types, and

their boundaries were less clearly demarcated on the ground. This may have lead to sampling errors from the difficulty of deciding whether the animals were in the ecotone or in one of the surrounding types. On the whole, such biases of over-and under-representation should be approximately equal and opposite, and can be disregarded. Thus, these c.g.i. values are taken as evidence that the hartebeest is an "edge" species, favouring the ecotones.

The mean c.g.i.'s show a net avoidance by the hartebeest of the Black Cotton soil types (06, 10, 35) despite the seasonally high selection of the burnt types 06 and 35. 06's unburnt equivalent, type 10, is avoided in every month of the year. The 2 ecotones and 2 unburnt types on the red soils (02, 04) show a net selection by the hartebeest through the year. Although they avoided the unburnt A. drepanolobium type 10 more than the burnt 06, the reverse situation happened with the red soil grasslands. Approximately the same degree of selection for 04 as for 01 is shown, but the former is selected in more months. Thus, the year - round mean c.g.i. of 04 (1.27) shows its net selection while 01 (mean 0.89) is avoided to about the same extent.

The water resources of the Nairobi Park and Athi Plains study areas.

The amount of standing water in any area is determined principally by the rainfall over some preceeding period and the balance between the flow in to and out of the area. The latter will depend on the slope of the ground, the location relative to the watershed, the size of the area over which the water is collected and the water retention and run-off properties of the area. Further losses of water are caused by surface evaporation.

Table 14.3 The total water density (m^2/km^2) and 2 - month effective rainfall, $P/E_t(2)$, for the park and plains study areas, with the biomass density (kg/km^2) and water density (m^2/km^2) excluding dams, for the park study area.

Nairobi Park

Month	Water density m^2/km^2	Effective rainfall, P/E_t (2)	Biomass density kg/km^2	Water density excl.dams m^2/km^2
1971 November	677	.11	8771	8
December	1527	.75	6278	435
1972 January	764	.62	7801	106
February	912	.21	8222	154
March	442	.26	5537	19
April	330	.10	7059	3
May	507	.34	7206	72
June	1427	.96	9321	414
July	1097	.68	15085	202
Aug.	889	.06	17186	97
Sept.	1046	.28	30775	133
Oct.	766	.91	15769	61

Athi Plains study areas

		Block					
Month		15	22	30	35	39	62
March	$P/E_t(2)$	.63	.66	.28	.57	.61	.53
	water density	206	47	540	206	73	802
June	$P/E_t(2)$	1.32	1.10	.71	.80	.61	.33
	water density	796	286	865	353	274	94
Sept	$P/E_t(2)$	.11	.22	.01	.04	0	.10
	water density	61	13	28	1	14	22

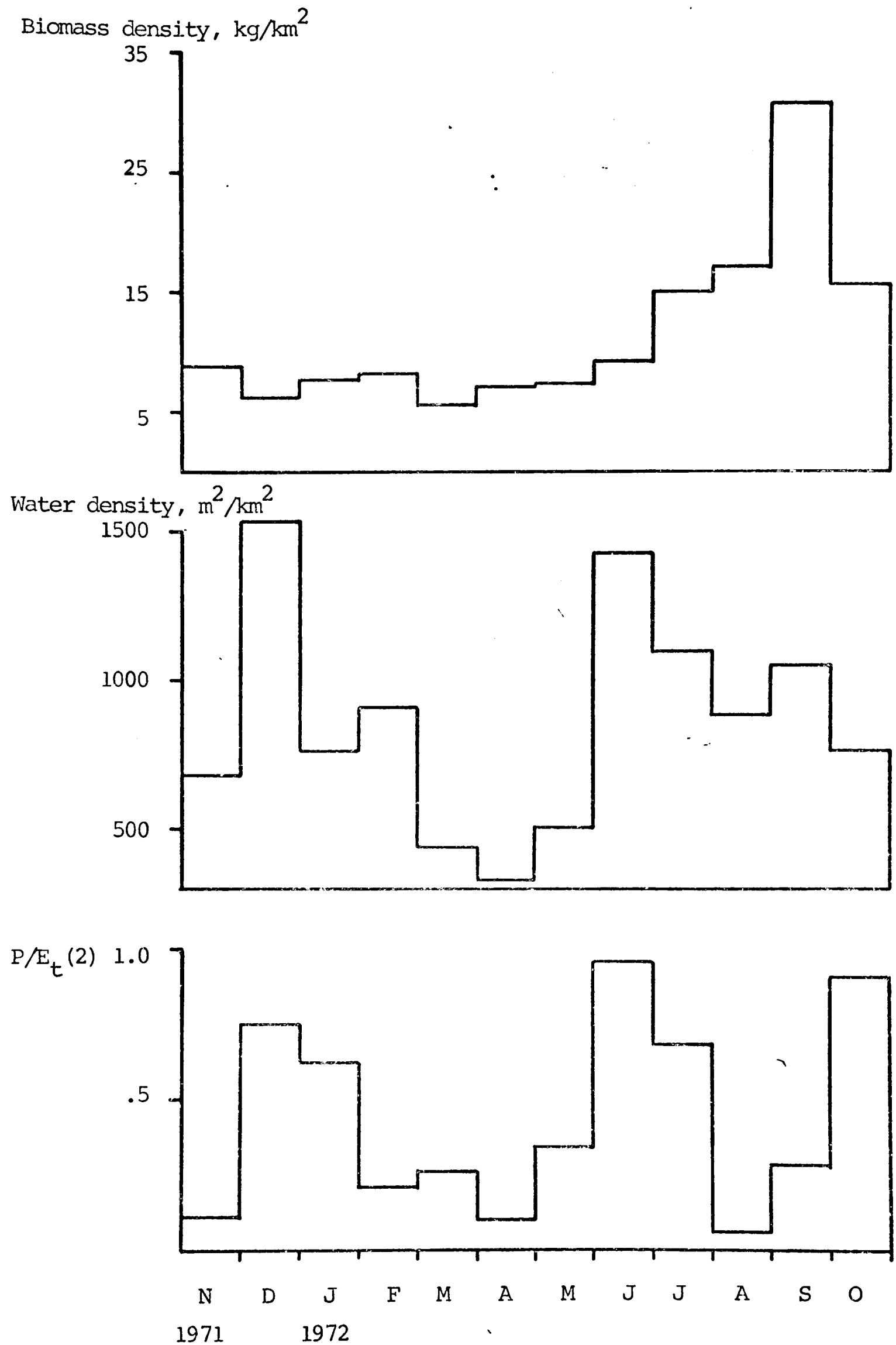


Fig.14.2. The effective rainfall over the previous 2 months, $P/E_t(2)$, the density of standing water (m^2/km^2), and the large herbivore biomass density (kg/km^2) in the Nairobi Park study area over 12 months.

The surface area of water in each of the 7 study areas was estimated on the occasion of each animal count. For the park, a 12 month run of data is available for relating to the rainfall. By using the evaporative power of the atmosphere as the potential evapo-transpiration (E_t) in the measure of the effective rainfall, P/E_t , the effects of monthly variation in the evaporation rate are removed.

The density of water (m^2/km^2) in the study area was correlated with the effective rainfall over the previous 1, 2 and 3 months. The best correlation was with the rainfall over the previous 2 months :

no. of months rainfall	r	d.f.	significance
1	.564	10	< 0.1
2	.604	10	< .05
3	.593	10	< .05

The data are shown in Table 14.3. The monthly P/E_t 's and water density are shown in Fig 14.2. The rainfall over two months shows a residual influence on the water resources in dry months such as February and August. The two parameters vary closely except for the last month when the amount of water decreased although both September and October were rainy months. Fig 14.2 also shows that this coincided with a large increase in the herbivore biomass in the study area. This biomass is that of the 11 species in the community study (p. 100). The large increase was due to the immigration of wildebeest, zebra and to a lesser extent, hartebeest. (Appendix 6).

It seemed possible that this increase in biomass was connected with the discrepancy between the rainfall and the area of water. On the assumption that the combined water requirements of these herbivores was approximately proportional to their total biomass, partial correlations

Table 14.4 The correlation coefficients and their significance between the effective rainfall over the previous 2 months and the density of surface water (m^2/km^2) for different numbers of months : simple correlations, and partial correlations, holding constant the biomass density (kg/km^2).

Correlation coefficients						
Months in correlation	simple r	d.f.	p	partial r	d.f.	p
Nov - June (8)	.822	6	<.02	.815	5	<.05
Nov- July (9)	.831	7	<.01	.811	6	<.01
Nov - Aug (10)	.756	8	<.02	.797	7	<.01
Nov - Sept (11)	.722	9	<.02	.790	8	<.01
Nov - Oct (12)	.603	10	<.05	.629	9	<.05

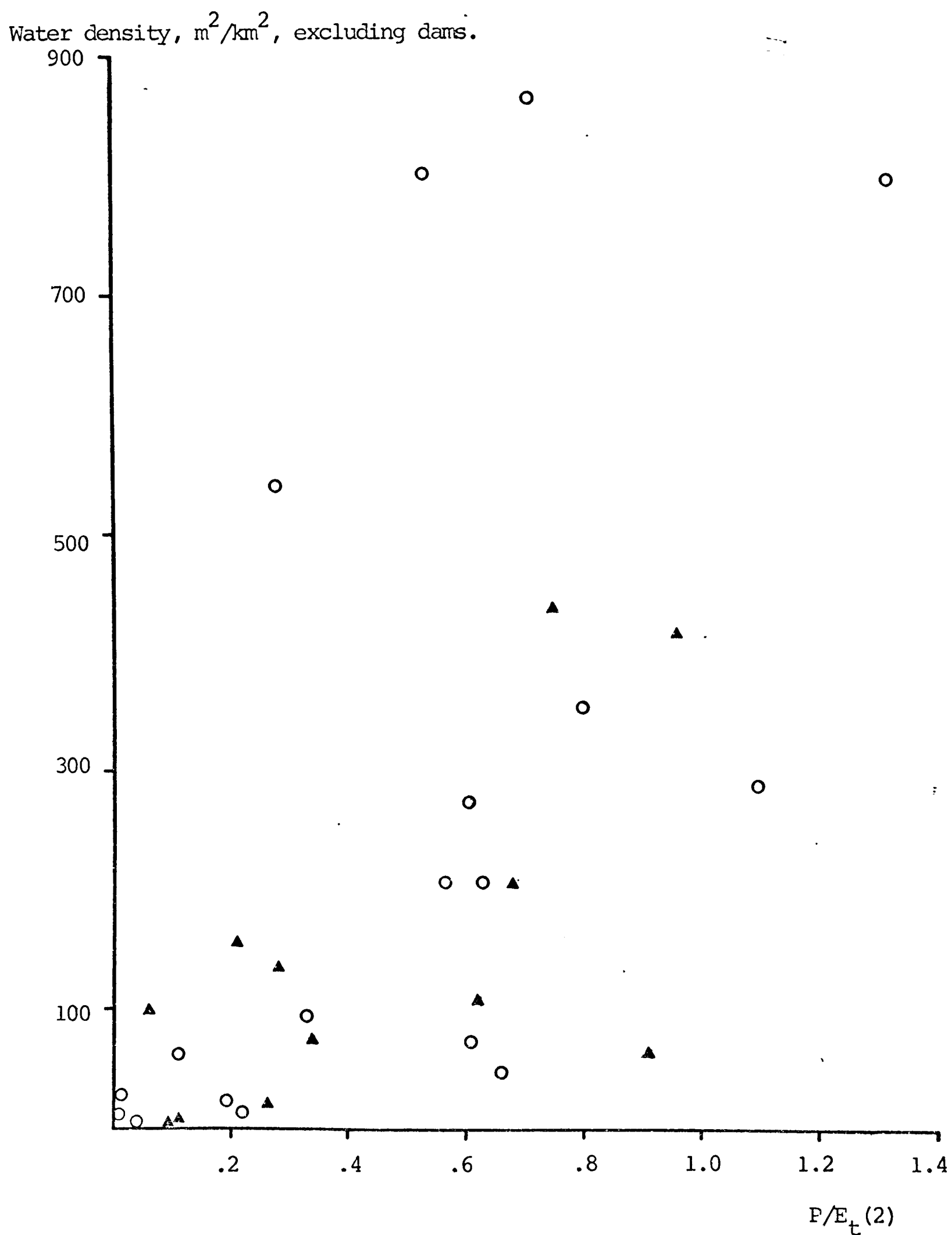


Fig.14.3. The density of standing water (m^2/km^2) in the plains study areas (o) and in the park study area excluding the water in dams (▲), with the effective rainfall over the previous 2 months, $P/E_t(2)$.

were calculated between P/E_t and the amount of water, removing the effect of the biomass by holding it constant (Table 14.4). For the 8 months November - June, when the biomass changed very little, the simple and partial correlations were nearly identical. The same was true when July's data was added, although the biomass had started to increase. With August and September's data added separately, the partial correlation was significantly greater. The addition of October reduced the difference.

July and October were wet months, and the high biomass of 15000 kg/km^2 had no significant effect on the water resources of the area. But when 2 nearly rainless months, August and September, coincided with even higher biomasses of 17000 and 31000 kg/km^2 , the amount of free water was significantly reduced. As these high biomasses were the result of immigration on a scale unprecedented since 1960-61, they can be considered an atypical feature of the park's ecology.

From the quick replenishment of the water resources with the October rain the supply of water in this part of the park is well in excess of the herbivores drinking requirements under almost all circumstances.

This superabundance could be the result of either creating artificial dams or because the dissected topography (p. 56) allows a large proportion of the incoming water to be retained. Their effects can be distinguished by comparing the park's density of water not in the dams with those of the study areas in the plains. In none of these had the natural water- storage capacity been improved.

Table 14.3 contains the relevant data for the park and the 6 plains study area, with their effective rainfalls over the previous 2 months (from Appendix 3). The values are plotted in Fig 14.3, from which it is clear that, for any given rainfall, the park retains no more water than

Table 14.5 The monthly dispersion of water sources and hartebeest sightings between 400 x 400 m grid squares in the Nairobi Park study area, with the current months effective rainfall, $P/E_t(1)$.

Month.	No. of grid squares containing :		
	water	hartebeest	$P/E_t(1)$
1971 November	15	38	.21
December	44	27	1.25
1972 January	17	42	.07
February	21	37	.35
March	9	34	.18
April	6	45	.01
May	29	42	.73
June	37	43	1.23
July	28	47	.09
August	16	46	.02
September	23	47	.51
October	21	57	1.24

the 6 plains areas as a whole, which include a variety of topographic forms, types of river courses etc (Ch. 5). From this it can be concluded that the present - day abundance of water in the park in the dry season is due to the construction of artificial dams.

One possible determinant of the hartebeest's distribution has been investigated further. This is its relationship to surface water which has been mentioned before as affecting its behaviour in the dry season.

Rainfall caused the amount of surface water in the study area to increase. It also became more widespread, shown in Table 14.5 as the number of 400 x 400 m grid squares (p. 17) in which water was recorded as present. Also shown is the effective rainfall in each month, with which the number of squares with water is significantly correlated ($r = .748$, d.f. 10, $p < .01$). By comparison, the number of squares occupied by hartebeest was not related to rainfall ($r = 0.008$, $p > 0.05$). The number of occupied squares shows a coefficient of variation of only 18%, compared to that of 49.6% for the number of squares containing water. On this measure, the hartebeest are evenly dispersed through the year, unlike the water sources.

This difference must be considered in any comparison of the hartebeest's mean distance from water at different times of the year. The monthly modal values of DRINK, the distance from water (Appendix 17) suggests a slight increase in the separation of hartebeest and water in the dry season. But whether the more localized water in the dry season influences the hartebeest's distribution will depend on whether the reduction in the dispersion of water is less than the increase in the animal's separation from water.

To answer this question, the frequency distribution obtained of the distance to water of all the hartebeest sightings in each monthly count was compared with the distribution which a randomly dispersed population would have. The study area contained 143 grid squares of which approximately

Table 14.6 Frequency distributions of the distance to the nearest water of hartebeest sightings (O) in each month, and the expected distributions (E), with the difference between them (D max) its significance, and the mean moisture content of grass in each month.

Month	N		D		J		F		M		A	
Distance,km	O	E	O	E	O	E	O	E	O	E	O	E
<.5	3	4	15	16	11	7	11	8	7	3	5	2
.5-1.0	12	9	23	20	17	11	27	14	15	9	6	5
1.0 - 1.5	8	9	14	9	21	10	10	10	9	9	29	8
1.5 - 2.0	7	17	5	7	15	13	3	10	7	13	15	16
2.0 - 2.5	10	0	1	0	4	2	1	2	7	8	11	6
2.5 - 3.0	8	3	0	0	1	5	1	3	5	5	9	4
3.0 - 3.5	12	4	0	0	0	2	0	3	0	3	3	9
D max	.37		.05		.15		.28		.20		.21	
sig.	.01		n.s.		n.s.		<.01		<.05		<.01	
moisture,%	-		-		36. 2		35. 4		20.1		5. 3	

Month	M		J		J		A		S		O	
Distance, km	O	E	O	E	O	E	O	E	O	E	O	E
<.5	22	11	25	11	4	9	16	5	15	5	15	9
.5 - 1.0	28	18	26	19	20	16	17	11	28	15	24	11
1.0 - 1.5	15	9	11	7	22	12	12	11	23	14	21	10
1.5 - 2.0	7	3	3	5	13	8	17	13	7	11	14	11
2.0 - 2.5	1	4	1	4	6	4	9	7	0	5	2	3
2.5 - 3.0	0	3	0	0	5	0	4	2	0	0	4	3
3.0 - 3.5	0	2	0	0	0	0	0	0	0	0	0	2
D max	.15		.14		.17		.11		.22		.14	
sig.	n.s.		n.s.		n.s.		n.s		<.01		n.s.	
moisture,%	62.0		63.0		45.4		16.2		23.0		25.1	

40 - 60 were occupied by the hartebeest in each month. (Table 14.5). Accordingly, 50 of the numbered squares were chosen at random, and the map distance from the centre of the square to the centre of the nearest square with water was measured in 500 m units. This was repeated using the squares in which each hartebeest sighting was made. As the distribution from the randomly distributed population constitutes an expected distribution, the 2 distributions were compared using the Kolmogorov-Smirnov 1 sample test (Siegel 1956).

Table 14.6 shows the frequency distributions for each monthly comparison, the test statistic ($D_{\max}$) and its significance. In 5 out of the 12 months the distributions differed significantly, showing that the hartebeest were not randomly distributed with respect to water. In February, March, April and September, the animals were nearer than would be expected. In November, on the other hand, they were further away. All these 5 months were rainless or nearly so (Fig 14.2). The last 4 months covered the period when hartebeest were seen to drink, and it is reasonable to conclude that in such months the location of suitable drinking sites partly determines the hartebeest's distribution. November presents a slightly different situation. On this month's count most of the hartebeest population were occupying type 02 in the extreme south of the study area (Fig. 5.3). This particular part of type 02 was not occupied to the same extent in any subsequent dry season. Moreover, the count was made as the rains were breaking. In these circumstances, no great importance is attached to the apparent avoidance of water in this "dry season".

Causal factors in the grazing cycle.

Each case of data for PCA in file NNPCOM referred to one vegetation type in one month. With the exception of some data fields occupied by declared missing values, data existed for the 8 major vegetation types in each of 12 months, a total of 96 cases. If these data are visualized as

an 12 x 8 matrix of values for each variable, 3 basic groupings of the data could be made for PCA, producing 3 sets of components :

1. PCA of each row of the data would show the pattern of variation in each vegetation type through the 12 months.
2. PCA of each column would show the patterns between vegetation types in each month.
3. If all the data were pooled, the resulting components would include 1 and 2 in a description of the overall spatial and temporal variation in the data.

The second approach was the most relevant one for the present purpose, but suffered the disadvantage that each month's PCA would be based on data from only 8 cases (the vegetation types). Similarly, the first approach could use only 12 cases in each component analysis. By comparison with published accounts of PCA, 8 and 12 cases are both inadequate, and the most reasonable course was to pool all the data in to a block of 96 cases for one PCA. But having done this, any interpretation of the components would have to recognise the dual nature of the variation in the data.

The data used in the PCA are shown in Appendices 17,15. The loadings for the 8 largest components are shown in Appendix 16. The raw data show that essentially parallel changes occurred through the months in all the vegetation types, and that these changes were much greater than the variation between types in single months. In effect, the data for each vegetation type would be treated as replicates for each month. This meant that although the first 8 components (App. 16) accounted for 99.1% of the variability, the components had to be given "seasonal" rather than "vegetational" interpretations. Consequently, the multiple regressions then only showed that the hartebeest were found in type 02 in the dry

season and type 06 in the wet. Nothing could be said of why they had chosen either at these particular times. PCA 's were also run in which the months were divided in to 3 "seasons" with the grouping using in ch. 7 (p.105), but these were no improvement. The unfortunate, but inevitable, verdict on this method of analysis was that by combining the data to obtain an adequate sample size, the components of possible interest as causal factors in the grazing cycle were swamped.

14.3 Discussion.

The data used in the PCA appeared suitable for this analysis by being inter-correlated and satisfying the requirements of normality and linearity. Although not described here, the components which were isolated were biologically meaningful, thereby achieving the "parsimonious summarization" (Seal 1964) of seasonal changes in the vegetation. The fact that the more interesting patterns of variation between vegetation types could not be detected because of inadequate sample sizes confirms Davies and Brown's (1972) experience that the results of PCA are "sensitive to the context", and that the data must be combined or divided in the appropriate way for the particular aim of the analysis.

The PCA was based on information collected in the Nairobi Park study area, covering 20 km². Large variations in the nutrient quality of the grasses in the vegetation types of such a small area would be surprising, and the data (Appendix 17) show that this is so. Therefore, unless their digestibilities varied more, a unit weight of grass from any vegetation type would contain an approximately constant quantity of digestible nutrients. In this case, the nutrient content of the grass may be less relevant to the analysis of the causal factors behind the grazing cycle than detailed information on the structure of the sward.

The influence of sward structure on the hartebeest's diet selection has already been discussed (p. 164). By feeding selectively in grassland of relatively optimal structure a grazer can increase its nutrient intake above the mean sward concentration (Arnold 1960) and also increase the rate at which dry matter is eaten (Allden and Whittaker 1970). In other studies of grazing cycles (Bell 1969) or mosaics (Vesey - FitzGerald 1965), the effects of herbivores on the sward structure, benefiting either themselves or other species, are described. Such effects, rather than changes in the food quality of the sward are emphasized, but, on the other hand, they are not necessarily independent. If animal use stimulates continued growth (Vesey - FitzGerald 1969), the structure and food quality will vary together. Information on the sward structure in terms of its leafiness and spatial arrangement may be more useful for an adequate analysis of the factors causing such grazing cycles.

The long - term effect of grass fires on the park's vegetation and the hartebeest can be examined from the monthly pattern of vegetation type utilization. Portions of the A. drepanolobium grassland and open plains were burnt in November 1970. The following figures show their mean standing crops of grass over the period November 1971 - October 1972, between 1 and 2 years after the fire. The burnt type 35 had no unburnt equivalent but it is included. For the 2 pairs of burnt and unburnt vegetation types, the mean c.g.i.'s from Table 14.2 are also given. The number of hartebeest in each type over the 12 counts estimates their relative utilization :

	standing crop kg/ha	c.g.i.	hartebeest
<u>A. drepanolobium</u> burnt (35)	890	.62	566
" (06)	1397	.78	1276
unburnt (10)	2661	.31	356
open plains burnt (01)	600	.89	581
unburnt (04)	1018	1.27	1033

The effects of the fire were long - lasting, for even in the second subsequent year the standing crops in the burnt A. drepanolobium (06) and open plains were only 53% and 59% of their unburnt counterparts. Since rainfall in both years was more than adequate to restore the grass biomasses of both types to their unburnt levels (Cassady 1973), utilization by herbivores maintained the shorter grassland. In the wet season the hartebeest consistently occupied the burnt A. drepanolobium types, 06 and 35, which were used by 5.2 times more animals than the equivalent unburnt area. Thus, burning this grassland enabled the hartebeest, as the most numerous herbivore, to maintain their wet season food supply in a more optimal condition for at least two years.

The opposite occurred on the open plains where the unburnt portion supported 1033 hartebeest over 12 days, and the burnt part only 581. The distribution of herbivores species among different grass biomasses (p.123 et seq.,) suggested that this burnt grassland (01) was suboptimal for the hartebeest through being too short. Its selection by wildebeest, Thomson's gazelle and warthog show that these species maintain this grassland nearer to their optimal structures. Thus, fires in this area affect the herbivore species differentially. Burning the A. drepanolobium areas after a period of some years opens up large areas to the hartebeest for their wet season use, but their habitat is made less optimal by burning the open plains.

Until 1968 the extent and frequency of fires in the park was insignificant. The movements of the hartebeest population in the period 1966 - 68 (Gosling 1974) emphasize the significance of fire on the hartebeest's ecology. Following rain in these years, the hartebeest dispersed to wherever there was fresh, sprouting grass more than 10 cm tall. As the rains finished, the "Acacia/grassland ecotone" (Type 03) was occupied, followed by the "Setaria/Ischaemum" grassland (Type 10). In the late dry season the hartebeest moved down in to the "Cymbopogon/Hyparrhenia" levels on the lower slopes (Type 02). In 1970 - 72 the hartebeest did not disperse after heavy rain, but moved in to the burnt Acacia types. In this latter period the unburnt Acacia areas of "Setaria/Ischaemum" grassland were avoided in all months of the year, suggesting that it was suboptimal habitat relative to the burnt portion and the vegetation types used later in the dry seasons. The consequences of burning the A. drepanolobium grassland, at the level of the hartebeest population are discussed in the next chapter.

By using vegetation type 02 in the dry season, the hartebeest population is deployed near the major river courses with the remaining water. This could be a fortuitous association, but the vegetation type may be attractive in its own right. Its standing crop remains high through the dry season, like that of the unburnt A. drepanolobium grassland which is not occupied, but these types are structurally different. Type 02 consists of distinct clumps predominantly of Cymbopogon poschippilii with tall culms (Appendix 17), unlike the dense sward of type 10. The uniformity of structure in type 10 is also partly due to its thick mat of dead but undecomposed plant material, responsible for its lower moisture content (Appendix 17). This mat is absent from type 02, making it easier for the hartebeest to feed selectively among the bases of these clumps.

The significant association of hartebeest and water sources in the dry season confirms subjective impressions, which were also reported by Gosling (1974b). In fact the association described above would probably have been more striking if based on the distribution of individuals rather than herds. However the use of individuals in the present analysis would assume that the members of a herd were independent samples, which seems highly unlikely. Therefore, the sample unit has to remain the herd.

When the hartebeest were in the burnt A. drepanolobium areas after rains, individuals were seen to drink only very rarely. In the period November 1971 - October 1972, the significant positive association of hartebeest and water started in February when the mean moisture content of the grass in the study area was 35.4% (Table 14.6). In the next dry season a significant association occurred only in September when the water formed only 23.0% by weight, although it had dropped to 16.2% in the previous month and in the next ^{was} 25.1%. The need to drink will depend not only on the intake of free water with the food, but also on the rate of water loss through, for example, evaporative cooling. The mean air temperature (Fig 4.6) and evaporative power of the atmosphere (shown as E_t in Appendix 3) are both higher in February, March and April than in August, September or October. If there were parallel differences in the level of heat stress and consequent water loss, drinking would be necessary in the former months when the grass still had a higher moisture content than in the later ones.

Because of the small area of the park study area, few of its 143 400 x 400 m grid squares could ever be more than 4 km from water in the dry season. Although this is not a great distance for a hartebeest to walk, the fact that they nevertheless aggregate around water in the

dry months argues that there are strong reasons for doing so. In Ch. 11 (p. 218), it was shown that the energy cost of walking to water in the dry season was considerable. It was also suggested that the energy saved by staying near water even when drinking every other day might be greater than the net energy gained by walking to and from feeding grounds which were further away but were more optimal in some way. Unless there are large differences in the digestibility, the information in Appendix 17 on crude protein, carbohydrate and gross energy contents shows that the food value of grass near water (types 02, 05) is no greater than that of more distant vegetation (types 10, 06, 04). On the other hand, the structure of the sward in type 02 may allow selective feeding (p. 268) in which case the hartebeest could maximise nutrient intake and minimize energy expenditure by remaining near water in the dry season.

If this reduction in energy expenditure is significant in even a small part of the well - watered park, it must be of greater importance to the hartebeest of the plains. This is suggested as one reason why the hartebeest distribution between the plains's vegetation zones varied so little between months through the year (p. 95), and also why the most selected zones were those with the highest rainfall. By occupying these zones the hartebeest would increase the probability that when it became necessary to drink free water, their requirements could be met in the same area or vegetation zone. Alternatively, this distribution pattern reduces the necessity of seasonal migrations.

Chapter 15.

HARTEBEEST ECOLOGY: A DISCUSSION

The various chapters of this thesis have dealt with specific aspects of either the hartebeest's environment or their ecology. The conclusions which I have drawn have been presented in the discussion at the end of each chapter. In this final chapter, I do not attempt to summarise these conclusions but try to point out the more interesting differences and similarities between the ecology of the hartebeest and other species, related and unrelated. In doing this, the relationship between hartebeest and cattle, both present and past, is considered in some detail. This leads to a final discussion of the differences between the Nairobi Park and the Athi Plains and their hartebeest populations.

15.1 The hartebeest in the herbivore community.

The analysis of the herbivore community's structure crudely describes the ecology of the hartebeest in relation to those of the other species. The diversity shown by each species in its occupation of vegetation zones and types, and its tolerance of the range of available grass biomasses measures the width of its niche. Two major points emerge:

1. Within the Athi Plains ecological unit, consisting almost completely of grasslands, the hartebeest shows a great diversity in its occupation of vegetation zones, which are recognized as natural divisions. There is also very little seasonal pattern in their occupation of these zones. On the other hand, the wildebeest and zebra use fewer zones on a year-round basis, and are migratory.
2. The constant number of hartebeest in the Nairobi Park is consistent with their sedentary existence in the plains. In the plains and the park, the hartebeest is the first and second-ranking species respectively in the diversity of vegetation type occupation. The plains animals occupy the

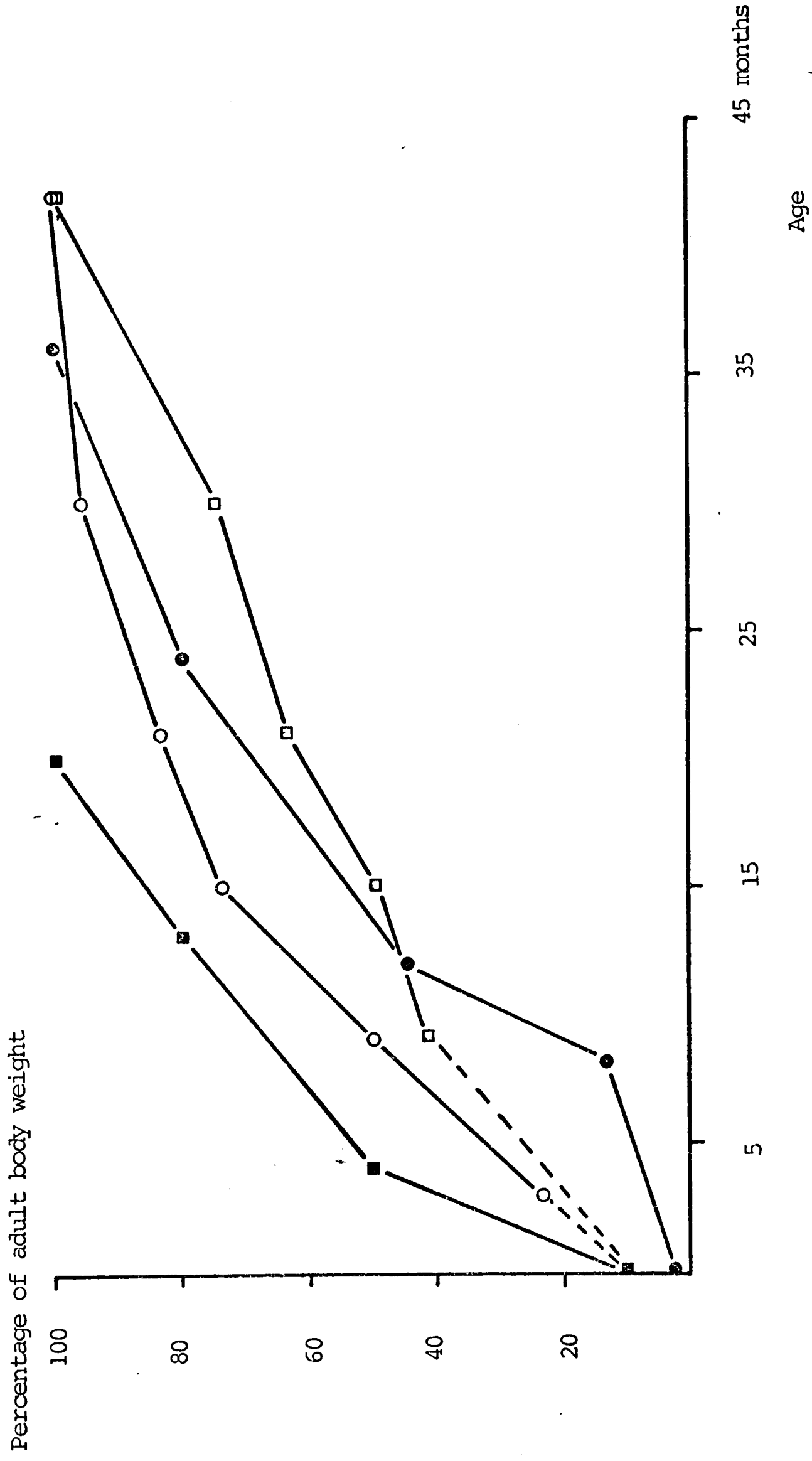


Fig.15.1. The rate at which full adult body weight is reached in the female sheep (■), the female euro (●), the female wildebeest (○) and the male and female hartebeest (○).

same types to the same extent through the year, but in the park seasonal occupation is highly developed, as described in the last chapter.

The standing crop of grass is one characteristic of the types. In both areas the hartebeest's use of the available standing crops is very catholic. In the wet and medium seasons, they show little selection for particular standing crops from amongst the range available. The hartebeest's diverse use of vegetation zones and standing crops indicates a broad niche relative to other species in terms of their habitat selection. That this happens in both areas, despite their differences, is good evidence that the hartebeest's ecology is essentially the same in both.

Differences in the habitat selection of the herbivore species are reflected in the degree of overlap between their distributions. In both areas the range of overlap values was wide, but with all high overlaps except that between hartebeest and cattle, ecological separation could be inferred. The overlap between these species was due to their similar habitat selection measured as vegetation zone or type or standing crop occupancy. On their gross feeding habits both are classed as "roughage grazers", and later evidence showed that there was good reason to think that the same single grass species was a major component of their diets. Positive evidence was presented which showed that the proportions of plant parts in their diets were very similar indeed. Under these circumstances, ecological separation between them appeared less than between any other species. The nature of this relationship is examined below.

15.2 Comparative aspects of hartebeest ecology.

The difference in the population distributions and movements of the related wildebeest and hartebeest are paralleled in other aspects of their ecology. This contrast is heightened by the similarity between the hartebeest's behaviour and that of certain of the Australian desert-living macropod marsupials, which have in common some adaptations to their environments.

In Chapter 12 the growth curve of the hartebeest was described. Full adult body weight was not reached in shot animals until the fourth year, confirming the results of Gosling's (1974) photographic measurements on living males in the Nairobi Park. In Fig. 15.1 the rate at which full adult body weight is reached is compared with Watson's⁽¹⁹⁶⁷⁾ data for wildebeest.

The maximum body weight of female wildebeest is calculated as 121.8 kg and is also reached at the age of 3-4 y. Data from both male and female hartebeest have been combined to obtain an adequate sample size. As the growth pattern of the sexes are the same (Fig. 12.1) and the adult body weights differ less than in the wildebeest, this seems justified. The figure also includes the female sheep and marsupial euro (Macropus robustus) from Ealey (1967). The sheep grows faster than any of the wild species. Of these, the euro grows slowly until it leaves the pouch because much of its pouch life is equivalent to the foetal development of the other species. Although both wildebeest and hartebeest reach their maximum weights at about the age of 3.5 y, the growth rate of the wildebeest increases in the second year of life, in a more typical sigmoid curve (Brody 1945), whereas the hartebeest grows at a more steady rate from birth to maturity.

The slow growth of the hartebeest and kangaroo is partly a consequence of their occupying environments in which the rainfall is unpredictable and the food quality poor. The hartebeest's dry season food can contain 2-4% crude protein (Table 10.1) while the main food item of the euro under the same conditions contains only 1.6% crude protein (Ealey and Main 1967). Despite such conditions both groups are relatively sedentary. Over 30-40 months, known red kangaroos were rarely seen at locations more than 10 miles apart (Frith 1964). The small scale of the hartebeest population movements has already been described. Under these conditions, the sedentary option is associated with slow growth and the late attainment of sexual maturity (p. 242), and the hartebeest, at least, has generally low reserves of body fat (p. 233).

Both hartebeest and kangaroo show many similarities in their reproduction. The strategy of the red kangaroo is "opportunistic" (Newsome 1965) in the face of periodic drought and sporadic rainfall. Under good conditions most females have a young-at-heel, which is still suckled, a smaller pouch offspring and a diapausing blastocyst (Tyndale-Biscoe 1973), so that although each young animal spends 600 days between conception and independence, a female can produce an independent offspring every 240 days. Except under conditions of extreme drought, a female can replace any pouch young which dies through inadequate lactation by the development of the blastocyst. The smaller young in the pouch is less of an energy drain and enables the quick production of independent young when conditions allow. There is no evidence of delayed implantation in the hartebeest, but their reproduction in the park was also controlled by the inter-related effects of rainfall, nutrition and condition. Under good conditions a calf was produced every 9-10 months (270-300 days). A response to rainfall of giving birth cannot be as swift, and probably does not need to be as rainfall has a longer lasting effect in East Africa. But within the limits imposed by being eutherian rather than marsupial, their reproduction can be fairly described as opportunistic.

The association of 2 young with a female kangaroo carrying a blastocyst is due to the slow growth but faster rate of production of young. The same happens in the hartebeest whose females are frequently seen followed by a juvenile and a subadult, separated in age by less than a year. Rarely, a female is followed by 3 successive offspring (Plate 2). The year-round diet of coarse material provides only modest surpluses of nutrients for growth above the maintenance requirements. This causes slow growth, which may be adaptive (p. 237).

The equivalent aspects of the wildebeest's ecology show considerable differences. By being migratory and following outbreaks of rain (Pennycuik 1974), its population effectively occupies areas with higher rainfall than

the average for the whole area. The proportions of green leaf in its diet in the Serengeti varies far more between seasons (Gwynne and Bell 1968) than that of the hartebeest in the Athi Plains (p. 155). This suggests that its nutritional plane also fluctuates more in a "feast to famine" manner. Concomitantly, the levels of body fat in the wildebeest are far more variable and more extreme values are recorded (Sinclair and Duncan 1972). These are related to different stages of the reproductive cycle in the two sexes. Wildebeest grow faster (Fig. 15.1) and reach sexual maturity earlier, with 37% of the females conceiving when 1 y 4 mth old, and 83% when 2 y 4 mth old (Watson 1969).

Great differences also exist in the timing and immediate success of breeding in the two species. In contrast to the hartebeest's calving in every month of the year (p.244), the wildebeest calving is highly synchronised with 80% born over a 3 week period (Watson loc. cit.). In East Africa the birth peak occurs in January and February so that the young are weaned on to the fresh grass produced by the rains of March-April. As this reproductive cycle includes an equally pronounced rutting season in May, the proximate factors controlling the timing of reproduction are presumably different from those of nutrition and condition postulated for the hartebeest.

The higher nutritional plane and better body condition of the wildebeest is associated with 96% of all females calving in a year (Watson loc. cit.), while the comparable figure for the hartebeest is only 50-80% (p.244). The pattern of subsequent mortality is very different. Young wildebeest are heavily predated (Estes 1966, Kruuk 1973), and further high mortality may ensue if lactation fails or weaning occurs before the short rains break. In the Athi Plains, 85% of the 1971 calf crop died in their first 4 months of life when lactation failed because no rain fell in late 1970 (Peterson and Casebeer 1972). By comparison, once conception has occurred, the course of the hartebeest reproductive cycle

seems relatively independent of the rainfall pattern. Although fewer calves are born, their survival of nearly 70% at the age of 1 year (Gosling 1974) is probably higher than the wildebeest in all except the most favourable years. The behavioural adaptations which help to reduce calf predation in both species have been discussed by Gosling (1969).

Reproductive behaviour in these two alcelaphines is therefore fundamentally different with the relative advantages of each depending on the habitat and climatic conditions. The wildebeest calving is prolific which, coupled with fast growth and high survival in some years, indicates a very high potential rate of increase. They are limited, though to producing only one calf a year despite a gestation period of only 8 months (Watson loc. cit.). The hartebeest's reproduction is more parsimonious and opportunistic, and although reproduction starts later in life, a calf is produced every 9 months under good conditions, with a much higher chance of survival for at least the first year.

15.3 The relationship between hartebeest and cattle.

In itself, the spatial coincidence of these two species says little of the nature of their relationship. Their presence together could be to their mutual benefit or one could be harmed by the presence of the other. From the evidence of other East African herbivore communities the relationships between species appear facilitatory in terms of their exclusive feeding habits and influences on the vegetation to the benefit of other species (Vesey-FitzGerald 1965, Bell 1969). In such diverse communities which have evolved together, one might suppose that the herbivore niches are relatively narrow (MacArthur 1955). The way in which the feeding behaviour and ecology of African herbivores can be categorised (e.g. Stewart and Hofmann 1972, Jarman 1974) suggests that this is likely. When an exotic species is introduced or imposed on to such a community, it would seem improbable that a vacant niche would exist and that, by occupying it, the resources of the area are then used more efficiently. From this argument, the presence of

cattle on the Athi Plains suggests a competitive situation.

Birch (1957) recognises two forms of interspecific competition. One is competition by exclusion, in which individuals of one species hinder the access to a resource of another species, which is harmed as a result. The second, competition by exploitation, can only occur if the members of two or more species utilize the same resources which are inadequate to meet the requirements of both. In a review, Grant (1972) points out that the critical evidence for interspecific competition among rodents falls in to two categories:

1. 2 sympatric species exhibit an inverse spatial relationship.
2. 2 sympatric species exhibit an inverse numerical relationship.

The first type of evidence is clearly lacking in the hartebeest - cattle situation because they tend to be found in the same place at the same time, but the mean densities of the two species in the Nairobi Park and the Athi Plains show an inverse numerical relationship:

	park	plains
cattle	0	27.3 km ⁻²
hartebeest	17.8	2.7 km ⁻²

Although the park differs in other respects than its lack of cattle, the two areas are essentially similar enough to allow this comparison. The densities of wildebeest and zebra, the other most abundant species, show less difference inside and outside the park (p. 88). On this criterion, therefore, interspecific competition between hartebeest and cattle occurs.

Grant (loc. cit.) continues that under laboratory conditions, interspecific competition is demonstrated if species A spends more time in species B's habitat in B's absence than its presence. The most readily observed aspect of the hartebeest-cattle interaction was that hartebeest moved away from approaching herds of cattle, thereby being displaced from their chosen sites. As the hartebeest never moved in this way when approached by any wild species, this is evidence of the competition of the two species for space. More specifically, as cattle moved in herds up to 500 strong, and

the hartebeest groups rarely exceeded 30 animals, approaching cattle caused the hartebeest to move, while the reverse never happened. The predictable outcome of such interactions was that the hartebeest was always the interfered species.

As both species have occupied the plains for a long, but unknown, period, the situation appears to be one of competitive coexistence. In such cases, the population level of one species must be depressed (Krebs 1972). The lower hartebeest density in the plains suggests that this requirement is met. The problem is whether the spatial exclusion can account for the size of the density difference.

If displacement occurred during a feeding period, grazing ceased while the hartebeest moved, but might continue at about 200 m from the cattle. The chances that feeding would be resumed in different, and presumably less optimal, vegetation would increase with the distance moved. If displacement resulted in a lower net nutrient intake, by whatever means, the hartebeest's productivity would also decline and could, in theory at least, cause the lower density. Three lines of evidence suggest that these effects of exclusion would be inadequate:

1. The distances moved by the hartebeest were small compared to the size of the vegetation types, so that large differences in grazing conditions were unlikely.
2. After the cattle had passed, the hartebeest did not immediately move back to their previous sites. This does not exclude the possibility, of course, that the passing of the herd rendered the vegetation less optimal.
3. The Maasai corral their cattle at night. Thus for a minimum of 12 h/day the location of cattle herds is not a factor determining the distribution of hartebeest. Also, any deficiency in feeding time caused by displacement during the day could be made up by feeding at night.

Competitive exclusion, therefore, seems unable to account for the different densities of the two hartebeest populations. As a corollary to

their ecological equivalence in terms of their distributions, these species also had the most similar diets. This similarity extended both to the grass species eaten, and the parts of those species. One line of evidence suggests that under some conditions, at least, their common food supply was inadequate to meet the requirements of both.

Between July and September 1972 no rain fell where the sample hartebeest were shot (Fig. 8.3). In the latter month leaf formed only 18% by weight of the sward, and the hartebeest were no longer selecting it. The less complete information on cattle diets over the same period shows the same changes. The absolute amount of herbage in the area was not inadequate (p. 164), but if "food" is defined as the amount of the grass component which was selected most in other months (i.e. leaf), it was in short supply in September, judging by the lack of selection. Because the hartebeest's intake in September was calculated to be below their maintenance requirement, the supply of leaf was inadequate.

The point at which a sub-maintenance intake is reached in a given area following a given amount of herbage growth will depend on the rate of grass offtake through the combined action of all the grazers. As the combined biomass of hartebeest and cattle in the plains was 3.7 times greater than the hartebeest's in the Nairobi Park, the level of nutrition would fall below the maintenance level sooner, or more often, in the plains. Here, cattle and hartebeest, with biomasses in the ratio of 25:1, were taking the same diet from the same vegetation types. With any additional effect of exclusion by cattle, this is strong evidence that the presence of cattle depresses the nutritional plane of the hartebeest. The accelerated defoliation of the sward results in competition for the limited amount of food in the manner defined by Birch (loc. cit.).

The reduced amount of food available to the hartebeest is a more likely reason for their lower density. The pattern and rate of breeding in the Nairobi Park population was shown to be largely determined by the nutrition and condition of the females through their effect on the birth rate (Ch. 13).

The number of newly-born calves in the plains appeared to be no lower than in the park (p.89), unlike the numbers of both juveniles and subadults. However, less reliability can be attached to a comparison of the numbers in an age class lasting only one month than of 2 age classes each covering 10-12 months. On present data the birth rate is the same in both areas, but mortality after the first month is higher in the plains.

The higher mortality may act only after weaning when the young animal is fully subject to the effects of adverse climatic conditions on the food resources. Growing animals, in common with lactating females, have higher nutrient requirements (A.R.C. 1965) than non-breeding adults. But whereas a lactating female will have accumulated reserves during pregnancy against the high cost of lactation, the small reserves of the immature animals (p. 231) suggest that much of their energy intake is diverted to body growth. Consequently, in a dry season, they are the most susceptible group to starvation.

In conclusion, the competition of cattle with hartebeest results in a lower density of the latter, and a lower proportion of young animals in their population. The intensity and occurrence of this competition will vary between places within the plains and in different seasons. One mechanism exists by which the intensity of dry season competition may be lessened fortuitously. In the last chapter it was argued that the distribution of dry season water sources was a major determinant of the hartebeest's distribution in the park and the plains. The proportion of the population affected by competition with cattle will depend on whether the hartebeest have to leave an area in which the natural water sources have dried up while the cattle can remain by using artificial sources which are now common in the Athi Plains. If this happens, competition for food is reduced. On the other hand, if both species continue to use the same water sources, they are likely to have the same feeding areas, thereby intensifying the competition. For the hartebeest both alternatives presumably have their advantages

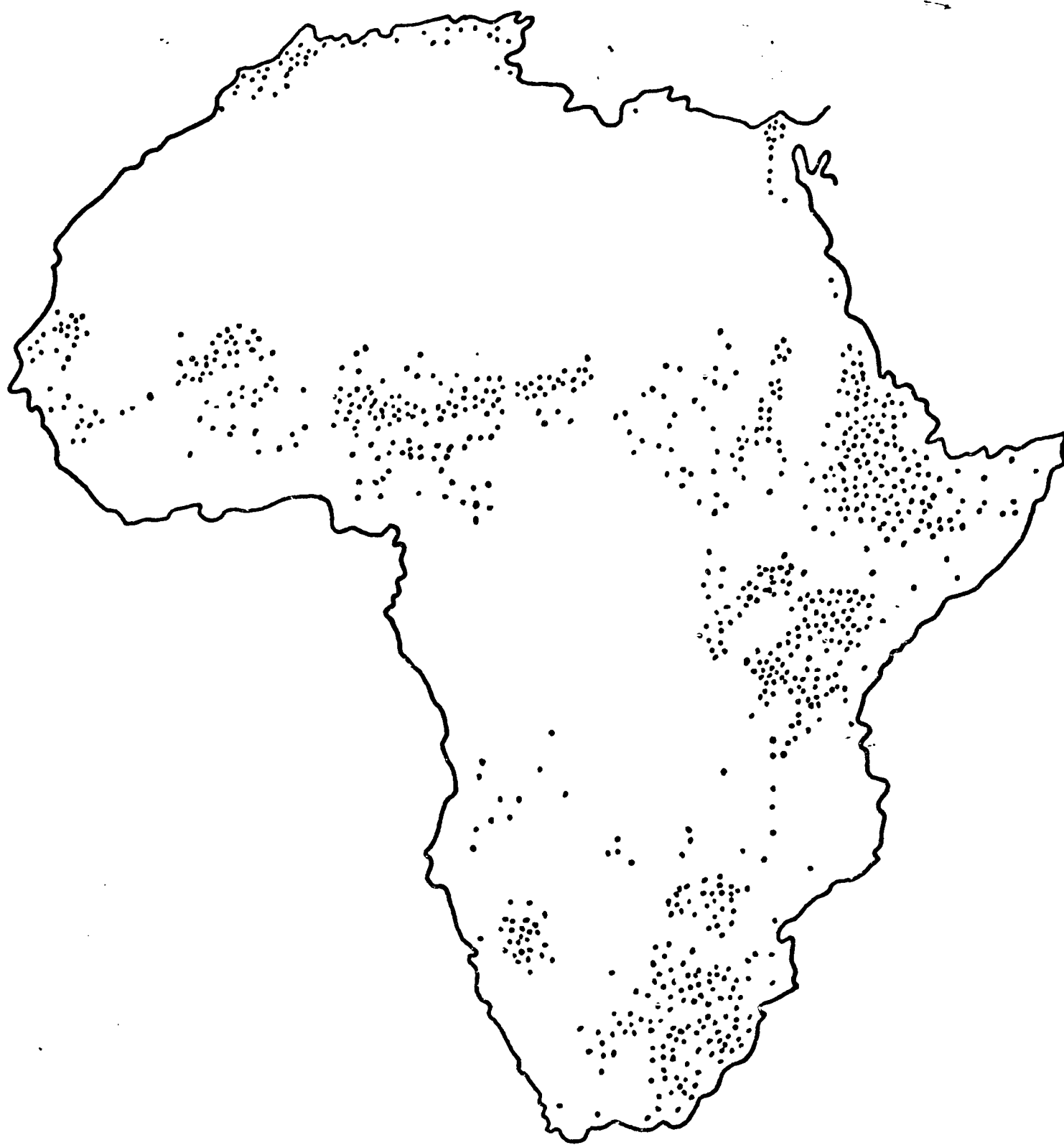


Fig.15.2. The distribution of cattle in Africa, 1959.

one dot represents 100,000 cattle

and disadvantages in terms of the energy cost of moving in to an area perhaps occupied by other herbivores against remaining and suffering a lower quality diet because of the activity of cattle.

15.4 The genera *Alcelaphus* and *Bos*: past and present.

The contemporary evidence from the Athi Plains shows that the habitat selection of hartebeest and cattle are almost identical, and this has resulted in a competitive situation. Their ecological similarity is of ancient origin. The cave of Haua Fteah in Libya contains strata dated from 70,000 to 2,000 B.P. Throughout this period remains of *Alcelaphus* sp. are found with those of *Bos* sp. (McBurney 1967). When the faunal composition in the cave changed, indicating climatic change, the proportional occurrence of both genera altered in the same way. Reviewing the associations between species on a presence or absence basis at 36 North African sites, McBurney (loc. cit.) showed that the commonest associations were between *Equus* and *Bubalis* (= *Alcelaphus*) (20 associations), followed by *Bos primigenius/Bubalis* (16 associations) while all the other species pairs occurred together less often. In Israel, the Kebarah caves contain 3 layers dated at 16-18,000 B.P. (Saxon 1974), with faunal remains deduced to be human kills. Again there are indications of climatic fluctuations, but throughout the layers the proportion of remains of *Bos* and *Alcelaphus* vary together in a way not shown by any of the other genera of *Equus*, *Cervus*, *Sus*, *Gazella*, *Dama* and *Capreolus*.

Except for the most recent layers in Haua Fteah, these sites pre-date the domestication of cattle (McBurney loc. cit.). This suggests that the habitats occupied by wild *Bos* spp. were very similar to those of the hartebeest. It is not surprising that when domesticated cattle were introduced to Africa south of the Sahara (Payne 1970), they should continue to use the same type of open grasslands, on which there were already indigenous *Alcelaphus* spp. Fig. 15.2 shows the distribution of cattle in Africa in

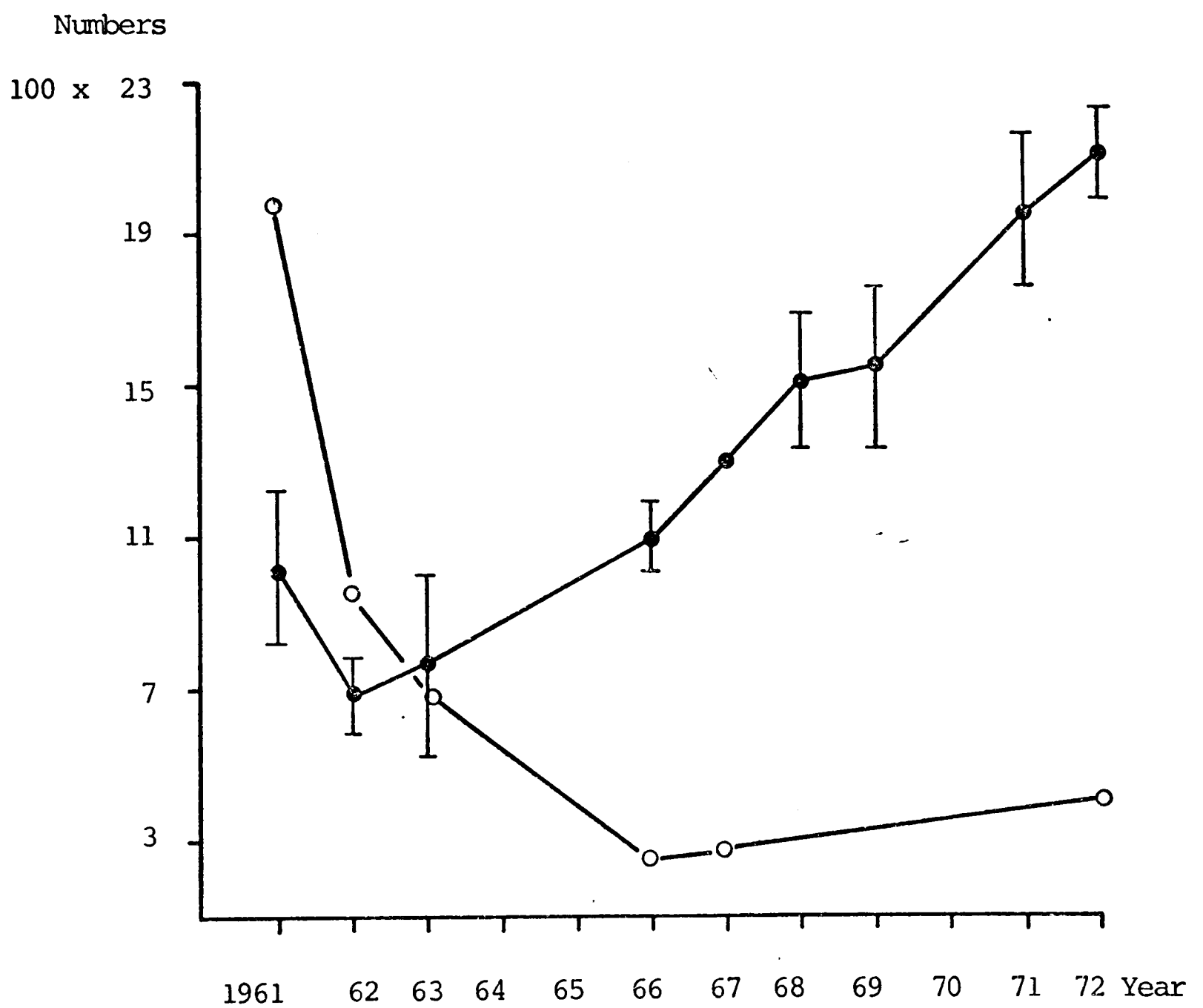


Fig.15.3. The mean population sizes of hartebeest (●) and wildebeest (○) in the Nairobi National Park, 1961-1972. The hartebeest means have standard deviations where possible.

1959-60 (Anon 1965). Comparison with Fig. 1.1 shows the distributions of cattle and Alcelaphus to be highly coincident. A major difference occurs in the range of Lichtenstein's hartebeest, but this arises because this hartebeest is a woodland species (Dowsett 1966). Throughout Africa cattle are largely confined to open grassland because of the prevalence of the tsetse fly, carrying trypanosomiasis in wooded regions (Payne loc. cit.). In South Africa the ranges of the Red hartebeest and cattle coincide less, but that of the hartebeest reflects its extinction from all but the more arid parts of its historic range by the beginning of this century (Sidney 1965).

The ecological equivalence of hartebeest and cattle and the competitive superiority of the latter indicate that as the grasslands of Africa are developed to increase the stocking rate of domestic animals, the hartebeest populations will gradually dwindle, as the Athi Plains population has done. The effects of rinderpest and heavy hunting are said to have caused the demise of Swayne's hartebeest in Somalia between 1891 and 1905 (Swayne in Simon 1962), but the large numbers of cattle in this country (Fig. 15.2) today may have been contributory to their original decline or their failure to increase again this century. The same fate may soon befall the last Ethiopian populations of this hartebeest, which occupy areas heavily used by cattle (Bolton 1973).

15.5 The park and the plains: a summary

The density of 17.8 hartebeest /km² in the park is a relatively recent phenomenon as Fig. 15.3 shows, using data from Foster and Kearney (1967), Foster and McLaughlin (1968) and this study. The situation prevailing before the severe drought of 1960-61 and its associated mortality is not known precisely, but it is generally agreed that the hartebeest were less numerous than wildebeest in the park. Gosling (1974) has explained the predominance of the hartebeest through the 1960's and early 1970's by saying that the mortality during the drought relieved the grazing pressure on the

park's vegetation. When the drought was broken by heavy rainfall in 1961, the number of wildebeest was no longer great enough to keep the sward at their optimum length. The longer grass favoured the hartebeest, which therefore increased faster, keeping the sward at their optimum length which was longer than the wildebeest's. This appears reasonable in the light of the different grass volumes selected by the two species(p.125 et seq.).

The 1200 hartebeest in the park in 1960 may be an overestimate of the resident population because of immigration from the plains. Despite the loss of 50% of this total between 1960 and 1963, the population had reached its former level by 1966. The problem is to account for the continued increase in which their density nearly doubled between 1966 and 1972. Some increase above the pre-1960 numbers might be expected because the lower numbers of wildebeest meant that the total biomass of herbivores was below the park's carrying capacity. In addition, a number of events occurred which increased the carrying capacity of the park, either generally or specifically for the hartebeest:

1. The rainfall was above average in each of the years 1966, 67, 68, and primary production can also be presumed to have been higher, increasing the carrying capacity.
2. In May 1967, the 900 cattle and 450 sheep, which had been allowed in the park since 1946, were evicted from the west end of the park (Foster and Kearney loc. cit.). An increased carrying capacity for the wild species would result, but in view of the equivalence of hartebeest and cattle, the former probably benefited most by the removal of domestic stock from an area with water throughout the year.
3. In May 1967, a policy of rotational burning of the park was initiated. By late 1970, approximately 70% of the park had been burnt once, but by far the largest fire was that of November 5th, 1970, which included 49.7% of the study area in its track. Fire can be an advantage or disadvantage to the hartebeest depending on which vegetation is burnt

(p.267), but the invariable selection of the burnt Acacia drepanolobium grassland and the avoidance of its unburnt counterpart shows that a fire here made available to the hartebeest a large area of hitherto suboptimal habitat. The fire removed virtually all the standing grass. The hartebeest started to feed on the new growth when it was long enough, and because they were already the dominant herbivore, they could maintain it in their optimal structure. The overall result was that although after 2 years the standing crop of grass was less than in the unburnt portion (p.267), the amount of available food was greater.

Although the hartebeest population of the park increased during 1966-68, Gosling(loc. cit.), found evidence that as the density increased in his study area, the birth rate dropped. Events in the period after 1968 show that this trend was not sustained, and the combined effects of the factors above allowed even higher numbers to be reached. However, Fig. 15.3 suggests that the population size was beginning to level off at about 2100 in 1970-72, representing the carrying capacity of the park under the drier-than-average conditions prevailing then. The parallel changes observed in the population size and surmised for the food supply are consistent with the action of female nutrition and condition as the ultimate and proximate factors determining the pattern and rate of reproduction.

The fine adjustment of the numbers of hartebeest to their food supply in both the park and the plains is shown by the events during the drought of 1973-74. As the vegetation was eaten down the hartebeest began to starve in both areas, while the wildebeest appeared able to collect enough food from the short swards (Hillman pers. comm. 1974). The situation was exacerbated by the lesser mobility of the hartebeest population. The result of the drought was that 90% of the hartebeest population died, as did a similar proportion of the cattle population. The wildebeest were relatively unaffected.

Sections of this chapter have shown that conditions in the park were

particularly favourable to the hartebeest population, while those in the plains were adverse because of their competition with cattle. The question arises of which conditions exerted the greater influence or, alternatively, what would be the "normal" density of hartebeest in the Athi Plains ecological unit before the creation of the national Park or the present high numbers of cattle?

No figures for the cattle population of the Athi Plains before 1942 have been seen but the increase to present levels probably only started in this year with the introduction of compulsory vaccination against rinderpest (Prole 1962). Until the 1920's, the chief haunt of Coke's hartebeest in Kenya was in the Athi Plains where "it was usual to have several thousand in view at one time, extending as far as the eye could see" (Simon 1962). The abundance of the hartebeest on these plains struck early travellers such as Radclyffe Dugmore (1913). His photographs, taken in the first few years of this century at the northern edge of the plains at Kamiti, 20 km

N.E. of the present Nairobi Park, show hartebeest in aggregations typical of the park in 1972. In 1902 Meinertzhagen walked the 16 miles between Nairobi and the Athi River railway station, to the south of the line of rail (Fig. 3.1). This would have taken him through the area of the Nairobi Park. On this journey he counted, amongst other animals, 4006 zebra, 845 hartebeest and 760 wildebeest (from Simon loc. cit.).

It is clear from these accounts that the high densities of hartebeest in the Athi Plains and particularly at their northern limit in the higher rainfall areas (Fig. 4.4) preceded the existence of the National Park by a long time. Thus, the density in the park in 1970-72 may be regarded more as the norm, and the lower density in the plains as atypical. The continued survival of higher numbers of wildebeest and zebra in the plains is evidence that competition with cattle, rather than direct persecution by man, is the reason for the plains situation. Compared to the range of Serengeti grasslands (Braun 1974), the Athi Plains support grass whose medium

length is determined by edaphic factors. The hartebeest's selection for such grass accounts for their original abundance in the plains. The lower herbivore biomass and lighter grazing pressure of the park enables the grass to approach its edaphically determined length to the benefit of the hartebeest population. Their increase has been helped further by the present policy of burning the longer grasslands.

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Appendix 1 . Glossary of animal species in the text.

Hartebeest	<u>Alcelaphus buselaphus buselaphus</u> (Pallas) <u>A.b. cokei</u> Gunther <u>A.b. Jacksoni</u> (Thomas) <u>A.b. lelwel</u> (Heuglin) <u>A.b. major</u> (Blyth) <u>A.b. swaynei</u> (P.L. Sclater) <u>A.b. tora</u> (Gray) <u>A. caama caama</u> (G. Cuvier) <u>A. lichtensteinii lichtensteinii</u> (Peters)
Wildebeest	<u>Connocnaetes taurinus albojubatus</u> Thomas
Zebra	<u>Equus burchelli</u> Gray
Thomson's gazelle	<u>Gazella thomsoni</u> Gunther
Grant's gazelle	<u>Gazella granti</u> Brooke
Ostrich	<u>Struthio camelus</u> L.
Warthog	<u>Phacochoerus aethiopicus</u> Pallas
Waterbuck	<u>Kobus ellipsiprymnus thikae</u> Matschie
Eland	<u>Taurotragus oryx pattersonianus</u> Lyuekker
Impala	<u>Aepyceros m-lampus</u> Lichtenstein
Giraffe	<u>Giraffa camelopardalis tippelskirchi</u> Matschie
Mountain kudu	<u>Redunca fulvorufula</u> (Afzelius)
Chanler's kudu	<u>Redunca fulvorufula chanleri</u> (W. Rothschild)
Rhinoceros	<u>Diceros bicornis bicornis</u> (L.)
Klipspringer	<u>Oreotragus oreotragus schillingsi</u> Neumann
Steinbuck	<u>Rhaphiceros campestris neumanni</u> (Matschie)
Buffalo	<u>Syncerus caffer</u> Sparrman
Topi	<u>Damaliscus lunatus topi</u> Blaine
Sheep	<u>Ovis aries</u> (L.)
Goat	<u>Capra hircus</u> (L.)
Cow	<u>Bos taurus</u> (L.) <u>Bos indicus</u>
Red kangaroo	<u>Macropus rufus</u> (Desmarest)
Grey kangaroo	<u>Macropus giganteus</u> Shaw
Euro	<u>Macropus robustus</u> (Fould)
Aardvaark	<u>Orycteropus afer</u> Pallas
Lion	<u>Panthera leo massaica</u> (Newmann)
Cheetah	<u>Acynonix jubatus</u> Scheber
Silver-backed jackal	<u>Canis mesomelas</u> Scheber
Side-striped jackal	<u>Canis adustus</u> Sundevall
Donkey	<u>Equus hemionus</u>
Blesbok	<u>Damaliscus dorcus phillipsi</u> Harper
White-tailed deer	<u>Odocoileus virginianus</u> Zimmermann
Black-tailed deer	<u>O. hemionus columbianus</u> (Richardson)
Oryx	<u>Oryx beisa beisa</u> (Rüppell)
Caribou	<u>Rangifer tarandus granti</u>
Reindeer	<u>R. tarandus</u> subsp.
Red deer	<u>Cervus elephas</u> L.
Camel	<u>Camelus dromedarius</u>

Appendix 2. The mean adult body weights used for calculation of biomass.

Species	Mean adult weight, kg.	Source
Wildebeest	218	Ledger (1968)
Zebra	238	Foster and Coe (1968)
Hartebeest	121	This study
Thomson's gazelle	21	Ledger (loc. cit.)
Grant's gazelle	50	Ledger (loc. cit.)
Warthog	50	Clough (1969)
Impala	50	Ledger (loc. cit.)
Ostrich	114	Austin and Singer (1961)
Waterbuck	209	Ledger (loc. cit.)
Eland	363	Foster and Coe (loc. cit.)
Giraffe	786	Average from Foster and Coe (loc. cit.) and Stewart and Zaphiro (1963)
Sheep/goat	16	Western (1973)
Cow	277	Foster and Coe (1968)

Appendix 3 . The monthly rainfall (mm) at 11 stations around the Athi Plains, and monthly evapotranspiration (E_t) mm, at Wilson and Embakasi.

	1970				1971							
Station	O	N	D	J	F	M	A	M	J	J	A	S
Wilson	46.6	69.0	30.5	64.0	1.2	14.0	285.3	335.7	12.7	8.0	20.4	20.6
Embakasi	29.2	34.0	21.0	33.9	1.6	5.1	270.6	165.0	12.0	8.1	38.1	11.7
Karen	23.6	51.3	18.8	90.6	11.9	7.6	242.5	306.1	19.0	9.2	59.4	39.6
Ngong	24.7	32.5	21.1	29.8	19.1	3.8	150.3	268.1	17.7	19.8	39.9	16.5
Mbagathi	29.1	67.9	38.6	49.6	7.8	5.1	252.9	270.8	14.3	5.6	24.9	41.4
Oloosseos	-	-	-	23.2	2.0	0.4	48.3	42.7	2.0	1.3	2.7	3.6
Kenplains	-	-	-	119.4	0	0	133.1	166.6	0	0	27.9	14.0
Stony Athi	8.4	5.3	22.6	85.8	0	7.4	161.8	85.3	0	0	8.4	0
Senya	13.0	25.8	0	4.1	0	0	34.3	18.8	5.7	0	0	8.9
Kajiado	0	9.4	5.0	59.7	0	7.9	107.4	104.7	0	0	9.2	0
Konza	15.7	26.4	39.6	18.0	0	4.3	191.2	77.3	8.0	0	0	0
E_t mm/month												
Embakasi	130	122	130	149	149	155	125	110	98	92	94	107
Wilson	114	112	130	137	145	140	100	95	94	86	93	107

Appendix 3. (Continued)

Total altitude,

		1971										1972										Oct-	
	J	O	N	D	J	F	M	A	N	J	J	A	S	O	N	Sept.	m						
Wilson		17.8	36.6	119.8	9.9	71.2	39.8	10.9	116.7	137.0	24.5	4.1	82.2	204.4	112.0	670.5	1976						
Embakasi		2.6	26.5	163.2	11.9	53.1	28.0	0.7	80.1	120.6	8.6	2.4	54.7	161.5	97.6	552.4	1903						
Karen		11.0	41.8	162.0	4.8	119.6	42.4	13.8	63.0	106.9	4.9	1.6	32.6	175.7	105.4	604.4	2196						
Ngong		11.4	26.5	124.1	0	96.6	72.6	5.1	191.5	147.4	4.9	0	36.0	118.1	113.5	716.1	2269						
Mbagathi		8.6	25.0	198.7	6.9	113.1	54.4	21.3	163.7	138.8	5.8	0	36.1	196.0	75.9	772.4	2122						
Oloossecs		3.4	31.9	172.3	3.5	88.9	103.4	1.5	146.9	83.3	3.1	0	35.9	58.2	106.0	674.1	2342						
Bl.22		4.5	15.0	162.0	3.0	125.0	65.0	86.0	128.5	80.0	4.5	2.5	43.0	51.5	63.0	719.0	2269						
Bl.16		115.	31.5	198.7	3.0	56.0	126.0	27.0	121.0	129.5	2.5	0	22.0	60.5	77.0	728.7	2122						
Bl.30		-	-	-	-	-	16.5	15.0	88.5	59.5	0	0	2.5	28.5	67.0	-	1903						
Athi		0	52.0	165.0	18.0	43.5	30.0	0	65.5	48.0	0	0	13.0	20.0	188.0	435.0	1830						
Kenplains		0	63.0	104.0	30.0	56.0	22.5	0	52.0	31.5	0	0	6.0	90.0	-	365.0	1903						
Stony Athi		0	83.7	30.5	0	69.7	9.9	0	56.4	69.1	0	0	12.2	64.0	46.7	331.5	1903						
Ol Doroto		4.0	48.0	106.5	0	63.0	97.5	2.0	48.0	12.0	0	0	7.5	56.0	64.0	388.5	1903						
Senya		10.4	33.3	217.4	11.8	95.2	68.3	55.8	102.5	50.0	0	0	9.3	40.0	47.9	654.0	1976						
Bl.39		7.0	36.5	217.4	7.5	96.5	79.0	0	111.0	4.5	0	0	0	22.0	29.0	459.4	2049						
Kajiado		2.0	30.2	190.9	27.4	153.9	25.3	0	51.9	50.4	0	0	24.7	42.7	49.1	556.7	2049						
Bl. 62		0	31.0	1106.5	9.5	63.0	84.0	1.0	54.5	13.0	0	0	69.0	71.0	93.0	431.5	1903						
Konza		0	27.7	193.8	9.0	2.2	110.0	0	81.0	31.0	0	0	3.0	85.0	56.5	457.7	1976						

Appendix 4 . Glossary of plant species in the text.

Acacia drepanolobium Harms ex Sjostadt
Aspilia mossambicense (Oliv.) Wild
Nesaea lythroides Welw. ex Hiern.
Becium obovatum N.E. Brown
Hibiscus flavifolius Ulbr.
Grewia similis K. Schum
Sericocomopsis hildebrandtii Schinz.
Lippia javanica (Burm f.) Spring
Omocarpum trichocarpum Taub.
Orthosiphon parvifolius Vatke
Senecio discifolius Oliv.
Balanites aegyptiaca De
Conyza aegyptiaca Ait.
Acacia xanthophloea Benth.
Acacia kirkii Oliv.
Solanum incanum L.
Akocanthera friesiorum Markgr.
Acacia gerrardii Benth.
Croton megalocarpus Hutch.
Brachylaena hutchinsii Hutch.
Calodendron capense Thunb.
Diospyros abyssinica (Hiern) F. White
Rhamphicarpa montana N.E. Br.
Acacia stuhlmannii Taub.
Hyparrhenia lintonii Stapf.
Cymbopogon poschipilii Hubbard
Eragrostis tenuifolia (A. Rich.) Steud
Sporobolus pyramidalis Beauv.
Harpachne schimperi A. Rich.
Themeda triandra Forsk.
Setaria phleoides Stapf.
Ischaemum afrum (J.F. Gmel.) Dandy
Microchloa kunthii Desv
Aristida adoensis A. Rich
Digitaria macroblephara (Hack.) Stapf
Panicum poaeoides Stapf
Rhynchosyris repens (Willd.) C.E. Hubb.
Pennisetum stramineum Peter
Eustachys paspaloides (Vahl) Lanza & Mattei
Bothriochloa insculpta (A. Rich) A. Camus
Brachiaria serrata (Spreng.) Stapf
Cynodon dactylon (L.) Pers
Pennisetum mezianum Leeke

Appendix 5. The numbers of each species counted in each block in the Athi Plains in each season, and the numbers in all blocks and the Nairobi Park study areas.

W = Wet season
M = Medium - wet season
D = Dry season

Species	Season	Block 15	Block 22	Block 30	Block 35	Block 39	Block 62	Plains = 15+22+30+35+39	Park study area
Cattle	W	758	780	713	1,596	1,401	12	5,260	
	M	369	317	1,012	233	496	307	2,734	
	D	537	499	777	1,334	3,410	199	6,756	
		1,664	1,596	2,502	3,163	5,307	518	14,750	0
Wildebeest	W	23	48	142	223	717	279	1,432	730
	M	26	114	7	7	308	551	1,013	351
	D	1,330	71	11	0	37	0	1,449	2,097
		1,379	233	160	230	1,062	830	3,894	3,178
Zebra	W	55	20	191	124	56	156	602	751
	M	448	27	44	7	0	102	628	193
	D	483	94	117	0	0	10	704	2,563
		986	141	352	131	56	268	1,934	3,507
Thomson's Gazelle	W	0	47	62	6	155	68	338	479
	M	9	57	29	5	181	121	402	223
	D	5	45	3	11	65	91	220	593
		14	149	94	22	401	280	960	1,295

Appendix 5 continued.

Species	Season	Block 15	Block 22	Block 30	Block 35	Block 39	Block 62	Plains = 15+22+30+35+39	Park study area
Grant's Gazelle	W	11	21	192	89	123	72	508	559
	M	31	137	73	73	128	134	576	327
	D	22	64	105	60	75	31	357	617
Hartebeest		64	222	370	222	326	237	1,441	1,503
	W	310	132	124	250	559	24	1,399	2,135
	M D	260 663	227 138	100 70	200 41	530 164	35 2	1,352 1,078	1,198 3,799
Sheep & Goats		1,233	497	294	491	1,253	61	3,829	7,132
	W	0	404	758	0	80	262	1,504	
	M D	0 0	518 237	240 440	0 449	100 50	501 570	1,359 1,746	
Impala		0	1,159	1,438	449	230	1,333	4,609	0
	W	0	40				3	43	329
	M D	30 0	43 0				0 24	73 24	86 526
Warthog		30	83	0	0	0	27	140	936
	W								115
	M D								100 185
		0	0	0	0	0	0	0	400

Appendix 5 continued.

Species	Season	Block 15	Block 22	Block 30	Block 35	Block 39	Block 62	Plains = 15+22+30+35+39	Park study area
Waterbuck	W	1						1	94
	M	1						1	15
	D	0						0	127
		2	0	0	0	0	0	2	236
	W	11	1	20	25	31	7	95	200
	M	19	5	19	25	18	33	119	104
Ostrich	D	17	0	12	15	12	9	65	259
		47	6	51	65	61	49	279	563
Eland	W	3	0		116	29	1	149	100
	M	1	0		0	168	0	169	26
	D	1	1		0	0	0	2	128
		5	1	0	116	197	1	320	254
	W	18	10				0	28	42
	M	32	0				0	32	4
Giraffe	D	1	0				5	6	16
		51	10	0	0	0	5	66	62

32,224 : total of all spp. in all months.

Appendix 6. Monthly total of each species counted in the Nairobi Park study area.

Month Species	1971		1972		Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Total
	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec	Total
Wildebeest	142	120	146	205	130	158	200	178	233	248	841	586			3,187
Zebra	296	21	130	63	5	68	15	104	611	755	1,127	312			3,507
Thomson's Gazelle	93	67	108	115	91	47	113	152	147	77	137	148			1,295
Grant's Gazelle	71	100	154	173	98	58	167	146	146	99	164	128			1,504
Hartebeest	457	417	551	654	498	605	576	597	545	571	1,086	586			7,143
Impala	68	137	68	41	125	59	82	72	33	104	89	81			959
Warthog	21	44	39	61	30	34	18	25	28	20	60	23			403
Waterbuck	10	28	15	0	22	27	12	22	32	22	18	28			236
Giraffe	3	11	0	4	1	1	7	17	7	0	1	10			62
Eland	7	16	18	8	2	8	6	41	37	62	29	20			254
Ostrich	36	88	15	53	19	16	32	45	35	43	53	92			527
Total	1,204	1,049	1,244	1,377	1,021	1,081	1,228	1,399	1,854	2,001	3,605	2,014			19,077

Appendix 7. The number of each species in vegetation types of Nairobi Park study area in each season, with the total and mean numbers seen each month.

		Nos. in Vegetation Type														
Species	Season	01	02	03	04	05	06	07	08	09	10	11	12	13	Total	Mean No. /Month
Wildebeest	Wet	177	3	85	123	3	69	0	1	0	1	0	0	0	730	182.5
	Medium	219	21	0	32	37	1	0	11	0	0	0	0	0	351	175.5
	Dry ⁽¹⁾	350	310	150	644	305	24	11	0	0	17	0	0	0	2097	349.5
	Dry ⁽²⁾	116	13	53	241	54	20	0	0	0	14	0	0	0	667	
Zebra	W	0	8	156	76	0	370	0	0	15	50	0	0	0	751	187.7
	M	11	16	0	74	69	19	0	0	0	0	0	0	0	193	96.5
	D	108	618	313	505	225	167	44	10	26	417	0	3	0	2563	427.2
Thomson's Gazelle	W	246	3	1	33	15	4	0	0	0	0	0	4	0	479	119.7
	M	153	11	1	27	19	0	0	0	0	0	0	0	0	223	111.5
	D	186	121	13	216	25	4	0	0	0	0	0	4	0	593	98.8
Grant's Gazelle	W	149	24	10	73	34	127	0	1	3	2	0	3	0	559	139.7
	M	165	38	0	64	36	13	0	0	0	0	0	0	0	327	163.5
	D	85	171	42	114	71	49	3	2	0	25	0	1	0	617	102.8

		Nos. in Vegetation Type															
Species	Season	01	02	03	04	05	06	07	08	09	10	35	11	12	13	Total	Mean Nc /Month
Hartebeest	W	139	106	91	49	103	1061	9	4	1	110	439	0	23	0	2135	533.7
	M	196	183	0	299	393	25	2	2	0	32	36	0	30	0	1198	599.0
	D	246	1192	399	865	569	190	90	55	7	214	91	0	29	32	3799	633.2
Impala	W	2	191	0	32	40	0	13	0	0	0	46	0	0	0	324	81.0
	M	1	59	0	0	7	0	0	0	0	0	19	0	0	0	86	43.0
	D	17	430	0	33	29	0	0	17	0	0	0	0	0	0	526	87.7
Warthog	W	22	3	20	10	23	7	1	1	5	5	18	0	0	0	115	28.7
	M	34	9	0	23	17	4	0	0	0	4	9	0	0	0	100	50.0
	D	62	19	11	62	6	3	0	0	2	5	15	0	0	0	185	30.8
Waterbuck	W	4	41	0	1	23	0	15	0	0	0	9	0	0	0	94	23.5
	M	0	0	0	0	9	0	6	0	0	0	0	0	0	0	15	7.5
	D	0	108	0	4	0	0	15	0	0	0	0	0	0	0	127	21.2
Ostrich	W	36	12	0	56	20	44	0	1	1	11	19	0	0	0	200	50.0
	M	28	8	0	9	8	7	0	0	0	26	17	0	1	0	104	52.0
	D	63	21	16	77	8	10	0	0	0	16	48	0	0	0	259	43.2

Appendix 7 continued.

		Nos. in Vegetation Type															
Species	Season	01	02	03	04	05	06	07	08	09	10	35	11	12	13	Total	Mean N /Month
Eland	W	0	9	16	12	3	39	0	0	0	1	20	0	0	0	100	25.0
	M	0	7	0	4	2	2	0	0	0	1	7	3	0	0	25	13.0
	D	3	111	0	3	3	0	1	0	0	0	0	0	0	0	128	21.3
Giraffe	W	0	6	0	0	5	4	0	0	0	25	2	0	0	0	42	10.5
	M	0	0	0	0	2	0	0	0	0	2	0	0	0	0	4	2.0
	D	0	3	0	0	0	0	0	0	0	13	0	0	0	0	16	2.7

Appendix 8. Seasonal distributions of herbivores between Athi Plains vegetation types.

Total 1 = Nos. in each vegetation type in all seasons.
 Total 2 = Nos. of each species in all vegetation types.

Species	Season	2	3	4	6	10	14	15	17	18	19	20	22	23	26	27	28	30	31	34	Total 2
Cow	Wet		188		181	389	731	513	0	12		667	274	506	320	276	1203	0			5260
	Medium		369		0	0	223	273	163	144		1012	281	36	233	0	0	0			2734
	Dry		0		0	537	1008	558	0	199		627	263	236	748	285	1894	400			6756
	Total 1	0	557	0	181	926	1962	1344	163	355	0	2306	818	778	1301	562	3097	400	0	0	14750
Wildebeest	W		7		0	16	197	184	101	178	0	44	48	0	114	31	469	23	0	20	1432
	M		24		0	2	136	68	292	229	30	9	113	1	2	3	55	34		0	998
	D		338		115	877	10	15	0	0	0	7	71	0	0	0	13	3		0	1449
	Total 1	0	369	0	115	895	343	267	393	407	30	60	232	1	116	34	537	60	0	20	3879
Zebra	W		2		0	53		26	80	76	0	117	20	0	91	0	118	19		0	602
	M		183		0	265		0	65	21	16	34	10	17	10	7	0	0		0	628
	D		11		65	407		0	10	0	0	44	94	0	54	0	19	0		0	704
	Total 1	0	196	0	65	725	0	26	155	97	16	195	124	17	155	7	137	19	0	0	1934
Thomson's Gazelle	W		0		0		115	24	62	6	0	46	29	18		0	31	7	0	0	338
	M		4		5		147	15	116	5	0	33	47	10		0	19	0	0	0	401
	D		2		3		29	8	63	18	10	13	34	11		1	20	0	4	4	220
	Total 1	0	6	0	8	0	291	47	241	29	10	92	110	39	0	1	70	7	4	4	959
Grant's Gazelle	W		11		0	0	17	20	10	62	0	2	10	11	108	13	124	41	0	0	429
	M		9		4	18	20	48	52	81	1	51	68	69	40	37	79	14	0	0	591
	D		1		2	19	2	17	4	27	0	12	37	27	55	19	125	13	3	7	370
	Total 1	0	21	0	6	37	39	85	66	170	1	65	115	107	203	69	328	68	3	7	1390
Hartebeest	W		210		26	71	190	204	4	20	0	50	126	6	132	12	253	80	10	2	1396
	M		109		51	100	86	159	13	11	11	60	201	26	160	77	293	21	0	0	1378
	D		49		318	296	7	32	1	1	0	51	110	28	29	16	53	74	1	12	1078
	Total 1	0	368	0	395	467	283	395	18	32	11	161	437	60	321	105	599	175	11	14	3852
Impala	W		0						0	3			21	19							43
	M		30						0	0			43	0							73
	D		0						24	0			0	0							24
	Total 1	0	30	0	0	0	0	0	24	3	0	0	64	19	0	0	0	0	0	0	140

Appendix 8 continued.

Species	Season	2	3	4	6	10	14	15	17	18	19	20	22	23	26	27	28	30	31	34	Total
Waterbuck	Wet		0	1																	1
	Medium		1	0																	1
	Dry		0	0																	0
	Total 1		1	1																	2
Ostrich	W		4	1	6	0	8	7	3	4		0	1		23	0	31	3	0	4	95
	M		6		7	6	9	0	6	27		4	5		35	0	5	9	0	0	119
	D		8		0	9	0	0	6	3		2	0		13	8	13	0	3	0	65
	Total 1	0	18	0	13	15	17	7	15	34	0	6	6	0	71	8	49	12	3	4	279
Eland	W	0	3		0			29	1				0	0	116		0	0			149
	M	1	0		0			0	0				0	0	0		62	106			169
	D	0	3		1			0	0				1	1	0		0	0			6
	Total 1	1	6	0	1	0	0	29	1	0	0	0	1	1	116	0	62	106	0	0	324
Giraffe	W				16	2				0			10								28
	M				12	20				0			0								32
	D				0	1				5			0								6
	Total 1	0	0	0	28	23	0	0	0	5	0	0	10	0	0	0	0	0	0	0	66
Sheep and Goats	W									262		30	0	404	0		808				1504
	M									501		240	403	115	0		0				1259
	D									570		440	0	237	449		50				1746
	Total 1	0	0	0	0	0	0	0	0	1333	0	710	403	756	449	0	858	0	0	0	4509

Appendix 9. The seasonal and overall distributions of each species in Nairobi Park broken down by standing crop of grass (categories 1 - 9), kg/ha, with the percentage coverage of each category.

W = Wet season; M = Medium wet season; D = Dry season; = No. in each category in all seasons;
Total = Total no. of each species in each season.

Standing crop kg/ha	Species	Season	0- 400	400- 800	800- 1200	1200- 1600	1600- 2000	2000- 2400	2400- 2800	2800- 3200	3200	Total
			1	2	3	4	5	6	7	8	9	
Wildebeest	W		0	215	230	119	113	2	1	0	0	680
	M		0	220	0	32	0	3	21	34	0	310
	D		16	504	241	579	454	20	0	156	11	1981
			16	939	471	730	567	25	22	190	11	2971
Zebra	W		0	26	13	134	513	0	0	0	50	736
	M		0	71	0	14	19	42	0	44	0	190
	D		0	108	214	759	408	453	7	410	115	2474
			0	205	227	907	940	495	7	454	165	3400
Thomson's gazelle	W		0	156	152	123	2	10	4	0	0	447
	M		0	156	1	24	0	29	1	0	0	211
	D		44	193	84	155	25	10	0	31	32	574
			44	505	237	302	27	49	5	31	32	1232
Grant's gazelle	W		0	136	129	83	126	20	19	0	2	515
	M		0	200	0	40	2	27	27	20	0	316
	D		44	193	84	155	25	10	0	31	32	574
			44	529	213	278	153	57	46	51	34	1405
Hartebeest	W		0	155	451	290	935	31	121	6	64	2053
	M		0	319	0	181	20	251	146	211	0	1128
	D		24	304	303	1390	653	211	19	336	297	3537
			24	778	754	1861	1608	493	286	553	361	6718
% of area covered	W		0	11.5	22.5	15.8	26.1	5.2	10.6	4.1	4.2	100.0
	M		0	18.0	1.3	21.8	16.6	11.7	18.6	12.0	0	100.0
	D		1.8	13.4	28.9	25.6	5.8	12.3	2.9	5.7	8.6	100.0
	ALL		0.9	13.1	19.3	21.0	15.5	8.2	7.7	6.0	8.3	100.0

Appendix 9 continued.

Standing crop kg/ha		0- 400	400- 800	800- 1200	1200- 1600	1600- 2000	2000- 2400	2400- 2800	2800- 3200	3200		
Species	Season	1	2	3	4	5	6	7	8	9	Total	
Impala	W	0	0	2	284	0	1	24	0	0	311	
	M	0	1	0	0	0	25	38	3	0	67	
	D	0	17	1	280	10	18	0	78	105	509	
		0	18	3	564	10	44	62	81	105	887	
Warthog	W	0	7	39	23	18	7	3	0	0	97	
	M	0	35	0	22	4	12	8	10	0	91	
	D	10	65	26	60	7	6	0	3	2	179	
		10	107	65	105	29	25	11	13	2	367	
Waterbuck	W	0	0	4	15	0	24	26	0	0	69	
	M	0	0	0	0	0	9	0	0	0	9	
	D	0	0	0	67	0	0	0	17	28	112	
		0	0	4	82	0	33	26	17	28	190	
Ostrich	W	0	32	71	8	41	30	11	0	2	195	
	M	0	30	0	7	7	11	19	12	0	86	
	D	10	118	28	62	9	12	0	9	9	257	
		10	180	99	77	57	53	30	21	11	538	
Eland	W	0	15	6	18	48	0	7	0	0	94	
	M	0	0	0	4	2	5	4	1	0	16	
	D	0	3	0	34	6	0	0	23	60	126	
		0	18	6	56	56	5	11	24	60	237	
Giraffe	W	0	0	2	8	7	0	9	15	0	41	
	M	0	0	0	0	0	0	2	2	0	4	
	D	0	0	0	2	0	10	3	1	0	16	
		0	0	2	10	7	10	14	18	0	61	
% of area covered	W	0	11.5	22.5	15.8	26.1	5.2	10.6	4.1	4.2	100.0	
	M	0	18.0	1.3	21.8	16.6	11.7	18.6	12.0	0	100.0	
	D	1.8	13.4	23.9	25.6	5.8	12.3	2.9	5.7	8.6	100.0	
	ALL	0.9	13.1	19.3	21.0	15.5	8.2	7.7	6.0	8.3	100.0	

Appendix 10 . The seasonal and overall distributions of 6 species in the Athi Plains, broken down by standing crop of grass (categories 1-9), kg/ha, with the percentage coverage of each category.
W = Wet season, M = Medium wet season, D = Dry season, = no. in each category in all seasons.
Total = no. of each species in each season.

Standing crop kg/ha		0- 400	400- 800	800- 1200	1200- 1600	1600- 2000	2000- 2400	2400- 2800	2800- 3200	3200	
Species	Sea- son	1	2	3	4	5	6	7	8	9	Total
Wildebeest	W	0	0	48	629	313	0	213	16	113	1332
	M	0	0	10	265	21	34	7	265	0	602
	D	0	75	475	22	877	0	0	0	0	1449
Zebra	W	0	75	533	916	1211	34	220	281	113	3383
	M	0	0	20	110	104	0	143	53	43	473
	D	0	0	10	265	21	34	7	265	0	602
Thomson's gazelle	W	0	123	76	44	407	0	0	0	0	650
	M	0	0	106	419	532	34	150	318	43	1725
	D	0	0	29	217	28	0	64	0	0	338
Grant's gazelle	W	0	0	194	135	9	63	0	0	0	401
	M	0	0	54	50	1	0	0	0	0	202
	D	0	97	277	402	38	63	64	0	0	941
Cattle	W	0	0	10	124	165	0	22	0	76	397
	M	0	0	102	134	83	176	37	18	34	584
	D	0	120	64	83	38	0	0	30	0	335
Hartebeest	W	0	120	176	341	285	176	59	48	110	1316
	M	0	0	274	1575	522	0	1180	389	320	4260
	D	0	0	504	568	144	1285	0	0	233	2734
% of area covered	W	0	713	2852	1620	823	0	0	748	0	5756
	M	0	0	3630	3763	1489	1285	1180	1137	553	13750
	D	0	0	126	392	287	0	250	71	101	1227
ALL	W	0	0	308	199	23	500	77	100	271	1478
	M	0	126	486	112	312	0	0	25	0	1061
	D	0	126	920	703	622	500	327	196	372	3766
	W	0	0	8.8	29.1	25.2	0	12.3	8.6	15.9	100.0
	M	0	0	16.8	16.4	9.3	28.0	5.0	8.6	15.9	100.0
	D	0	26.7	21.0	22.7	13.6	0	0	15.9	0	100.0
ALL		0	8.7	15.0	22.2	15.6	9.0	5.7	13.5	10.3	100.0

Appendix 11 . Matrix of seasonal species' overlaps (R₀) between 14 vegetation types in the Nairobi Park. Decimal points have been omitted from the body of the table. W = Wet season, M = Medium season, D = Dry season.

	W	M	D	Wbst	Zebra	Thom	Grant	Imp	Whog	Wbuck	Ost	Eland	Gir	Hbst
Wildebeest				1.0										
Zebra				658										
	W	M	D	593	1.0									
				836										
Thom.Gaz.				859	314									
	W	M	D	956	600	1.0								
				931	781									
Grants Gaz.				898	668	843								
	W	M	D	906	779	953	1.0							
				931	942	871								
Impala				384	281	405	523							
	W	M	D	529	451	404	527	1.0						
				575	686	563	635							
Warthog				783	623	688	831	516						
	W	M	D	887	827	887	950	507	1.0					
				943	836	952	892	398						
Waterbuck				301	207	396	533	906	581					
	W	M	D	408	568	372	420	321	457	1.0				
				585	717	543	635	892	347					
Ostrich				776	667	669	920	549	799	524				
	W	M	D	763	613	729	764	508	886	354	1.0			
				935	858	804	906	357	965	318				
Eland				789	920	466	837	503	713	428	757			
	W	M	D	647	667	542	664	727	733	326	740	1.0		
				677	771	655	741	965	462	937	424			
Giraffe				278	553	251	447	411	552	467	611	477		
	W	M	D	467	560	441	472	406	679	645	777	565	1.0	
				363	824	255	578	286	409	319	524	329		
Hartebeest				742	855	623	866	536	804	607	822	926	721	1.0
	W	M	D	747	935	779	877	678	946	626	806	760	781	
				870	954	834	961	788	854	793	842	845	724	

Appendix 12 . THE CALCULATION OF CORRECTION FACTORS TO ADJUST THE PROPORTIONS OF FOOD COMPONENTS IN THE RUMEN TO THOSE OF THE DIET AT INTAKE.

A.1. Introduction.

If plant species or their parts are differentially digested in the herbivore gut, the proportions observed in the faeces or stomach are not necessarily those of the ingested food. Stewart (1967) showed that not only did the leaves of a number of different grass species fragment to varying extents when fed to herbivores and retrieved from the faeces, but that the degree of fragmentation of a single species varied with the animal species eating it. Quantitative deductions from faecal frequencies of grasses are therefore limited. He ascribed this fragmentation to differential digestion and remarked that under these circumstances the calculation of correction factors would be a considerable undertaking, requiring much experimentation to obtain empirical results for each herbivore species and each grass. This is obviously impractical under field conditions even if only one herbivore is considered. For the reasons described in Chapter 8, the hartebeest rumen contents were analysed for plant parts rather than species. Because the main grass components of leaf, sheath and stem have characteristic chemical compositions (Gibbs 1947) and digestibilities (Terry and Tilley 1964) which were confirmed by this study (see Results, p.334) there appeared to be a basis for developing methods of adjusting the proportions of parts observed in the rumen to those at intake.

Campling, Freer and Balch (1962) showed that straw particles were retained in the digestive tract for 25-30% longer than hay particles, and that most of this difference was accounted by differences in the period spent in the rumen rather than the hind gut. On the basis that the difference in crude fibre (CF) contents of the hay and straw diets was in the range of values of grasses in the diet of Serengeti buffalo, Sinclair and Gwynne (1972) adjusted the observed proportions of leaf + sheath and stem in the rumen by 1:1.3 to calculate the proportions at intake. This approach

makes several assumptions :

1. That CF is an important determinant of retention time (RT) in the rumen.
2. That changes in RT are directly proportional to, and of equal size as, any changes in CF.
3. That the rumen behaviour of the leaf and sheath portion was the same as that of the hay, which was a mixture of perennial rye-grass and white clover (Campling, Freer and Balch, loc.cit.), and that grass stem behaved like oat straw.

The growing body of information on the physical aspects of rumen functioning and changes in the digesta after feeding (e.g. Evans et al 1973, 1974) encouraged a more refined approach to the problem of deducing the diet from the data obtained from dead animals.

A.2. Factors determining the retention time in the rumen.

The natural diets of ruminants contain large amounts of coarse herbage or roughage. Diets which lack fibrousness have adverse effects on the performance of cows (e.g. Powell 1941), and Glover and Duthie (1958) demonstrate the superior digestive efficiency of ruminants over non-ruminants on high fibre diets. Their fore-stomach is greatly expanded and differentiated into the rumen, reticulum and omasum for the fermentation of the cellulose of roughage diets by bacteria and protozoa (McDonald 1969). Physical breakdown of food particles is achieved largely by rumination, and the amount of time spent per day during eating and ruminating measures the fibrousness of the diet (Balch 1971).

Compared with feeds in temperate countries, sward samples from the Athi Plains would be classed as poor quality hays or straws. When such roughages are fed to ruminants, much of the ingesta floats because of the air caught in the hollow stems, producing a characteristic stratification through the reticulo-rumen (Hungate 1966), referred to subsequently as the

rumen. This layering is opposed by mixing due to the contractions of the ruminal musculature, and by the upward passage of particles with attached bubbles of CO_2 and CH_4 produced by the fermentation processes (Balch and Kelly 1950). As the gas phase equilibrates with the liquid phase, the air trapped in the lighter particles is gradually displaced, allowing them to sink. When all the gas has been lost, the digesta have a specific gravity (SG) which is little higher than that of water or the rumen liquor viz. 1.03 (Balch and Kelly loc.cit.).

Even on a diet of medium-quality pasture hay offered once a day to cows, conditions in the rumen are neither uniform nor constant (Evans et al 1973). The dorsal sac contains a higher proportion of low density particles than high density particles, and the reverse holds for the ventral sac, where the digesta also contain less dry matter because of lower particle concentrations. High density particles are digested faster (Baumgardt 1970) resulting in shorter retention times (RT's). Coarse material is confined to the dorsal sac, and as the particles become smaller ventrally, their sizes become more uniform (Evans et al, loc.cit). This stratification by particle size and density persists but declines through 24 hours on the regime of one meal a day. Maximum concentrations of light, coarse material, producing the lowest density digesta are found in the dorsal sac soon after feeding. Minimum concentrations occur 19.5 - 23.5 hours later.

The same experiments showed a 1:1 relationship between the particle concentrations by size and density, suggesting that in general large particles tend to be of low density and small particles tend to be of high density. Digestion in the rumen therefore involves changes in both, and food particles are retained until small enough to pass through the reticulo-omasal orifice (Freer, Campling and Balch 1962).

Ration density is recognized as a factor in determining the voluntary intake of food by ruminants (Baile and Pfander 1967, Montgomery and

Baumgardt 1965). The retention time of rubber particles in the rumen of cows receiving a hay diet was inversely related to their specific gravity (SG) in the range 1.01 - 1.21, and was directly related to the size of the particles with diameters 4.8, 4.0 and 3.2 mm and SG 1.20 (Campling and Freer 1962). Particles with SG's between 1.02 and 1.06 stayed in the whole gut of all the experimental cows for the same time as stained hay particles.

The lower voluntary intake by cows of straw compared to hay (Campling, Freer and Balch 1961) was associated with longer RT's, slower digestion in the rumen and a lower crude fibre (CF) digestibility. The hay diet contained 8.7% crude protein (CP) and the straw 2.9%. Their dry matter portions contained 31.1% and 40.6% CF respectively. In sheep also, the retention time of organic matter (Thornton and Minson 1973) was highly significantly correlated with the organic matter digestibility (OMD) and the fibre and lignin contents. It was not related to the quantity of digesta or organic matter (OM) in the rumen nor with the number of jaw movements made by the animals or the cellulolytic activity in the rumen.

From such studies it is evident that RT in the rumen is determined largely by characteristics of the diet rather than by physiological factors of the animal (Thornton and Minson 1972). This generalisation is not inconsistent with the results of Stewart (1967 and p. 327) where the times of throughput and elimination of food particles were very similar in the wild ruminant species tested, although there were inter-specific differences in the end products of digestion. Among these characteristics, particle SG and digestibility appear important and seemed possible starting points from which to calculate the relative RT's of the components of the hartebeest diet. Their relative rates of passage ($1/RT$) could then be used to correct the rumen proportions to those at intake for comparison with sward composition. Particle size is not suitable, for, without fistulated animals, it is impossible to measure the size of the ingested

particles, and nothing can be deduced from the rumen particles when the precise time of ingestion is unknown. On the other hand, measurement of the SG of the diet components allows one to predict their behaviour in the rumen when taken in conjunction with the results of rubber particle experiments (Campling and Freer, loc.cit.). As the tame hartebeest, which were used for other purposes (Chap. 9,10) were not available for measuring RT by experiment, indirect methods such as measuring the rate of excretion of stained particles (Castle 1956, Campling, Freer and Balch 1962) and direct methods such as the total emptying of the rumen (Minson 1966) could not be used.

A.3. Methods

The measurement of specific gravity

The materials on which SG determinations were performed consisted of the leaf, sheath and stem components of the sward samples collected at the same time as the hartebeest of the second series were shot (p.153).

Although absolute measurements of SG were obtained by Evans et al (1973) using a SG bottle, this proved fruitless with the East African samples. The volume of air trapped in the dry samples was large and defeated attempts at accurate filling of the bottle, despite efforts to expel the air by warming the bottle or displacing it with CO₂.

The SG of the sample was eventually determined by pelleting a subsample of about 1 g dry weight. The cylindrical pellet was weighed to 0.0001 g, and its height and diameter were measured with vernier calipers. Each measurement was made at 3 points on the pellet, and their mean used. Differences of more than 2% between the maximum and minimum measurements of height and diameter were exceptional. Four subsamples were taken from the first sample (the September sheath), but only 2 pellets were made from subsequent samples. The volume of each pellet was calculated, and its SG determined from its known weight.

Table A12.1. The measured specific gravity and mean values, moisture content and calculated field S.G.'s of grass components in each month.

Month	Part	Specific gravity		Mean	Moisture content %	Field S.G.
		(i)	(ii)			
January	Leaf	.8896	.8765	.883	34.9	1.19
	Sheath	.8500	.8547	.852		1.15
	Stem	.8240	.8063	.815		1.10
April	Leaf	.9171	.9433	.930	24.3	1.15
	Sheath	-	-	.840*		1.04
	Stem	.8089	.8437	.826		1.03
July	Leaf	.8611	.9155	.888	35.0	1.20
	Sheath	.8221	.8119	.817		1.10
	Stem	.8043	.8513	.828		1.12
September	Leaf	.8890	.8886	.889	13.9	1.01
	Sheath	.8297	.8802	.853		0.97
	Stem	(iii).8901	(iv).8131			
		.8754	.8702	.873		0.99

* value assigned as described on p.

Mean retention time, hours

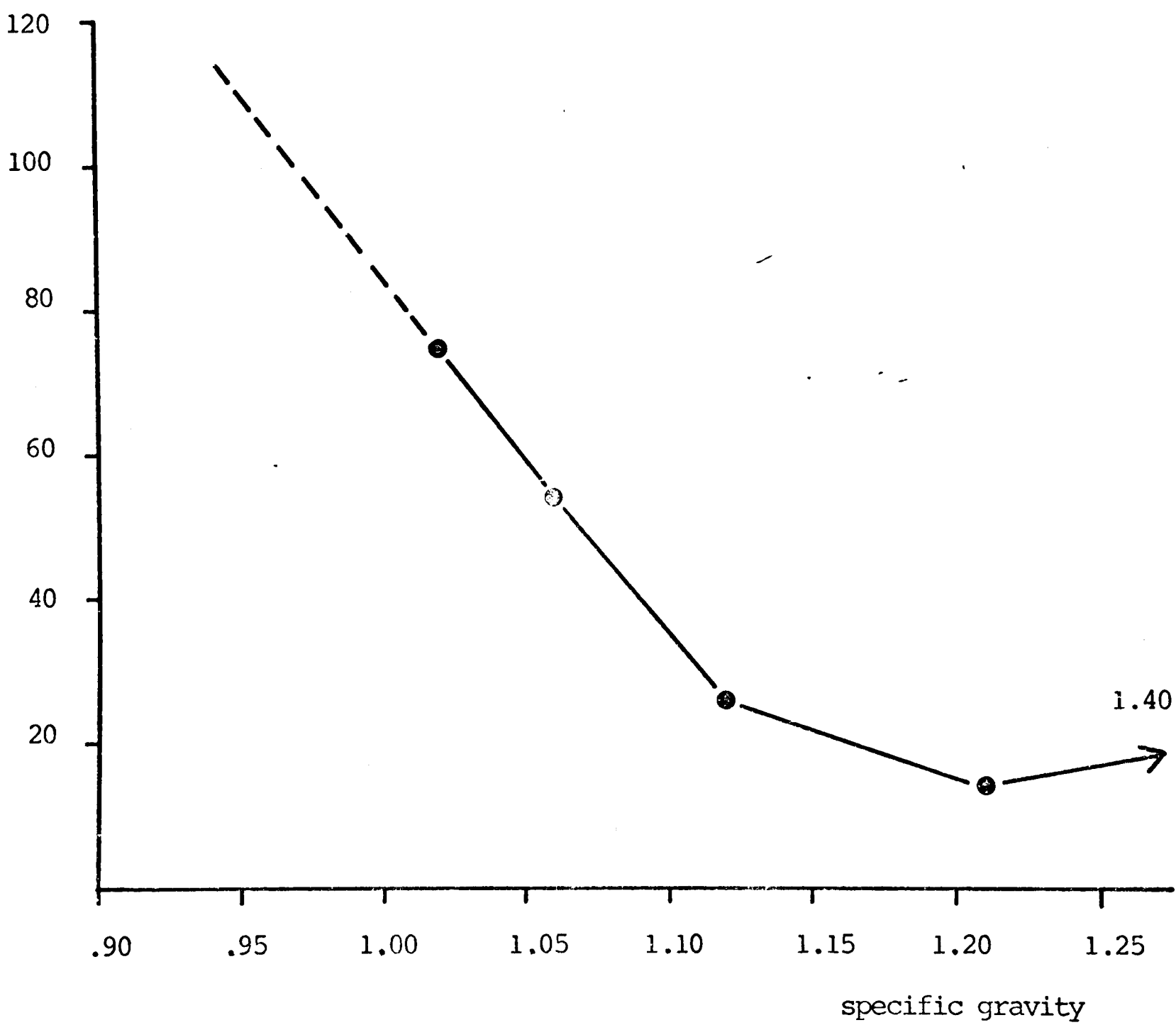


Fig.A12.1. The retention time (hours) of rubber particles of different specific gravities in the rumens of cows, from Campling and Freer (1962)

The volume and, hence, the calculated SG depended on the degree of compaction of the sample during pelleting. Although no torsion spanner was attached to the mill, each sample was compressed to the limit of the strength of the operator who was always myself.

The calculated SG's were those of oven-dried material whose original moisture content in the field was known from the difference between fresh and dry weights (p. 19). These SG's were then multiplied by $(100 + \% \text{ water in sample}) / 100$ to obtain the "field" SG (Table A. 12.1). Because the grass samples were sorted when dry, the moisture percentage is an overall figure. In the absence of any positive information, the water contents of leaf, sheath and stem have been assumed equal.

This method has admitted inaccuracies but it is easy and relatively quick compared to using SG gradient columns for rumen digesta (Evans et al, loc.cit.). Amongst dry methods, grinding and pelleting has the advantage of reducing possible differences in the packing capacity between samples (see Discussion p. 339). It also provides a measure of the food particle SG as they are passed in to the rumen. Measurements on the digesta provide SG's of particles which have been in the rumen for an unknown period.

The results of Campling and Freer (1962) have been used to relate SG and the RT of particles. Their Expt. 2 measured the rate of passage ($1/RT$) of rubber particles through cows receiving a diet containing 83.8% DM which was composed of 8.4% crude protein, 4.2% ether extractives, 33.2% crude fibre, 46.3% N-free extract and 7.9% ash. Of the hay, dried grass and concentrate diets used, this diet had the most similar composition to those of East African grasses (Ch. 14). Their relationship between SG and RT in the rumen is reproduced as Fig.12.1. The lightest particles used had a SG of 1.02, but the graph has been tentatively extended to include the range of lowest SG's measured here. However, calculated RT's for the lighter particles are almost certainly much shorter than would be found by feeding experiments because polyethylene and polypropylene

Table A12.2. The composition of plant parts and random sward samples.

CP = crude protein, CF = crude fibre, OMD = organic matter digestibility.

Month	Part	% CP	% CF	% Ether extract	% Ash	% OMD
January	Leaf	6.2	30.2	1.6	15.7	44
	Sheath	4.3	-	-	14.5	38
	Stem	2.9	41.3	0.5	7.2	17
April	Leaf	6.2	27.3	1.6	15.4	46
	Sheath	4.5*	-	-	-	40*
	Stem	2.9	-	-	6.8	23
July	Leaf	5.7	-	1.5	15.4	43
	Sheath	4.7	-	-	16.0	42
	Stem	2.6	-	-	8.6	37
September	Leaf	3.4	31.9	1.3	16.6	42
	Sheath	3.2	30.9	1.3	18.0	33
	Stem	2.1	43.8	0.7	8.1	19
Sward samples						
	1	4.2	34.7	1.1	14.6	37
	2	6.5	29.3	1.1	13.5	33
	3	4.1	31.9	1.2	16.4	42
	4	4.4	32.0	1.2	16.4	40
	5	4.9	40.0	2.1	12.0	41
	6	8.1	28.6	1.9	12.9	50
	7	5.4	30.5	1.4	16.0	39
	8	2.9	34.9	1.1	14.2	34

* value assigned as described on p.

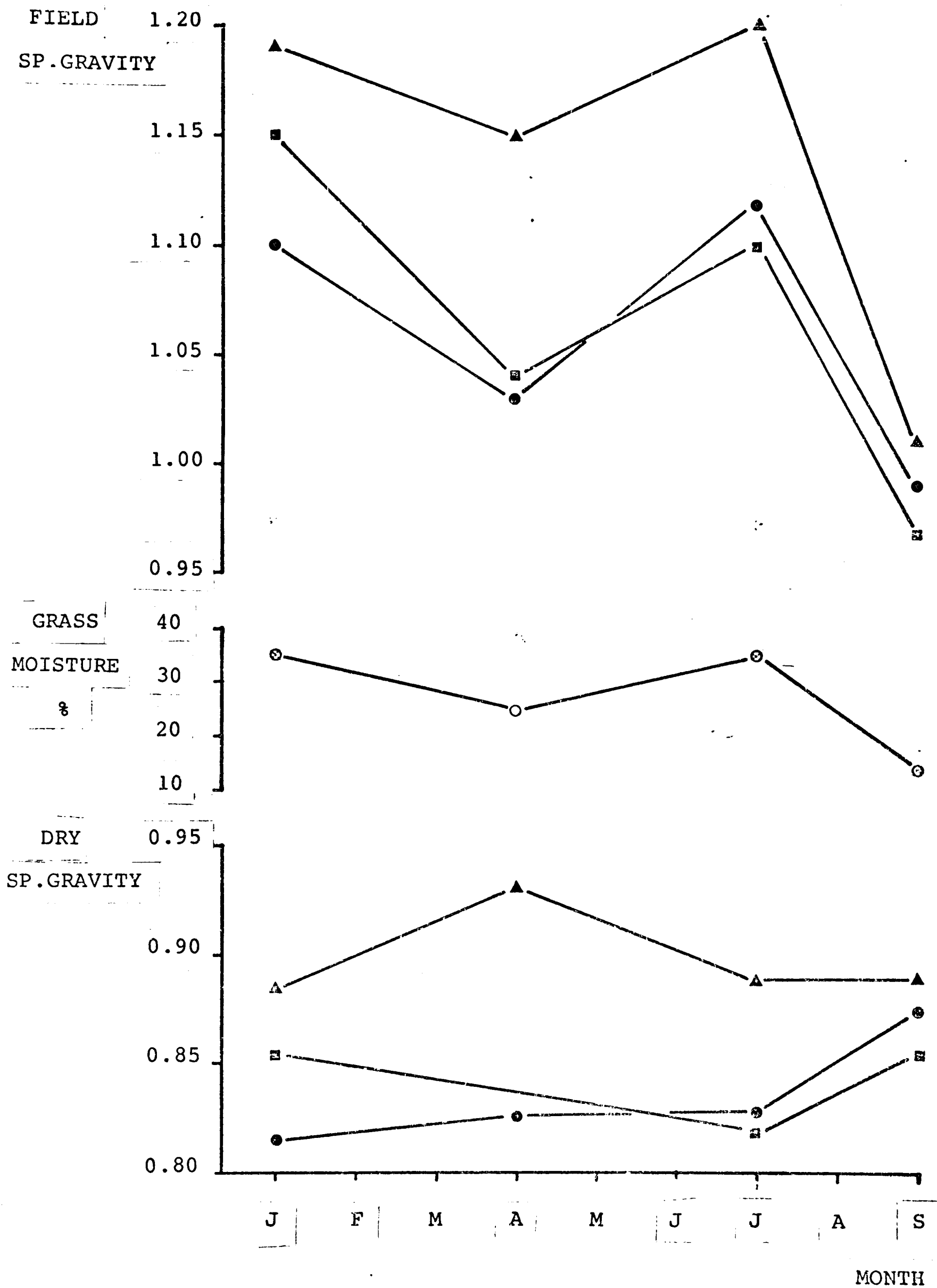


Fig.A12.2. The dry specific gravities of 3 grass components, the moisture content (%) and the calculated field specific gravities in 4 months.

▲ leaf, ■ sheath, ● stem.

particles of SG 1.0 could remain in the rumen for weeks (Campling and Freer, loc.cit.). The rumen liquor of hay-fed cows has a SG of 1.012 (Balch and Kelly 1950).

A.4. The chemical analysis of grass samples, and use of OMD.

A small number of grass samples were analysed by the Agricultural Development Advisory Service (the Ministry of Agriculture, Fisheries and Food) for crude protein (CP), crude fibre (CF), ether extractives (EE) and ash. In vitro determinations of organic matter digestibility (OMD) were also made. The samples consisted of the leaf, sheath and stem components on which the SG measurements were made, and a selection of mixed species samples of whole grass from the Athi Plains and Nairobi Park.

The relationships between these quantities are discussed on p. 334 . The OMD results have been used to calculate the retention time of organic matter (RTOM) from the regression

$$\text{RTOM (h)} = 35.5 - 0.32\text{OMD} \quad (\text{Thornton and Minson 1973})$$

This relationship was developed from sheep and, strictly, is only applicable to them. The calculated RTOM'S are the times for which a diet of known OMD would be retained in the sheep rumen. But, in view of the similarity in rumen function of different species (Glover, Duthie and French 1957) it is reasonable to assume that the relative RTOM's are equally applicable to the hartebeest.

A.5. Results

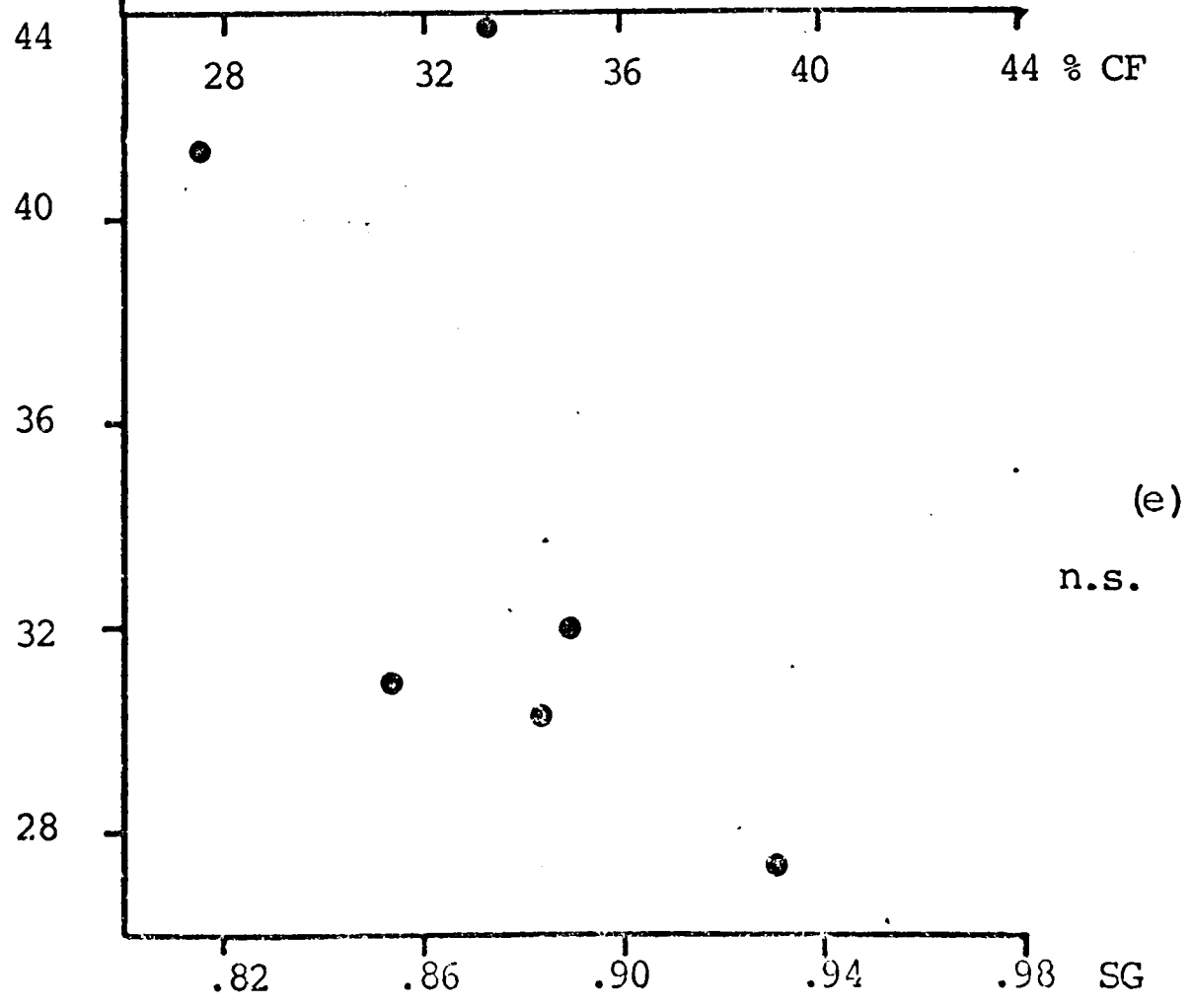
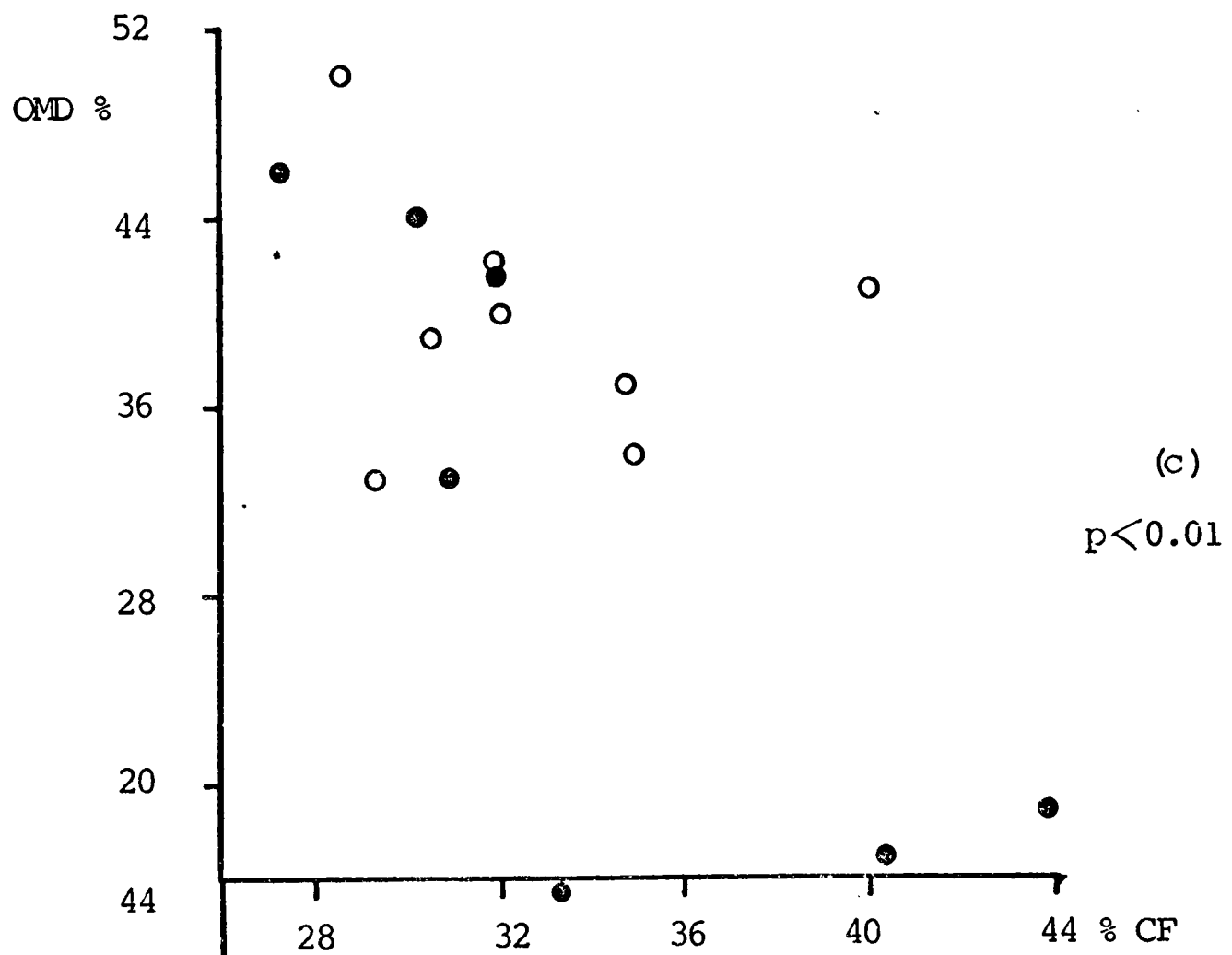
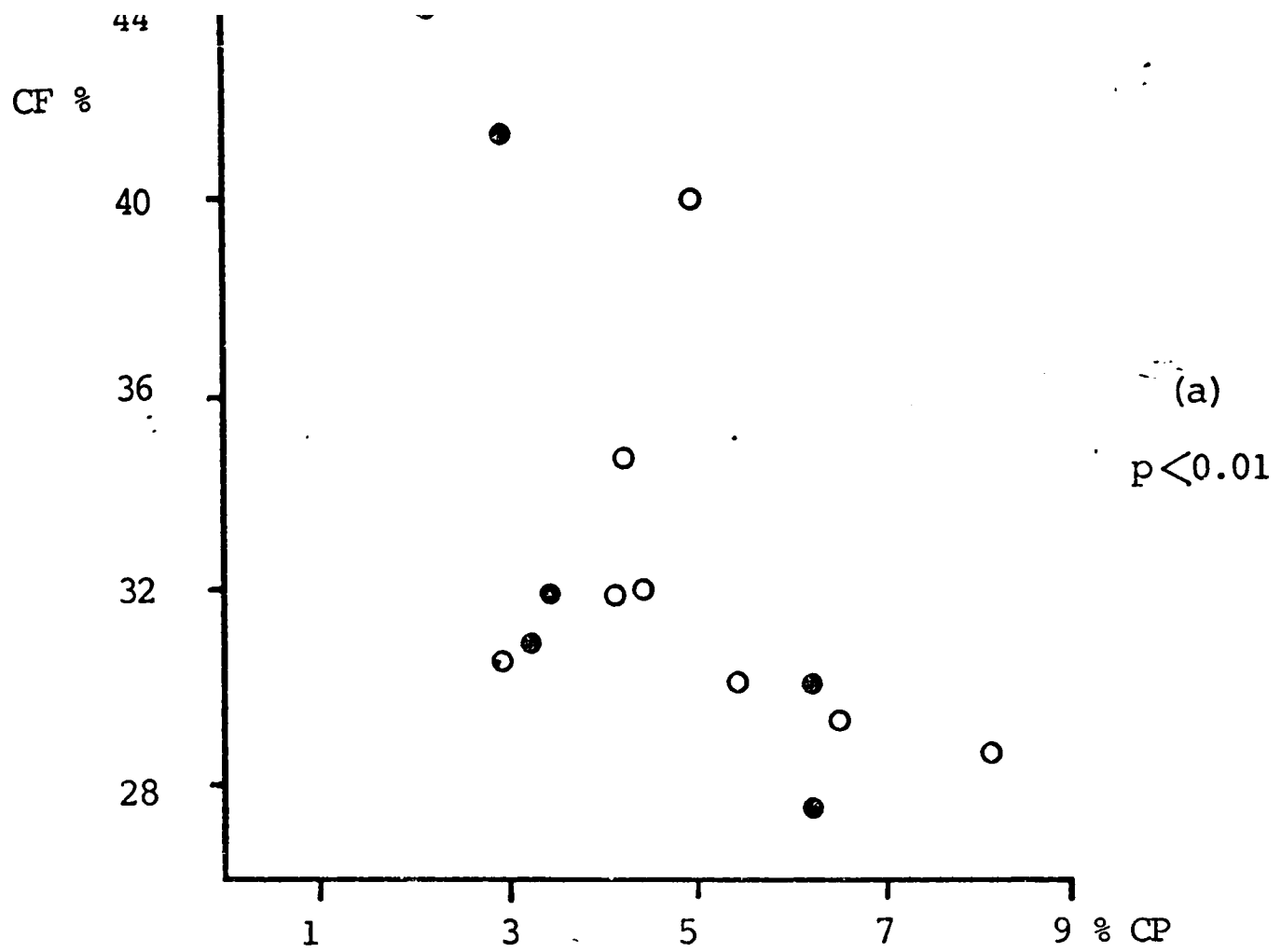
The SG's of the plant components with their measured water contents and the calculated field SG's for each month are presented in Table A 12 .1. There was no sheath sample for April, but it has been assigned a dry SG of 0.840, the value which would be expected by linear interpolation between the measured SG's of January and July.

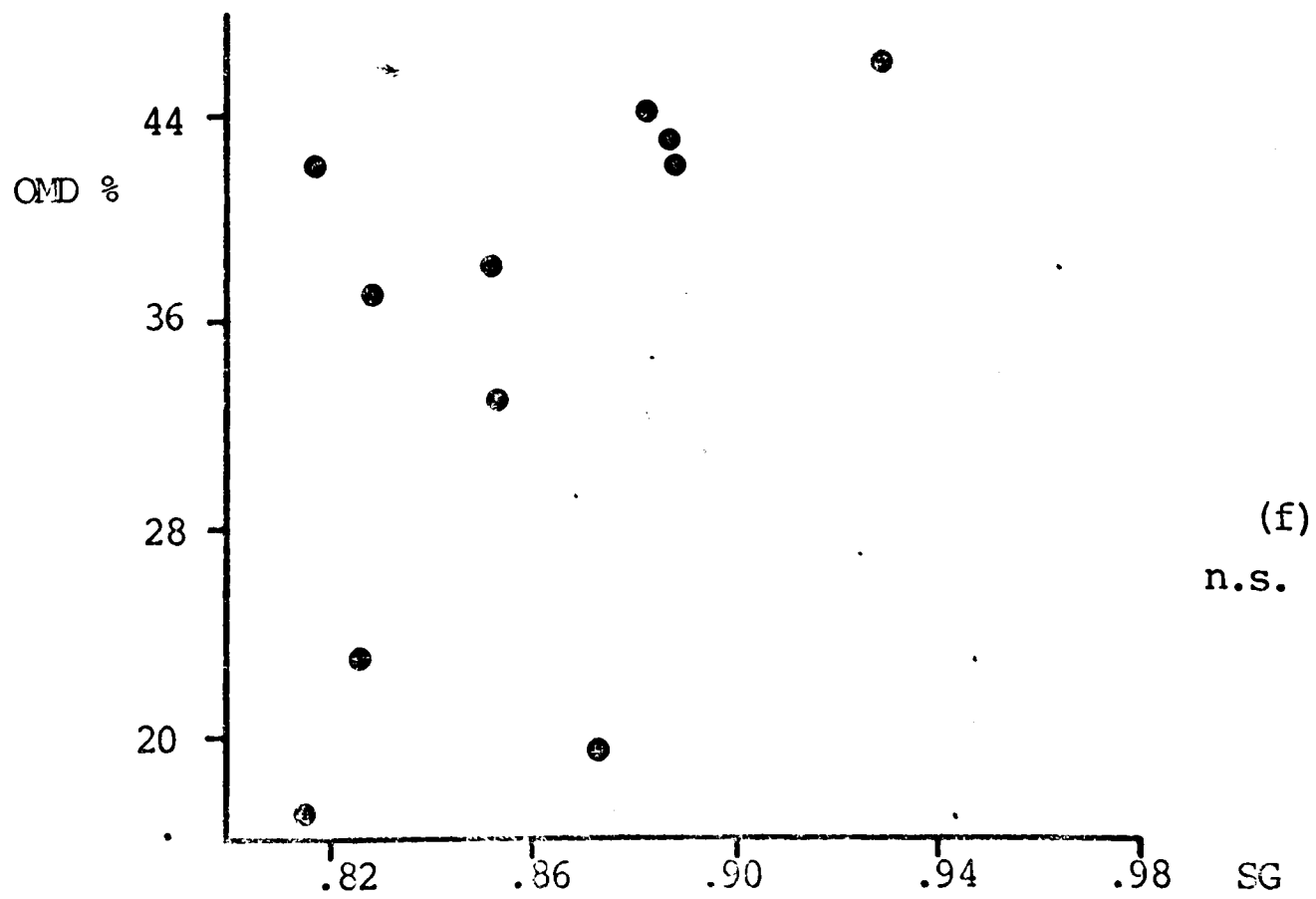
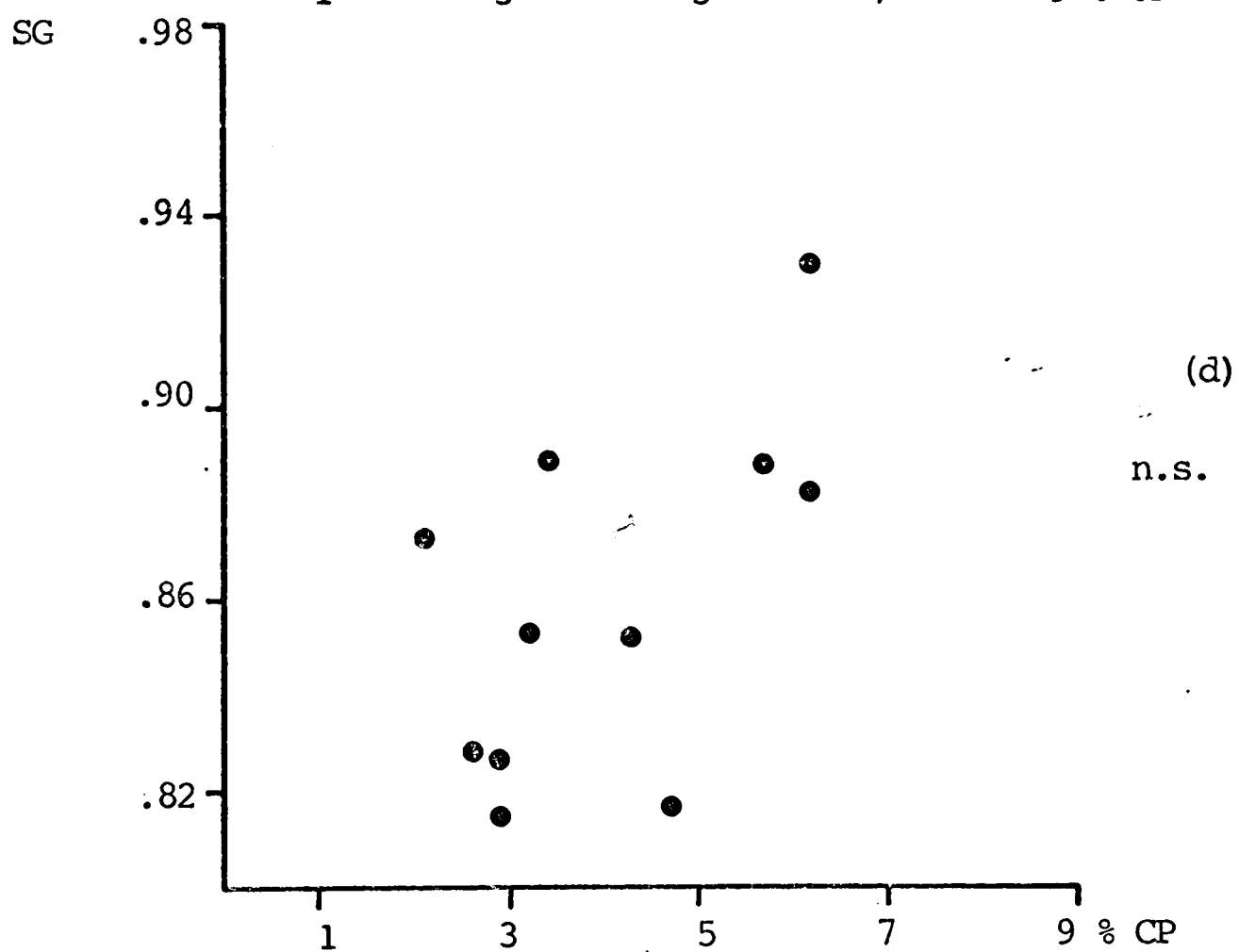
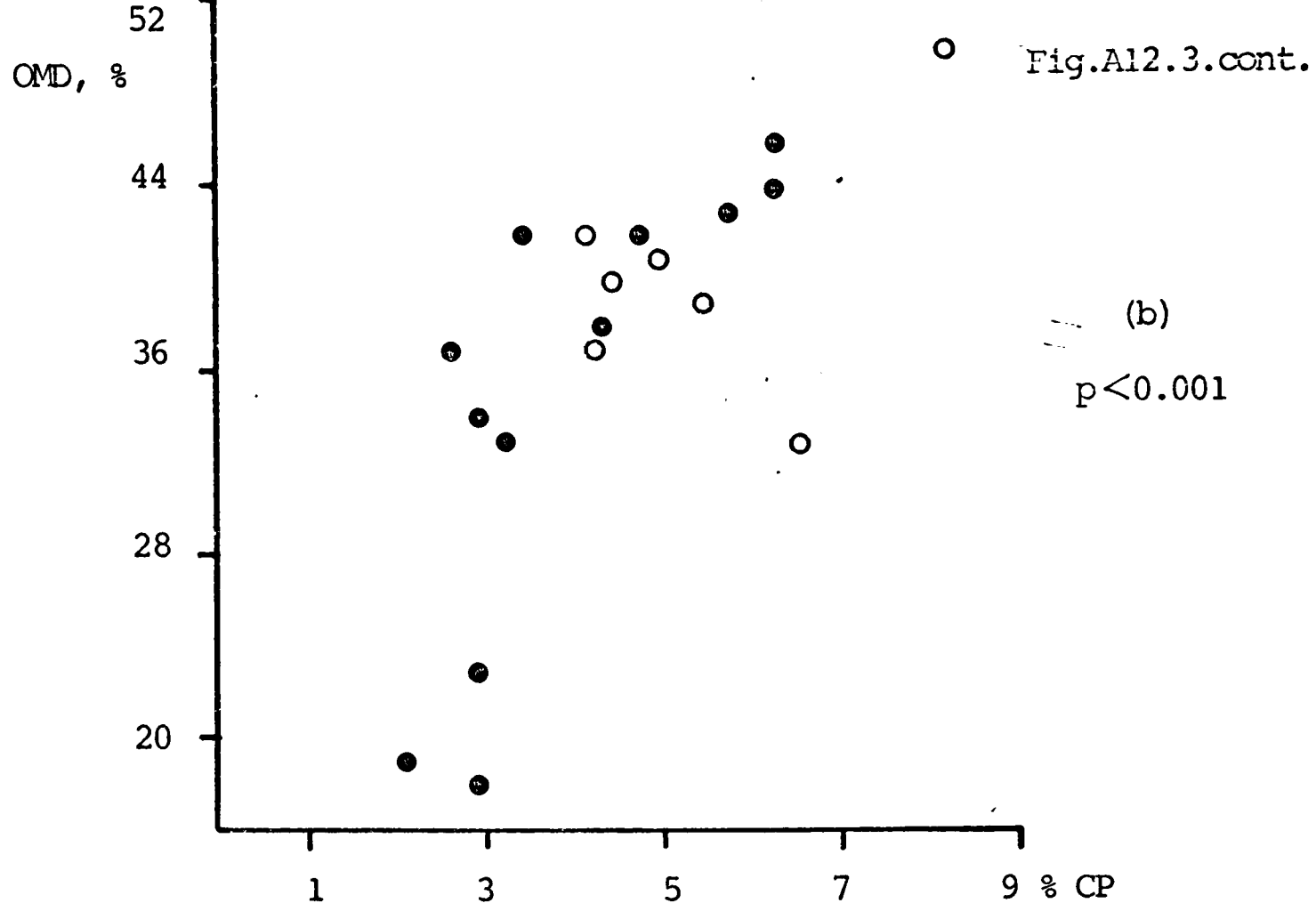
The measured SG's vary little between months (Fig. A 12 .2), although leaf is consistently the most dense component. The sheath and stem values

Fig.A12.3. The correlations between the crude fibre (CF) and crude protein (CP) contents (% dry weight), the in vitro organic matter digestibilities (OMD %) and specific gravities (SG) of grass samples.

- a. CF and CP
- b. OMD and CP
- c. OMD and CF
- d. SG and CP
- e. CF and SG
- f. OMD and SG

- whole grass sample
- grass component sample





increase in the dry season (September), approaching the leaf value. By comparison, the field SG's vary more between months in parallel with the changing moisture content of the sward. This results in the lowest field SG's in the dry season when values for all three components are nearly the same.

The proximate analysis results are shown in Table A 12.2. The small volume of some samples prevented measurement of their CF and/or EE contents. Because of this reduction of sample size, the relationships discussed below include the results of the analyses on samples of whole grasses. These are distinguished in Fig. A12.3. The missing April sheath sample has been given CP and OMD values of 4.5% and 44% respectively by the same method as used above for SG.

Table A12 .2 shows that the CP content of leaf is consistently higher than that of stem, and its CF percentage is lower in the few samples with fibre values. The values for sheath are intermediate. Fig A.12.3a shows that these two quantities are significantly and inversely related ($r = -.686$, $p < .01$, 12 df). They are important determinants of digestibility and Fig. A.12.3b shows the positive relationship between CP and OMD ($r = .702$, $p < .001$, 17 df). The negative relationship between CF and OMD is presented as Fig. A.12.3c ($r = -.756$, $p < .01$, 12 df).

The slight differences in the parts SG's are related to their CP contents (Fig. A 12.3d). Although not significant the relatively dense leaf tends to have a higher CP content than stem ($r = .579$, ns, 9 df). An inverse relationship between SG and CF would, therefore, be expected. This is shown in Fig. A.12.3e, but although the relationship is highly suggestive and the correlation high ($r = -.638$, 4 df), it is not significant because of the shortage of samples with both CF and SG determinations.

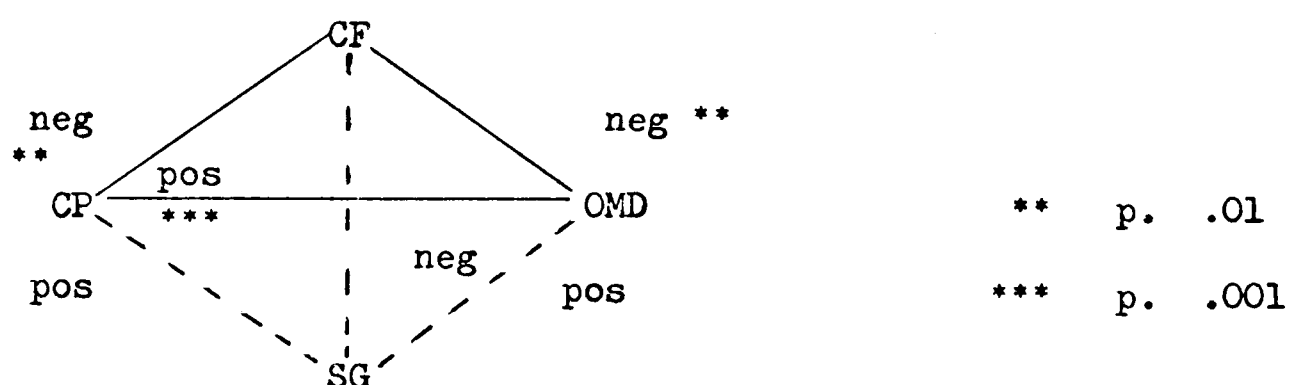
From the relationship between CP and SG, and between CP and OMD, there should be a positive relationship between SG and OMD. Again, this is

Table A12. 3. The specific gravity (SG) and calculated retention time in the rumen of dry matter (RTDM), and the organic matter digestibility (% OMD) and its calculated retention time (RTDM) for grass parts in 4 months.

Month	Part	SG.	RTDM (h)	OMD %	RTOM (h)
January	Leaf	1.19	17	44	21.4
	Sheath	1.15	22	38	23.3
	Stem	1.10	35	17	30.1
April	Leaf	1.15	22	46	20.8
	Sheath	1.04	65	40	22.7
	Stem	1.03	69	23	28.1
July	Leaf	1.20	15	43	21.7
	Sheath	1.10	35	42	22.1
	Stem	1.12	26	37	23.7
September	Leaf	1.01	79	42	22.1
	Sheath	0.97	99	33	24.9
	Stem	0.99	89	19	29.4

strongly suggested by Fig. A.12.3f, but the correlation is not significant ($r = .530$, 9 df).

These relationships are summarised by :



Assuming that the rumen processes described in cattle and sheep above are, for present purposes, identical to those in the hartebeest, I suggest the following interpretation of these relationships, which is consistent with the results of the studies described earlier (p.329). Stem is consistently less dense than leaf, and will therefore predominate in the dorsal sac of the rumen, where the rate of fermentation is lower. The CP content and OMD of stem are lower than those of leaf, so that it will be retained in the rumen for longer. Sheath is intermediate in both.

A.6. The calculation of retention time.

Retention times for the grass parts are taken from the graph relating RT and SG (Fig. A.12.1), and are calculated from the regression with OMD (Fig. A.12.3). Both are shown in Table A.12.3 with the SG and OMD of each component. The RT calculated from SG is strictly that of dry matter (RTOM). Although the mean RTOM is about 25 minutes shorter than the mean RTDM in sheep (Thornton and Minson 1972), they are highly significantly correlated ($r = .99$, $p < 0.001$), and are here treated as equivalent.

The regression method shows that in each month the RTOM of stem is longer than that of sheath, which is longer than that of leaf. Their mean values are 27.8, 23.3 and 21.5 hours respectively, in the ratio 1.29 : 1.08: 1.00. No seasonal trend is apparent in these figures.

The range of RTDM's calculated from SG is much greater. Although the lowest RT's of leaf are almost the same from both methods, the slowest passage time for DM (99 h for sheath in September) is much greater than that for OM (29.4 h for stem in September). In January and April, the RTDM in stem is greater than those of leaf and sheath (as with RTOM), but the positions of sheath and stem are reversed in July and September, reflecting the low SG of the former in these months. The mean RTDM's are 54.7: 58.0: 33.3 h respectively for stem, sheath and leaf, in the ratio 1.65 : 1.74: 1.00. The RTDM values show more variation between months than do those of RTOM, contrasting the seasonal changes in field SG through varying water content with the relative constancy of OMD for each component.

The two RT's calculated for each component by these methods are obviously highly divergent in some cases. Nonetheless, the low RT of stem in July, confirmed by both methods, is interesting in that the increase in its SG since April is paralleled by an increase in its OMD.

A.7. The correction of the rumen proportions to those in the diet.

The method of Sinclair and Gwynne (1972) has been used to correct the rumen proportions to the proportions entering the mouth. The rumen proportion of a component is an overestimate of its occurrence in the diet if it spends longer than average in the rumen, and the opposite is true for a component whose passage is relatively speedy. Therefore, to calculate the ingested proportion of a diet component, the rumen percentage must be corrected by a factor inversely proportional to its retention time:

$$I_a = \frac{R_a}{RT_a} \quad \text{where } I_a = \text{proportion of component a at intake}$$

$$R_a = \text{observed proportion of a in rumen}$$

$$RT_a = \text{retention time of a in rumen}$$

or $R_a = k \cdot I_a \cdot RT_a$ where k is a rate constant. When the proportions of two

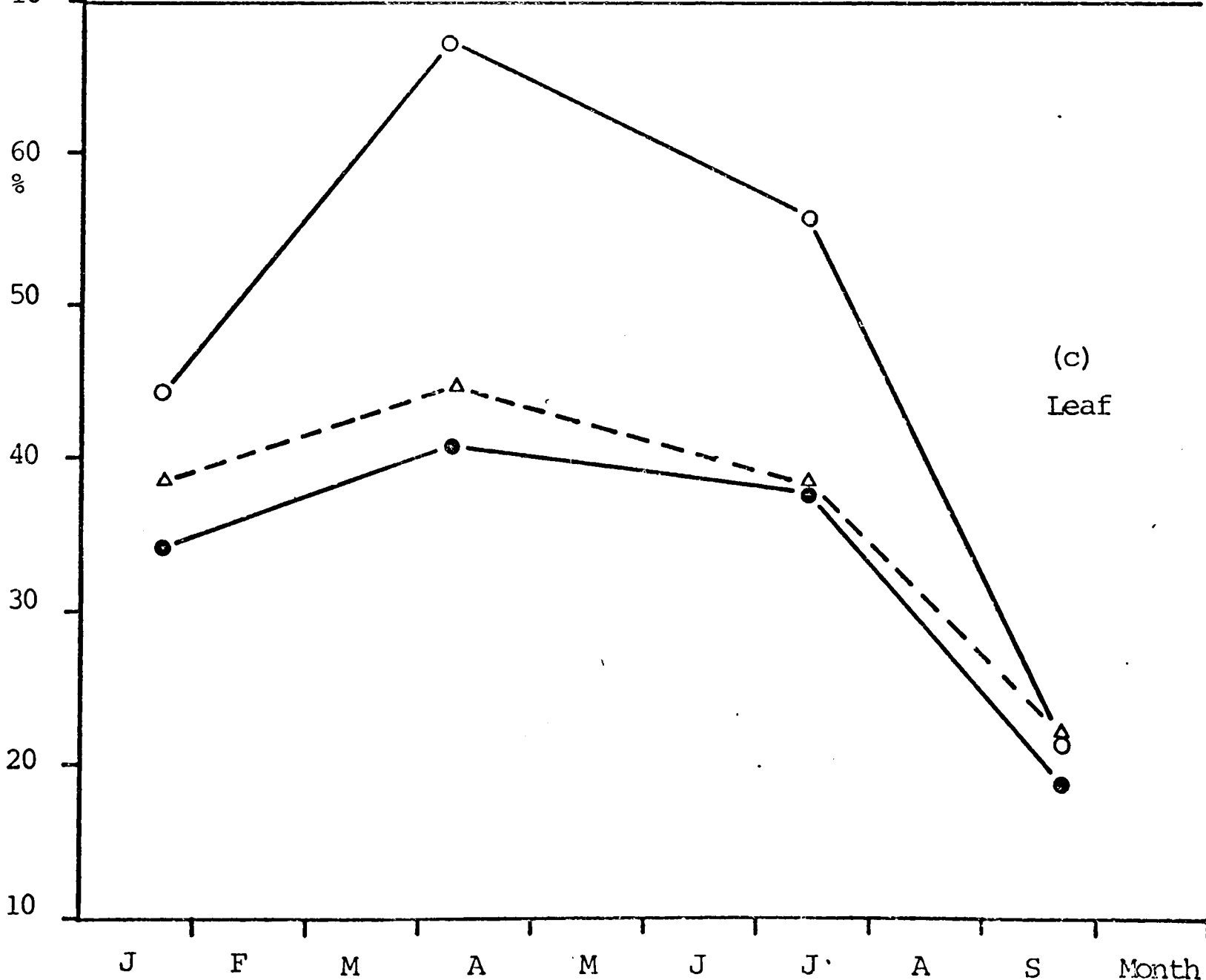
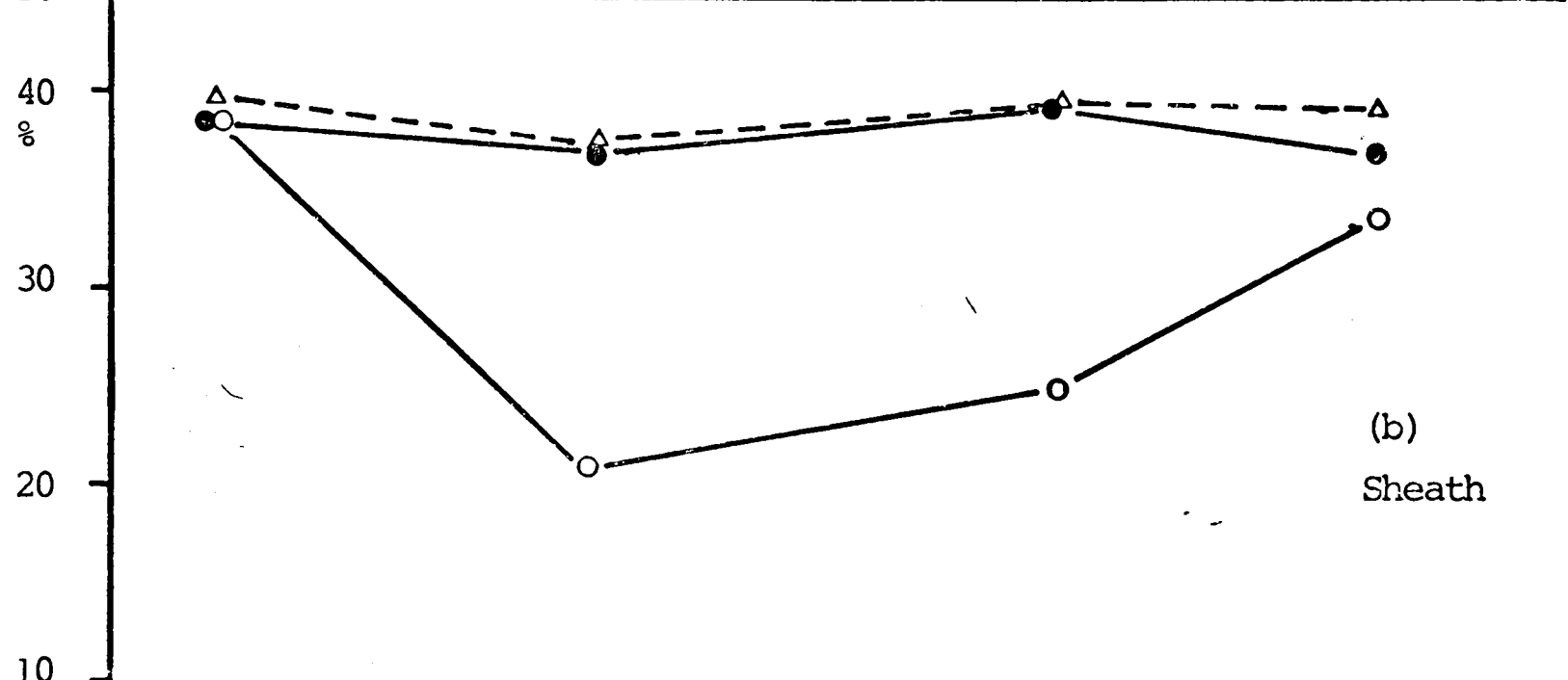
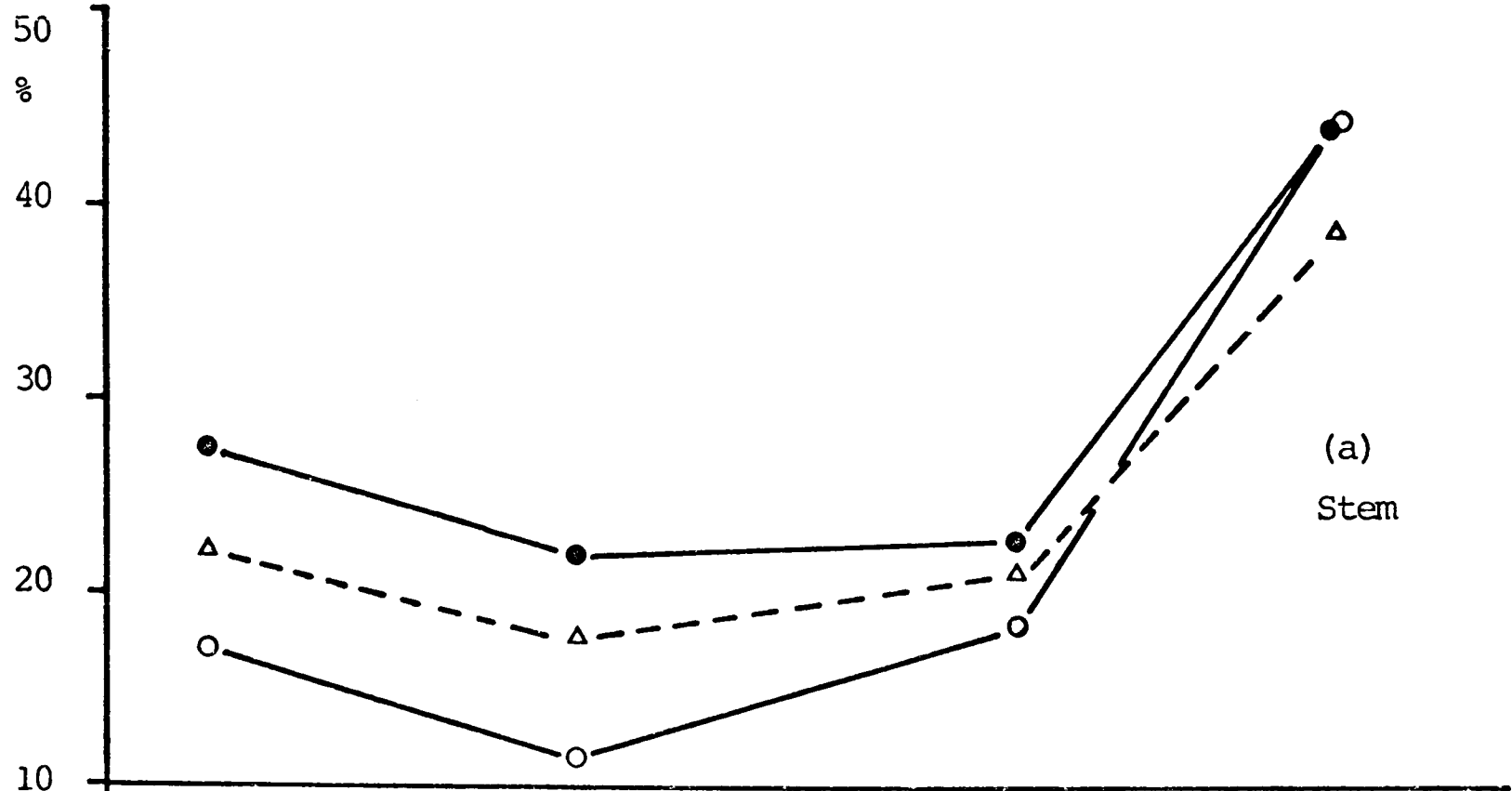
components are considered :

$$\frac{R_a = I_a \cdot RT_a}{R_b = I_b \cdot RT_b}$$

Table A12.4. The mean rumen proportions with 95% confidence limits for grass parts in each month, with their dietary proportions calculated from (i) sp. gravity, SG (ii) organic matter digestibility, OMD.

Month	Part	% in rumen	95% conf.limits	% in diet from SG correction	% in diet from OMD correction
January	Leaf	34.1	$\pm$ 8.2	44.3	38.4
	Sheath	38.3	4.8	38.5	39.5
	Stem	27.7	7.9	17.2	22.1
April	Leaf	40.8	4.6	67.4	44.8
	Sheath	37.1	5.2	21.0	37.4
	Stem	22.0	2.9	11.5	17.9
July	Leaf	37.6	9.6	55.5	38.6
	Sheath	39.4	2.9	25.0	39.7
	Stem	23.0	7.6	19.5	21.6
September	Leaf	18.5	10.5	21.2	21.8
	Sheath	37.1	4.8	33.9	38.8
	Stem	44.4	10.6	44.9	39.3

Fig.A12.4. Series II hartebeest: the mean percentage in each month of (a) grass stem, (b) sheath and (c) leaf in the rumen (●——●) and in the diet using the specific gravity correction (○——○) and the organic matter digestibility correction (Δ— — —Δ).



Three such expressions can be made for a system of three components (a, b, c), and their combined intake equals unity :

$$I_a + I_b + I_c = 100.$$

Knowing the rumen proportions and retention times of each component, ($R_{a,b,c}$ and $RT_{a,b,c}$), the simultaneous equations can be solved for the intake proportions ($I_{a,b,c}$).

The ingested proportions of leaf, sheath and stem have been calculated using their mean proportions in the rumens of the hartebeest shot in January, April, July and September 1972 (Ch. 8). RT's based on SG and OMD have been used to obtain two sets of dietary proportions. These results, with the observed proportions in the rumen, are shown in Table A12.4 and Fig. A. 12 .4.

A.8. Discussion

Retention times calculated by OMD

The expression ($RTOM = 35.5 - 0.32 \text{ OMD}$) used to calculate the retention times of organic matter in the hartebeest rumen is one of three relating RTOM, OMD and OMI which were derived for sheep fed a variety of grasses of mean OMD of 63% (range 45.8 - 77.0%) (Thornton and Minson 1973). The OMD's of the Kenyan grasses only just overlap with this range, so that calculating their RTOM's assumes that the linear relationship holds with low OMD's up to a maximum retention of 35.5 hours. Blaxter, Wainman and Wilson (1961) showed that the voluntary intake of sheep dropped increasingly rapidly at low forage digestibilities. As retention time and intake are related (p.330), this suggests that RT's of low OMD feeds are disproportionately longer than the regression would predict, which could account for the rough agreement between the RT of leaf from both methods (p.336), but the considerable discrepancy between the times for stem. On the basis of passage time, Blaxter, Wainman and Wilson (loc. cit.) found that hay with a digestibility of 74.2% spent 41 h in the sheep rumen, but, when the

digestibility fell to 44.7%, RT increased to 83 h. Although other factors such as the CP content of the feed will affect RT, the increase in RT over such a digestibility range is comparable to that calculated for the hartebeest using the SG relationship.

The usefulness of relationships derived from such feeding studies may be limited. First, two varieties of a single grass may be sufficiently different to warrant separate regressions for predicting intake (Milford and Minson 1967). Second, the changes in overall digestibility and intake of a cut herbage may only reflect the changing proportions of relatively digestible leaf and less digestible stem (Lambourne and Reardon 1962). Differences between these components were recognized by Laredo and Minson (1973) who found that although RT and OMI were related to OMD of a range of grasses, the intake of leaf was always higher than that of stem at a given level of fibre, or OMD. Although the in vivo digestibility of leaf was higher, the in vitro OMD's of the two components were the same. Samples for the latter tests were milled first, and the greater energy required to grind the stem fraction was taken to indicate the destruction of a particular arrangement of the fibre component which depressed its in vivo digestibility and intake. This suggests that in vitro OMD can never completely predict intake.

Retention times calculated by specific gravity

If the air space within roughage particles is largely responsible for their behaviour in the rumen, the relevant SG is that of the food particles under these conditions, rather than the absolute SG of solid plant material. The volume, and hence SG, of a known weight of chaffed material will depend partly on the air trapped in each particle and the air trapped between adjacent particles. The latter is a function of the closeness of packing of the sample, and again is not realistic of conditions in the rumen where mixing separates the particles and makes them more accessible to the

micro-fauna (McDonald 1969). By reducing the inter-particle air spaces, coarse grinding allows close packing but perhaps affects the internal air spaces rather less. If so, then it is more meaningful than measuring the SG of chaffed material. The confounding effect of inter-particle air spaces through differences in packing may be the cause of Laredo and Minson's (1972) results that the mean density of chaffed stem was 3 times greater than that of leaf. Their conclusion that voluntary intake was therefore negatively correlated with feed density is directly opposite to the experience of many other workers (e.g. Baumgardt 1970).

The stems of the Kenyan grasses have lower OMD's than the leaves (Table A 12.2), which is clearly related to their higher fibre contents (Fig. A.12.3), but when, as described above, the in vivo OMD of chaffed leaf is greater than that of stem at any given level of CF (Laredo and Minson loc.cit.), the structural arrangement of the fibre appears to affect the digestibility. Certainly, differences in the fibre content are not surprising in view of the different functions of the plant parts. Except at the nodes, grass culms are usually hollow but rigid, and their photosynthetic activity low (Metcalf 1960). Consequently, their CP content is low and although highly fibrous, their effective SG is low because of the air they hold.

As an intercalary meristem, the sheath is a zone of elongation of the leaf cells and is less differentiated than the leaf tissue (Esau 1965). Although the rings of sheath support the culms basally (Metcalf loc.cit.), they are not subject to the deformation stresses of leaf and stem, and the single measurement of sheath fibre content is lower than the comparable leaf value. (Table A12.2). The leaf and sheath vascular bundles are continuous, and with the slight photosynthetic activity of the latter, it has a higher protein content than stem material. Although possibly more fibrous, leaf has the highest protein content, and its mean OMD is consequently 5 units higher than that of sheath (Table A 12.2).

Although OMD is determined by the amounts of CP and, to a lesser extent, CF (Fig. A12.3c, and Glover and French 1957), SG measures the composite effects of CF and its arrangement, a cell content parameter, measured here as CP, and, in the case of stem, the volume of trapped air. The importance of the last factor increases as the diet becomes more stemmy. Because the Kenyan sward and hartebeest diet both contain large proportions of roughage, I conclude that the rumen retention times of particles can be more meaningfully calculated on the basis of their specific gravity than from their digestibility. Despite the approximations inherent in the method of SG determination, this approach provides a mean of calculating the composition of the diet when only the composition of the food residues in the rumen is known.

Appendix 13. . Series I hartebeest. Their sex, age, eviscerated weight, and the reproductive status of adult females.

Female reproductive status:

NPNL - non-pregnant, not lactating
 PNL - pregnant, not lactating
 NPL - not pregnant, lactating
 PL - pregnant, lactating

Number	Sex	Age y	Reproductive status of adult females.	Eviscerated weight, kg.
2	F	-	NPNL	84.3
4	F	-	NPL	96.5
5	F	12-14 mth.	-	58.9
6	M	8- 9	-	91.2
7	F	-	PL	89.3
8	M	16-17 mth.	-	58.8
10	F	-	NP	93.8
13	M	3- 4	+	103.3
14	F	-	NP	69.6
17	M	7- 8	-	112.6
18	F	17-18 mth.	-	59.2
19	F	2-2.5	NP	75.9
20	M	21-24 mth.	-	84.7
21	F	2.5- 3	NP	81.9
22	M	8- 9	-	116.1
23	M	3- 4	-	122.7
24	F	8- 9	NP	91.0
26	M	14 mth.	-	64.1
27	M	2.5- 3	-	90.4
28	F	4- 5	P	98.1
31	F	-	P	105.0
32	F	-	P	100.1
35	F	-	NP	95.2

Appendix I3 . Series II hartebeest. Their sex, age, eviscerated weight, hind foot (HF) length, their kidney fat index, muscle weight index, dry matter (DM) content of the marrow, and the reproductive status of the adult females.
 Female reproductive status. NPNL - non-pregnant, not lactating, PNL - pregnant, not lactating, NPL - not pregnant, lactating, PL - pregnant and lactating.

Number	Sex	Age y	Reproductive status of adult females	Eviscerated weight, kg	HF length cm	Kidney fat/HF	Muscle wt/HF	Marrow % DM
40	F	4-5	PNL	92.6	48.5	2.19	36.0	87.7
41	F	12-18m	-	74.0	46.3	0.93	28.9	78.5
42	F	24m	NPNL	88.0	48.8	1.23	33.2	85.4
43	M	5-6	-	111.0	50.5	0.94	40.4	75.1
44	F	2-2.5	NPNL	81.7	47.0	1.26	32.4	66.9
45	M	8-9	-	115.1	48.1	1.23	37.1	80.6
46	M	8-9	-	116.6	49.4	2.34	37.0	70.1
47	F	9m	-	46.4	41.5	0.23	20.4	0
48	F	7-8	NPNL	110.2	50.9	3.34	37.3	91.0
49	M	7-8	-	109.6	48.5	0.62	35.6	56.9
50	F	11-12	NPL	90.5	47.3	0.72	31.5	50.4
51	M	2-3	-	94.5	50.4	1.25	31.7	87.2
52	M	4-5	-	128.6	51.9	2.80	41.0	89.8
53	F	7-8	NPL	102.3	49.1	1.21	35.8	81.3
54	F	21-24m	-	83.5	48.2	1.70	34.4	84.6
55	F	17-18m	-	67.8	45.2	0.81	29.5	64.7
56	F	6-7	PL	105.1	51.2	1.82	39.3	99.2
57	F	5-6	PNL	104.4	46.0	8.92	41.6	91.4
58	M	-	-	52.7	45.5	0.64	21.9	90.4
59	M	3-4	-	113.1	50.8	3.99	43.0	99.0
60	M	3-4	-	116.9	48.7	2.86	41.3	94.8
61	M	17-18m	-	76.5	47.9	1.18	30.8	96.2
62	F	21-24m	NPNL	88.2	49.1	2.49	34.6	94.7
63	M	5-6	-	119.7	50.0	1.26	41.1	77.6
64	M	5-6	-	120.1	50.6	0.82	36.6	47.7
65	M	6-7	-	112.3	50.5	0.72	33.7	76.5
66	M	10-11	-	108.8	51.5	1.26	34.3	77.6
67	F	6-7	PNL	106.8	49.0	1.95	34.7	81.1
68	F	6-7	PNL	114.6	49.2	5.06	40.0	71.8
69	F	9-10	PNL	96.0	50.9	1.46	34.4	81.8
70	F	-	-	48.9	45.3	0.24	20.5	59.3
71	M	21-24m	-	83.5	49.9	0.87	30.0	81.3

Appendix I4. Principal components analysis (PCA)

In attempting to account for the distribution of animals, it would be reasonable to assume that a variety of factors exert an influence. Some of the more obvious influences might be climatic, the distribution of water sources, spatial variation in the nutrient content of the sward, the numbers and distribution of other species, local topography etc. On the other hand, these may not be independent, for a climatic factor such as rainfall is a determinant of the protein content of the sward. If one or both are shown to be partial predictors of animal distribution, can one say which is the better independent variable, or can both be used?

The data-reducing capacity of principal components analysis (PCA) allow questions like this to be answered, because it enables the detection of underlying patterns of relationships between a set of variables. This allows the data to be reduced to a smaller set of components which can be used as source variables for examination of any observed relationships in the set of data.

The theory behind PCA and its use are described by Lawley and Maxwell (1971), Child (1970) and Seal (1964). Its biological applications include the classification of plant communities (eg Ivimey-Cook and Proctor 1967), and in analysing the changes in animal species abundance (eg Williamson 1963). The advantage of PCA over other analytical methods is shown by Davies and Brown (1972) in their analysis of the growth patterns of insects. The use of PCA by Dudzinski and Arnold (1974) to compare the diets of sheep and cattle grazing together in terms of the sward structure and its nutritive value, is similar to the application reported here.

PCA proceeds in 3 steps in this context:

1. The set of variables which are of interest are specified and the matrix of correlation coefficients between them is prepared.

2. This matrix is used to derive the principal components which are linear functions of the original variables. The first component is the linear combination which accounts for more of the variance in the data than any other linear combination. The second component is defined as the second best linear combination, which is orthogonal (uncorrelated) to the first. To be orthogonal this component must be the linear combination of variables which accounts for the highest proportion of the residual variance left unaccounted by the first component. The next and subsequent components are found iteratively by the same process until no variance remains in the data. Unless one variable is perfectly determined by the rest of the variables, there will always be as many components as there are variables.

In each component each variable has a loading. These are used, first, to assess the importance of each component in terms of the variance in the data which is explained by it. This is done by summing the squared loadings in each components to obtain the eigen-value or latent root. The first component has the highest latent root, the second has the second highest, and so on. The components are more easily compared in terms of their variances. Ideally, each variable has a total variance of unity. Thus if n variables are in use, the total variance is n , and the percentage of the variance extracted by each component is

$$\frac{\text{latent root}}{n} \times 100$$

3. The components defined in this way are new, composite and orthogonal variables of the original data. In the present case, they are the environmental parameters considered as possible determinants of animal distribution.

The components loadings can then be used in multiple regressions to predict the animal distribution, using a suitable measure of their density or location as the dependent variable. Each data case contains one value of the dependent variable and one for each of the environmental variables. The relative importance of the latter in each component is incorporated by multiplying each variable value by its loading in each component. In addition each variable is standardized by subtracting its value from its mean and dividing by its standard deviation (SD). Thus, for a component containing 7 variables, a factor score is calculated as:

$$\begin{aligned} \text{SCALE 1} = & (\text{loading}_1 (\text{var1} - \bar{X}_1) / \text{SD}_1) + \\ & (\text{loading}_2 (\text{var2} - \bar{X}_2) / \text{SD}_2) + \\ & (\text{loading}_7 (\text{var7} - \bar{X}_7) / \text{SD}_7 \end{aligned}$$

and the same is done for each component.

Ideally, the data used in a PCA must be normally distributed, but provided the distributions are not excessively skewed, multimodal or truncated, an approximation to normality can be obtained by transforming the data (Child loc. cit.). Another possible restriction is in the model's assumption that the initial correlations between the variables are based on linear relationships. If some of the variables show, for example, curvilinear relationships, they may fail to contribute any information to the analysis. The data can be examined at the start for normality and linearity by generating scattergrams of the values of all possible variable pairs.

The identification of the components is largely subjective, relying on the biological knowledge of the analyst. An assumption of PCA is that having extracted the maximum variance from a set of variables, the components "ought" to have some "ecological meaning" (Austin loc. cit.). On occasion, a component may be the result of fortuitous association, to which no biological interpretation can be given (eg Austin loc. cit.).

Appendix I5. The means and standard deviations (S.D.) of 13 habitat variables, and their correlation matrix.

	DO	MA	MI	VG	CU	CR	AQ	EN	DR	MO	PR	FB	CB
Mean	.207	.445	.128	.604	.744	3.188	1.966	3.606	.110	.604	.259	.597	.682
S.D.	.490	.462	.486	.209	.414	.319	1.487	.015	.154	.220	.054	.045	.042
Dominant height DO	1.0												
Maximum height MA	.909	1.0											
Minimum height MI	.954	.875	1.0										
Vegn.greenness VG	.435	.424	.416	1.0									
Culm height CU	.828	.905	.788	.386	1.0								
Standing crop CR	.740	.833	.667	.322	.868	1.0							
Water density AQ	.169	.151	.198	.450	.119	-.012	1.0						
Energy content EN	.261	.006	.095	.151	-.121	.048	.112	1.0					
Water scarcity DR	- .135	-.126	-.123	-.420	-.202	-.057	-.265	-.175	1.0				
Grass moisture MO	.264	.103	0	.819	.172	.083	.357	.156	-.396	1.0			
Protein content PR	- .101	-.317	-.141	.604	-.351	-.242	.276	.070	-.173	.647	1.0		
Fibre content FB	.384	.551	.194	-.289	.536	.570	-.198	.138	.239	-.149	-.592	1.0	
Carbohydrate content CB	- .213	-.128	-.099	-.197	-.215	-.245	-.066	.188	-.142	-.557	-.353	-.149	1.0

ppendix I6. The factor loadings on 13 habitat variables, with the eigen values, variance and cumulative variance accounted for by 8 principal components.

Component	Eigen value	% var.	Cum % var.	DO	MA	MI	VG	CU	CR	AQ	EN	DR	MO	PR	FB	CB
1	5.008	38.5	38.5	-.945	-.963	-.874	-.518	-.942	-.870	-.214	-.112	.205	-.288	.163	-.482	.266
2	3.157	24.3	62.8	-.008	.167	.049	-.784	.156	.201	-.521	.145	.467	-.838	-.874	.609	.312
3	1.467	11.3	74.1	-.082	-.045	-.178	-.073	.050	.124	-.246	-.510	.505	.258	.197	.213	-.822
4	1.060	8.2	82.3	.094	-.101	-.193	-.071	-.176	.046	-.149	.818	.120	.228	.051	.425	-.156
5	.805	6.2	88.4	.197	.026	.327	.009	-.176	-.095	.273	.147	.624	-.234	.187	-.209	.007
6	.722	5.6	94.0	.126	-.009	.174	.127	-.049	-.082	-.719	.050	-.006	-.050	.214	-.271	.094
7	.408	3.1	97.1	.157	-.077	.209	-.311	-.036	-.157	.012	.065	-.265	-.092	-.043	-.122	-.333
8	.255	2.0	99.1	.125	.081	.030	.059	.021	-.369	-.081	-.049	.079	.208	-.170	.036	.055

Appendix 17 . Measurements of grass structure and volume, water density and dispersion, and grass chemical composition for 8 major vegetation types in 12 months.

DOMHTVEG, Dominant height layer of vegetation.

Veg.type	Month											
	N	D	J	F	M	A	M	J	J	A	S	O
01	1	1	1	1	1	1	1	1	1	1	1	1
02	5	3	5	2	2	1	2	2	2	2	2	2
03	1	1	1	1	1	1	1	1	1	1	1	2
04	1	1	1	1	1	1	1	1	1	1	1	1
05	2	2	2	1	1	1	1	2	2	2	1	1
06	1	1	1	1	1	1	2	2	1	1	1	1
10	1	1	1	1	1	1	2	2	2	1	1	1
35	-	-	-	-	-	-	1	1	1	1	1	1

Key 1 = 0-10 cm, 2 = 10-20 cm, 3 = 20-30 cm, etc. 0 = absent.

MAXHTVEG, maximum height layer of vegetation.

01	1	1	1	1	1	1	1	1	1	1	1	1
02	5	5	5	4	5	3	4	3	4	3	4	4
03	2	3	3	3	2	2	2	3	3	2	3	3
04	2	1	1	1	1	1	1	1	1	2	3	1
05	3	5	3	3	3	2	2	3	3	3	3	3
06	1	4	1	3	1	1	2	3	3	3	3	3
10	4	3	4	3	3	3	3	3	4	2	3	3
35	-	-	-	-	-	-	3	2	3	2	3	2

Key as for DOMHTVEG

MINHTVEG, lowest height layer of vegetation.

01	1	1	1	1	1	1	1	1	1	1	1	1
02	2	1	1	1	1	1	1	1	1	1	1	1
03	1	1	1	1	1	1	1	1	1	1	1	1
04	1	1	1	1	1	1	1	1	1	1	1	1
05	1	1	1	1	1	1	1	1	1	1	1	1
06	1	1	1	1	1	1	1	1	1	1	1	1
10	1	1	1	1	1	1	1	1	1	1	1	1
35	-	-	-	-	-	-	1	1	1	1	1	1

Key as for DOMHTVEG

VEGGREEN, grass greenness, excluding culms.

Veg.type	N	D	J	F	M	A	M	J	J	A	S	O
01	2	6	4	4	4	2	6	6	4	2	4	3
02	1	5	6	6	4	2	5	6	5	3	2	3
03	2	6	5	4	3	2	6	6	6	4	6	5
04	2	6	4	6	3	2	6	6	6	5	5	4
05	2	5	5	4	3	2	6	6	6	3	4	4
06	2	5	4	3	2	1	6	6	5	3	3	2
10	2	4	4	4	4	2	5	6	6	4	3	3
35	-	-	-	-	-	-	6	6	6	5	5	2

Key 1 = 0%, 2 = 1-20%, 3 = 20-40%, 4 = 40-60% 5 = 60-80%, 6 = 80-100%

CULMHT, height of culms.

10	0	0	2	2	0	0	2	4	3	2	3	0
02	10	8	9	6	6	5	6	8	8	9	8	8
03	6	5	6	5	5	4	4	8	6	8	8	5
04	0	0	3	2	0	3	2	4	4	4	5	6
05	6	5	8	5	5	5	3	7	8	6	6	7
06	7	6	5	4	4	4	6	7	8	7	8	6
10	7	8	7	5	7	5	7	9	8	7	7	7
35	-	-	-	-	-	-	4	5	4	5	5	5

Key as for DOMHTVEG

CROP, standing crop of grass, kg/ha

01	596	476	574	454	403	447	521	1119	989	571	756	291
02	3752	1584	2368	2402	1488	1226	1563	2477	2374	4320	2976	1410
03	828	811	1111	1936	1302	1210	1059	1691	1874	1852	1616	1012
04	940	994	645	1272	821	1218	703	1105	1425	1348	1288	458
05	2016	2260	2174	2867	1405	1881	1329	2457	2538	1762	1913	1784
06	1016	1043	1637	1480	1134	951	1757	1647	1683	1641	1399	1379
10	2528	1855	3062	2456	3528	2255	2472	3184	3283	2804	2262	2242
35	-	-	-	-	-	-	982	1245	730	951	868	605

AQUADENS, water density, m²/km²

Veg.type	N	D	J	F	M	A	M	J	J	A	S	O
01	2	496	521	534	55	1	82	282	25	1	43	3
02	27	729	35	109	22	1	102	980	928	243	390	190
03	8424	16329	3939	12343	5158	4292	7941	27170	22012	25121	30878	25931
04	1697	3614	3027	2655	1467	1287	1956	2638	1668	2426	2256	1501
05	1	395	1	1	1	1	1	1	140	1	91	1
06	1	82	1	1	1	1	1	78	18	2	2	1
10	2	120	14	1	1	1	1	122	53	5	10	2
35	242	3970	2247	2248	1281	786	793	2513	2318	691	786	176

ENERGY, energy content, cal/g

01	4116	4076	4028	4071	4061	4034	4029	4202	4026	4141	4032	3996
02	4165	4127	4152	4032	4191	4142	4242	4185	4182	4084	4122	4243
03	4149	4046	4178	4070	4085	3983	4078	4019	3960	3940	3612	4108
04	4144	4073	4125	4117	4092	4187	4164	4178	4205	4185	3926	4187
05	4149	4109	4060	4056	4181	4238	4203	4171	4062	4036	3881	4111
06	3853	4095	4093	3951	3816	3512	3873	3918	3907	3831	3784	3848
10	3917	4143	4199	4055	3874	4002	4061	4026	3958	3966	3975	3952
35	-	-	-	-	-	-	3836	3855	3911	3994	3881	3559

DRINK, distance to water.

01	2	0	0	1	1	0	0	0	0	0	0	0
02	0	0	0	0	0	0	0	0	0	0	0	1
03	0	0	1	0	1	1	0	0	0	0	0	0
04	3	0	1	0	0	2	0	0	1	0	1	1
05	2	0	1	1	0	1	0	0	0	0	0	2
06	1	0	1	2	2	2	1	0	2	1	1	2
10	0	1	1	1	0	0	0	0	0	2	1	2
35	-	-	-	-	1	2	1	0	1	0	0	2

Key 0 = 500 m, 1 = 500-1000m, 2 = 1-2 km, 3 = 2-3 km, etc.

PROTEIN, grass crude protein concentration, % dry weight.

Veg.type	N	D	J	F	M	A	M	J	J	A	S	O
01	5.3	12.7	6.3	10.1	8.3	4.6	15.3	10.5	9.8	6.1	7.4	7.9
02	3.5	6.3	6.3	7.0	5.2	3.5	6.1	9.6	7.0	4.8	3.9	3.1
03	4.4	10.0	5.7	5.7	5.2	4.4	10.5	7.4	11.4	4.8	5.7	4.6
04	5.1	12.8	7.1	9.6	7.9	6.6	17.9	10.5	11.0	4.4	6.6	2.2
05	4.9	3.1	5.2	4.8	6.1	7.0	8.7	8.3	9.2	6.6	5.3	4.6
06	3.8	6.1	5.0	5.2	3.9	5.1	9.6	8.7	8.9	5.7	4.4	6.5
10	3.9	4.4	4.6	4.4	4.8	4.4	7.0	7.4	10.1	6.6	5.2	5.9
35	-	-	-	-	-	-	9.6	9.6	12.5	5.2	7.0	2.8

FIBRE, grass crude fibre concentration, % dry weight.

01	37.1	21.3	27.2	22.9	25.5	26.4	25.1	28.9	27.4	31.5	26.8	30.4
02	39.5	33.4	30.8	33.1	34.7	35.3	36.8	36.0	35.4	35.0	37.9	35.8
03	36.2	26.0	31.1	32.5	29.0	33.3	29.2	32.7	29.8	33.5	32.6	31.7
04	36.0	23.9	27.8	27.4	26.8	27.6	23.1	31.2	30.4	32.5	31.7	33.6
05	38.0	40.9	30.1	38.8	27.6	39.9	30.0	32.4	34.7	33.6	35.6	36.9
06	32.1	34.2	27.6	34.8	34.9	30.9	29.0	36.2	32.6	33.6	34.2	29.4
10	31.3	36.8	33.6	33.1	28.7	32.0	30.4	35.2	35.8	34.1	34.4	29.6
35	-	-	-	-	-	-	28.6	27.8	23.8	32.0	26.6	29.7

CARBHYD, grass carbohydrate concentration, % dry weight

01	38.3	45.7	42.5	46.3	42.2	44.4	35.7	35.5	43.4	43.1	40.7	40.7
02	36.0	40.9	40.8	39.9	41.1	44.4	37.8	32.1	38.5	39.4	42.1	42.1
03	40.1	35.2	39.9	37.9	41.3	41.3	39.2	31.3	37.1	41.4	42.3	42.3
04	40.0	42.0	43.1	38.0	42.0	44.9	36.1	34.6	40.8	46.4	44.0	44.0
05	38.7	40.0	41.7	44.1	45.6	35.8	39.2	35.6	35.0	40.7	39.2	39.2
06	37.0	53.8	48.3	34.0	36.4	36.2	35.6	31.3	35.4	39.1	41.1	41.1
10	41.2	44.7	39.3	43.3	39.1	40.1	38.3	34.3	32.5	37.3	42.4	42.4
35	-	-	-	-	-	-	34.2	27.9	35.9	44.0	41.0	41.0

MOISTURE, grass water content, %

Veg.type	N	D	J	F	M	A	M	J	J	A	S	O
01	-	-	49	45	16	1	73	66	29	6	16	12
02	-	-	41	55	25	11	58	61	47	17	15	35
03	-	-	33	24	28	17	68	62	53	18	29	33
04	-	-	44	37	15	6	74	70	46	17	24	30
05	-	-	35	28	16	6	61	62	44	14	23	28
06	-	-	22	30	14	6	59	60	42	17	26	18
10	-	-	29	29	27	3	48	58	52	17	24	21
35	-	-	-	-	-	-	56	64	51	24	28	23