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FEEDING ECOLOGY OF THE KUDU *TRAGELAPHUS STREPSICEROS* (PALLAS) IN THE KRUGER NATIONAL PARK

by

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For Eugenie and Jacqueline

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FEEDING ECOLOGY OF THE KUDU TRAGELAPHUS STREPSICEROS (PALLAS) IN THE KRUGER NATIONAL PARK

by

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ABSTRACT

The study investigated aspects of the feeding ecology of kudus that could indicate their nutritional status, and which might affect their population performance; i.e. (i) potential food abundance, measured as the biomass of available forb and woody plant leaves (ii) the nutrient content of potential food (iii) an index of accepted food abundance, given by feeding time achieved per unit distance moved while foraging (iv) an index of food intake rate while foraging, given by the proportion of foraging time spent feeding (v) diet composition (vi) differences between food types in acceptance, as indicated by selectivity ratings.

Potential food was most abundant in the late wet season at 60 g dry weight per m^2 and least abundant in the late dry season at 12 g per m^2. Forbs were less abundant than woody plant foliage,

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but comprised about 65 per cent, as opposed to woody plants 35 per cent, of the kudus' diet during most of the year.

The selectivity ratings of the various food types were positively correlated with their leaf protein, phosphorus and water contents in the wet season, suggesting that the kudus selected for plants with a high nutrient content. In the dry season, however, there was no relationship between acceptance and leaf nutrient content. This was because the kudus favoured woody plants armed with thorns during the wet season, but increased their acceptance of unarmed woody species in the dry season, despite the fact that the armed species averaged higher in nutrient content throughout the year. Thus plant structural defences may have outweighed leaf nutrient content as a factor influencing selection in the dry season.

The index of accepted food abundance provided a satisfactory reflection of seasonal and between-habitat variations in food abundance as experienced by the kudus, but its reliability would be increased if it were accompanied by measurements of the rate of food intake per unit time spent feeding. This index offers a means of monitoring long-term changes in the quantity of food available to kudus, and of determining whether their population is limited by food availability.

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INTRODUCTION

Food is considered by many authorities to be the ultimate resource limiting animal populations (e.g. Wilson 1975, White 1978). The point has been seriously questioned (Chitty 1967) but for large African herbivores there is some evidence to support it.

The biomass of large herbivores in different savanna regions shows a close positive correlation with mean annual precipitation (Coe, Cumming and Phillipson 1976, Sinclair 1977). Since annual precipitation is known to be the major determinant of primary production in the arid and semi-arid regions of the world (i.e. regions with less than 700 mm precipitation per annum) the correlation indicates that the carrying capacity of savanna ecosystems for large herbivores depends of food availability, which is in turn related to primary production (Phillipson 1975, Coe et al. 1976).

Precipitation in the Kruger National Park (like that of southern African summer rainfall areas in general) tends to follow a 20 year oscillation, with about 10 years above average and 10 years below average (Tyson and Dyer 1978, Gertenbach 1980). There are indications that past fluctuations in ungulate numbers in the Kruger Park were associated with variations in rainfall (Gertenbach 1980). Long-term studies of ungulate populations in the Park could therefore yield valuable insights into relationships between population dynamics, precipitation and food availability. The Kruger Park kudu population is in many respects well suited to such a study (see Owen-Smith 1979). Kudus are individually recognizable by the pattern of the stripes on their flanks and this, together with the fact that adult cows associate in discrete groups, allows accurate monitoring of population changes. Starting in 1974 Owen-Smith has made annual counts in two study areas, one near Tsokwane in the Central District of the Park and the other near Pretoriuskop Rest Camp in the south.

Results have shown that the 1970's was a period of steady increase in the kudu population, numbers more than doubled from 1972 to 1978. This may be associated with the fact that the 1970's fell within a high rainfall phase (Owen-Smith unpublished)

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The present study, extending from 1975 to 1977, concerned the feeding ecology of the kudus in the Tsokwane study area during the phase of population expansion. Its aim was to measure parameters that reflect the nutritional status of the population. Comparison of the results of this study with those of future studies done during a population decline phase may reveal the importance of the food supply as a factor limiting the population. Before discussing the actual parameters that were measured the interrelationships between nutrition and population performance are reviewed briefly.

In order to meet its requirements for maintenance, growth and reproduction an animal needs to maintain a certain rate of assimilation of nutrients into its tissues. The relationship between the nutrient assimilation rate on the one hand and nutrient requirements on the other indicates the nutritional status of the animal. The greater the deficit between assimilation rate and requirements the lower will be the animal's fitness and capacity to reproduce. Relationships between nutrition and fitness can be subtle; malnutrition tends to interact with disease and predation in reducing survival and reproductive output. Inadequate nutrition, for example, can impair the immune system, leading to pathogenic infection. The infection reduces the animal's capacity to feed itself, resulting in further reduction in disease resistance and yet more serious malnutrition (Sinclair 1977). The dependence of reproductive capacity on nutrition is well established (Sadleir 1969). Undernourished females show reduced ovulation rate (e.g. Fletcher 1981), and malnutrition during pregnancy reduces the size of the offspring and its chances of survival (Thorne, Deane and Hepworth 1976). The high nutrient cost of lactation places even more strain on maternal nutrition than pregnancy (Sadleir 1969, Moen 1973).

Under conditions of reduced food availability the rate at which a ruminant can assimilate nutrients may be limited in two ways. If the animal accepts only items offering a high nutrient content the scarcity of such items would mean a high searching time during

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foraging, and consequently a low food ingestion rate. If the animal accepts greater quantities of lower quality food, not only is the nutrient concentration of the diet reduced but the rate at which it digests and passes through the digestive tract is slower (Blaxter, Wainman and Wilson 1961, Van Soest 1965). In either case the net result is a lowered rate of nutrient assimi= lation.

Whether or not nutrition is likely to limit population perfor= mance could be most directly determined by evaluating the nutri= tional status of the animals, that is by measuring their daily intake of metabolizable nutrients and assessing whether this is sufficient to meet their daily requirements. However, data re= quired for reliable estimates of nutrient intake rate are diffi= cult to obtain for free-ranging wild ungulates. For the kudu study a more feasible approach was to measure aspects of feeding ecology which provide a reflection of the nutritional status of the population. These measurements could then be used as indices to determine whether fluctuations in the food supply are associa= ted with population changes.

With the objective of deriving such indices Owen-Smith (1979) advanced a conceptual model identifying relationships between nutrient intake rate, foraging performance and food abundance in the habitat. Summarized briefly these relationships are as follows: The vegetation structure of the habitat in conjunction with the body size and digestive capabilities of the animals de= termines the abundance of vegetation components that could poten= tially be accepted. Potential food abundance is thus defined as all the vegetation components that the animals might eat at some time or other. But herbivores will not accept all of the poten= tial food available at any one time; their response may change with habitat conditions, for example when food is scarce they may accept lower quality items which are rejected under more favourable circumstances. Within any defined period potential food can be divided into accepted and rejected fractions. The criteria where= by the animals accept or reject potential food items therefore defines accepted food abundance. Daily food intake is determined by the rate at which the accepted vegetation components are ingested per unit time spent foraging together with the proportion of the day devoted to foraging. (As used here the term foraging includes feeding, moving between food items, as well as short bouts of other activities - such as defaecation, urination or standing alert - which occur within the main foraging spell.) The nutrient content of the accepted food determines the daily nutrient intake and ultimately the nutritional status of the animal.

Thus to provide a reflection of habitat conditions that are related to nutritional status data are required on the following:

(i) The abundance of potential food in dry weight per unit ground area.

(ii) Differences in acceptance between the various food types available to the animals, and the way in which acceptance changes with changing conditions. (The term acceptance is used to mean the fraction of a particular food type encountered by an animal that it actually eats - Owen-Smith 1979). The acceptance of a food type can be estimated by comparing its relative contribution to the diet with its relative availability in the habitat (see Petrides 1975, Chesson 1978).

(iii) The abundance of accepted food.

(iv) The rate of food intake while foraging in dry weight per unit time.

(v) The activity budgets of the animals (the proportion of the day devoted to foraging, resting and other activities).

(vi) The nutrient contents of the various vegetation components included in the diet.

Given the maximum height at which the animals can feed plus general information on their diet it is possible to estimate potential food abundance by using appropriate vegetation sampling techniques.

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However one cannot predict the vegetation components that a given herbivore population will accept under particular conditions, and so acceptable food abundance cannot be measured by sampling from the vegetation. The rate at which free-ranging ungulates ingest food is also extremely difficult to measure. Thus as an index of accepted food abundance Owen-Smith (1979) measured the feeding time achieved per unit distance moved while foraging, and as an index of food intake rate while foraging he measured the proportion of foraging time spent actually feeding. These indices include the assumption that feeding time provides a reliable reflection of quantitative food intake.

Owen-Smith (1979) made a preliminary evaluation of the two indices for kudus in the Tsokwane study area in the Kruger National Park during 1974-75, and also examined seasonal variations in diet composition and activity budgets. His results indicated that the indices are sensitive to variations in habitat conditions. However since no measurements of the abundance and nutrient content of potential food were made the relationship between the indices and habitat conditions needed closer evaluation.

In the present study potential food abundance in the Tsokwane study area was estimated with two main aims in mind:

(i) to examine relationships between potential food abundance and the indices of accepted food abundance and food intake rate while foraging

(ii) to estimate the acceptances of different food types by comparing their relative contribution to the kudus' diet with their relative abundance in the habitat.

Specific questions which the study attempted to answer were:

(i) What are the seasonal and between habitat variations in potential food abundance, and how sensitive are the indices to these variations?

(ii) How does the nutritional value of the different food plants vary over the seasons?

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(iii) What are the differences between food plants in acceptance, how does this vary between seasons, and what are the factors underlying acceptance?

(iv) To what extent are the indices likely to give a meaningful reflection of habitat quality and nutritional status of the kudu population?

The results are presented in three chapters; the first dealing with the abundance and average nutrient content of potential food, the second with diet composition and estimation of acceptance, and the third with relationships between the indices and potential food abundance. In the fourth and final chapter the daily nutrient requirements of kudus are estimated from data on domestic and other wild ruminants. A rough approximation of daily nutrient intake is derived for comparison with the estimated requirements. This is done with the aim of identifying data requirements for reliable assessment of the nutritional status of the population.

Previous studies on the diet of kudus

A number of studies have reported the composition of the diet of kudus (Brynard and Pienaar 1960, Wilson 1965, 1970, Conybeare 1975, Giesecke and Van Gylswyk 1975, Owen-Smith 1979) but none have included quantitative estimates of the availability of different dietary components. All have shown that kudus are predominantly browsers, eating leaves, shoots and reproductive parts of woody plants as well as forbs, but generally accepting only small quantities of grass. The number of species accepted is large; Brynard and Pienaar (1960) list 147 species of food plants in the Kruger National Park. Diet composition has been shown to vary seasonally. Conybeare (1975), in Wankie National Park, Zimbabwe, and Owen-Smith (1979) in the Kruger National Park, both report that although leaves and shoots of trees and shrubs are eaten throughout the year they make up the bulk of the diet in the early wet season. Herbaceous plants are more prominent in the diet in the late wet season than at other times of the year.

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As is typical of browsers, kudus have a relatively small rumen capacity, and the rumen is adapted to a rapid throughput of food (Hofmann and Stewart 1972, Giesecke and Van Gylswyk 1975). Grass tends to be digested more slowly than browse (Short, Blair and Segelquist 1974) and grazers typically have a capacious rumen designed to retain the food longer (Hofmann and Stewart 1972). The digestive capabilities of kudus would thus limit them from accepting mature grass.

THE STUDY AREA

The study area was the surroundings of the Nwamuriwa Hills, situated 4,5 km due east of the Tsokwane Ranger Station, in the Central District of the Kruger National Park. There are two hills which rise abruptly from the surrounding plain: Nwamuriwa, the larger southern one (highest point 410 m a.s.l.) and Nwamuriwane, or Little Nwamuriwa to the north of it (highest point 330 m a.s.l., see Fig. 1). The two hills are linked by a saddle which rises slightly higher than the surrounding flats, which vary between 240 m and 260 m above sea level.

The rocks of the region are volcanic. The Nwamuriwa Hills are composed of granophyre while the underlying rock of the plains is basalt. As with many hills in the African savannas (King 1967) there is a sharp break in profile between the steep (roughly 30°) hill slopes and the gently sloping (5 - 10°) to almost level ground surrounding the hill base (termed the pediment). The distinct angle formed by the junction of the pediment and the steep hill slopes is termed the knick or piedmont angle (Small 1972). The slopes are strewn with loose boulders from the knick to the crest of the hills. Scattered outcrops of bare rock occur generally at the hill crests but there is no free face or cliff. On parts of the pediment close to the knick there are scattered loose boulders but these are much less frequent than on the slopes.

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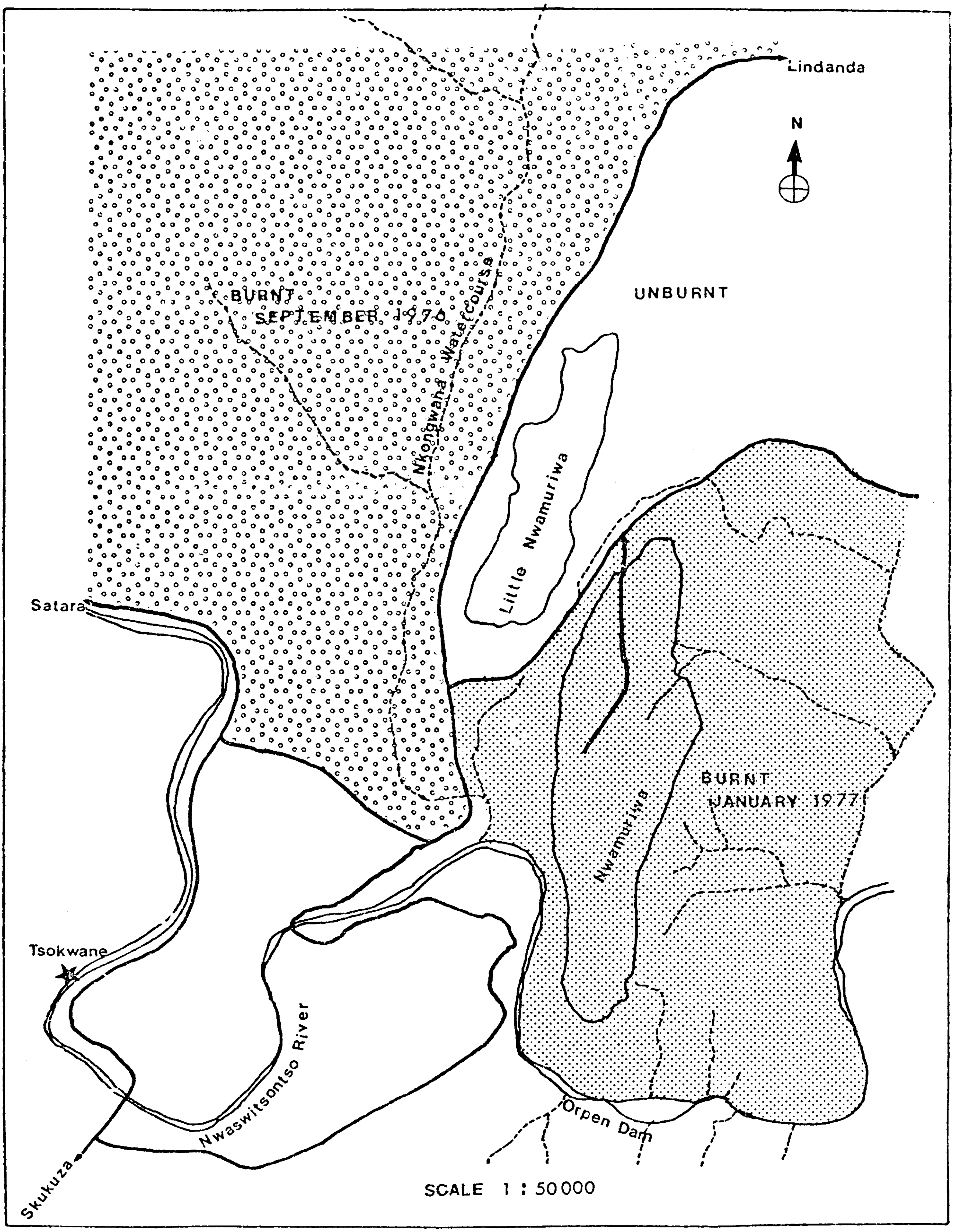

FIG. 1 THE STUDY AREA; THE NWAMURIWA HILLS, TSOKWANE DISTRICT, KRUGER NATIONAL PARK, SHOWING THE AREAS BURNT DURING THE STUDY PERIOD

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There is good soil cover on the pediment and the underlying rocks are exposed in only a few places. There is virtually no surface stone more than 100 m out from the knick.

As may be expected there is a gradient of increasing percentage clay in the soils from the hill tops to the base and out across the pediment. Soil samples taken in National Parks Board surveys (Coetzee 1977) show 8,0% clay near the highest point of Nwamuriwa, 11,4% at the mid-slope of Little Nwamuriwa and 37,1% on the basaltic plains at a distance of over 500 m from the hills.

The vegetation of both the hills and surrounding plains is a moderately open savanna in which three main strata can be recognised: a herb layer composed mostly of grass with some forbs, dwarf shrubs and seedlings of woody plants, an intermediate layer of shrubs and saplings, and an upper layer of tall trees. Although physiognomy varies little over the study area there is a pronounced difference in species composition between the vegetation of the hills and that of the surrounding plains. The dominant woody plant throughout the basalt plains is the knobthorn, _Acacia nigrescens_. This tree prefers clayey soils although it is seldom found in close proximity to water (Van Wyk 1972). On the crests of the broad interfluves _Acacia gerrardii_ replaces it as the dominant woody plant. The dominant grass on the flats. on clay soils, is _Themeda triandra_, with _Panicum maximum_, _Panicum coloratum_, _Digitaria pentzii_ and _Bothriochloa insculpta_ as associated species (Coetzee 1977). Where there is less clay, such as on the pediment, the _Panicum_ species are dominant.

On the hills the dominant woody plant is the red bush-willow, _Combretum apiculatum_, a tree which is virtually confined to well-drained sandy or rocky soils (Van Wyk 1972). The east facing slopes of the Nwamuriwa Hills are characterised by the presence of patches of _Pterocarpus rotundifolius_ growing as a multi-stemmed shrub. This species is virtually absent from the west facing slopes. The difference in species composition between the west and east facing slopes may be due to a soil water difference resulting from a different angle of bedding of the underlying rocks.

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The grasses tend to be shorter and more sparse on the hills than on the flats, the dominant species on the slopes being *Panicum maximum* and *Digitaria pentzii* with occasional *Themeda triandra* (Coetzee 1977).

Although the species composition of woody plants on the hills is quite distinct from that on the flats there is in fact a gradual change in composition from the hill tops to the knick and out across the pediment. *Acacia nigrescens* is dominant on the pediment and most sections of the lower slopes, but it declines in density with increasing height above the hill base. The density of *Combretum apiculatum* is higher on the upper slopes than lower down above the knick. Very few specimens of this species occur away from the hill base or outlying terraces. Between the pediment and the outlying flats further from the hills there is no sharp distinction in the vegetation. Rather a gradual quantitative change is noticeable as one moves further from the knick (described in more detail in Chapter 1).

Owen-Smith (1979) divided the study area into two major subdivisions. The first, termed the hill base ecotone, comprised the lower hill slopes (up to about 100 m from the knick) and the pediment. The outlying flats he termed the knobthorn savanna. Owen-Smith arbitrarily chose the tourist roads running parallel with the knick (Fig. 1) as the boundary between them.

Two other distinct vegetation types in the area are the riparian fringe along the bank of the Nwaswitsontso River (Fig. 1) and the *Acacia tortilis* savanna on the base-rich soils to the south-west of the hills.

Further subdivisions of the hill base ecotone recognised in the present study are discussed in Chapter 1. All vegetation samples intended to represent the hill base ecotone came from the zone extending 80 - 100 m upslope from the knick and up to 400 m out from the base across the pediment. Samples representative of the knobthorn savanna were all taken more than 400 m from the hills.

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Climate

The region is one of hot humid summers and warm-to-cool dry winters. Eighty-five per cent of the annual precipitation falls between October and March. The rain tends to fall in short intense thunderstorms, so that a high proportion of the annual precipitation can arrive within a few days. The pattern of rainfall over the study period (October 1975 to August 1977) and preceding years is shown in Fig. 2. The mean annual precipitation recorded at the Tsokwane Ranger Station for the period 1935 to 1979 is 561 mm (Gertenbach 1980). The means for both study years (taken from July to June) were both considerably higher than this, 651 mm for 1975-76 and 668 mm for 1976-77. In both summers of the study (1975-76 and 1976-77) the rains arrived late (Fig. 2), the first good rain in 1975 came at the end of November and in 1976 in mid-November. In 1976-77 there was a drought between mid-December and the end of January.

Temperatures in the Kruger Park can vary from 0°C to over 40°C. Mean daily temperatures (calculated by dividing the maximum plus the minimum by two) at Skukuza are about 27°C at the hottest time of the year (November-December) and 17°C at the coldest (June-July) (Smuts 1972). Temperatures are not recorded at the Tsokwane Ranger Station.

Fires

Two fires occurred during the study period. In September 1976 the knobthorn savanna west of Little Nwamuriwa was burnt in accordance with the rotational burning program of the National Parks Board. In mid-January 1977 the vegetation was dry as a result of the drought and lightning started a fire which burnt Nwamuriwa Hill and surroundings (the area burnt in each fire is shown in Fig. 1).

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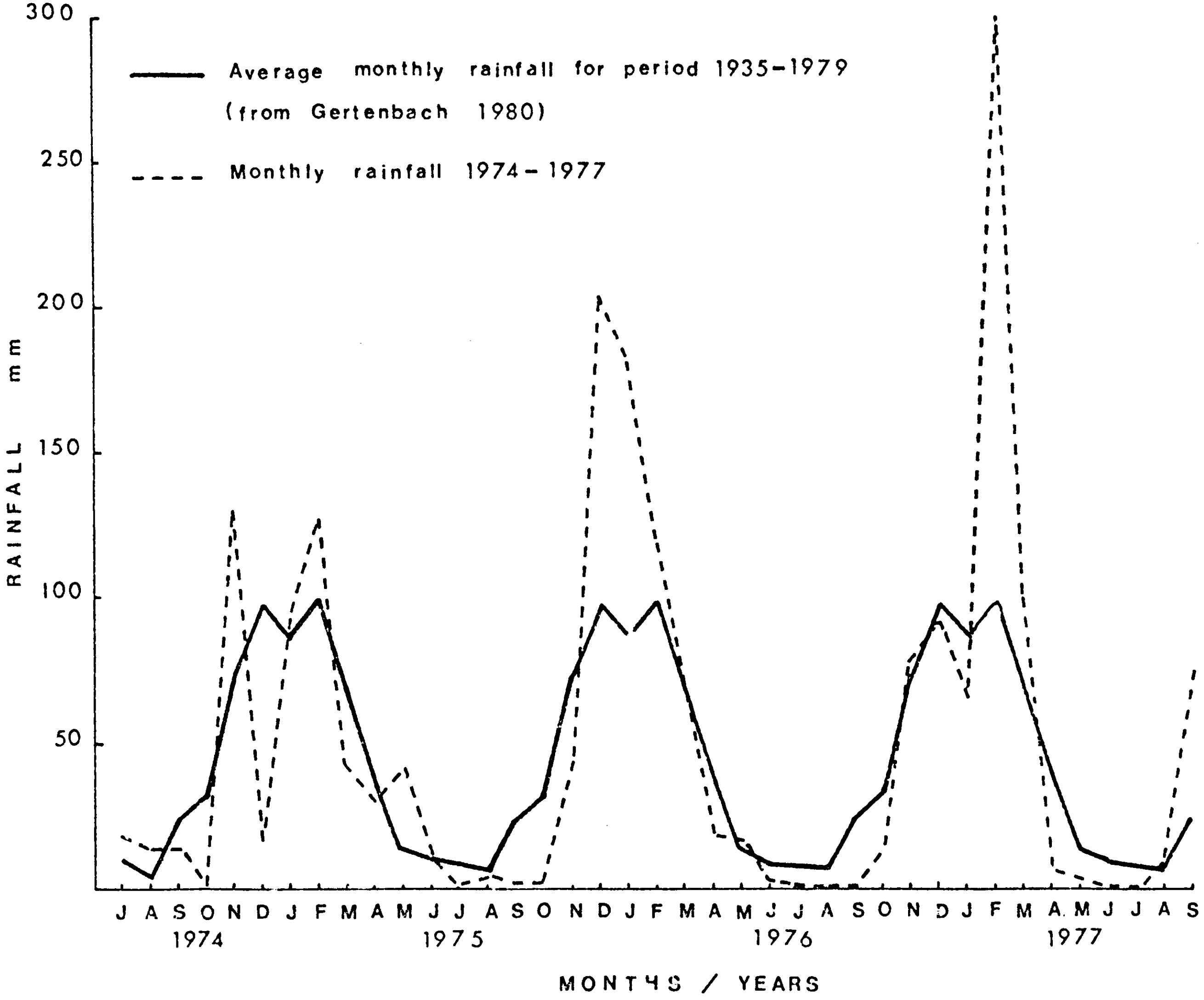

FIG. 2 MONTHLY PRECIPITATION RECORDED AT THE TSOKWANE RANGER STATION, KRUGER NATIONAL PARK FROM JULY 1974 TO SEPTEMBER 1977, COMPARED WITH THE MONTHLY AVERAGES FOR THE PERIOD 1935-1979

The study population

Kudu cows associate in discrete groups, averaging four adult cows per group plus offspring at Tsokwane in 1976. Male young leave the cow group when about two years old, but females usually remain with their maternal group into adulthood. Each female group remains within a specific home range, the boundaries of which remain very consistent from year to year (Owen-Smith unpublished). The home ranges of neighbouring groups overlap extensively but in the study area there were no cases of complete overlap between groups.

Breeding is seasonal, most conceptions occurring between April and June, and most young being born between January and March. The adult bulls consort with the female groups only during the rut in April, remaining till July. There is no sign of territoriality among bulls, each bull simply attaching himself temporarily to a cow group (Owen-Smith unpublished). Young calves lie out for the first few months after birth. The mother visits the calf periodically for suckling but in between rejoins her group. From about May the calves no longer lie out but remain with the mother's group.

There were four cow groups whose home ranges included the Nwamuriwa hills (see also Owen-Smith 1979). Most observations were made on the adult cows of three of these groups:

(i) The Nwamuriwa West Group, ranging on the west side of Nwamuriwa and the southern part of Little Nwamuriwa,

(ii) The Nwamuriwa East group on the east and north side of Nwamuriwa,

(iii) The Little Nwamuriwa group, ranging over Little Nwamuriwa and the knobthorn savanna to the west and north of it.

The range of all three groups overlapped in the saddle between the two hills.

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Other large mammals in the study area

The browsing ungulates most commonly seen in the study area, apart from kudus, were giraffe (*Giraffa camelopardalis*) and impala (*Aepyceros melampus*). Both these species were seen on the pediment and sometimes the lower slopes of the Nwamuriwa Hills but not on the upper slopes. Impala were more common in the adjoining *Acacia tortilis* savanna than in the study area itself. The waterbuck (*Kobus ellipsiprymnus*), predominantly a grazing antelope, occurred periodically throughout the study area, including the hill slopes and hill tops. Zebra (*Equus burchelli*) and wildebeest (*Connochaetes taurinus*) passed through the study area on migration but did not remain there year-round. Of the smaller antelope klipspringer (*Oreotragus oreotragus*) were fairly common on the hills, and steenbok (*Raphicerus campestris*) were sighted occasionally in the knobthorn savanna near the Nkongwana watercourse. Grey duiker (*Sylvicapra grimmia*) were seen twice on the pediment of the hill base ecotone and reedbuck (*Redunca arundinum*) occurred in the knobthorn savanna on the northern end of the study area. Lone elephant bulls (*Loxodonta africana*) quite frequently passed through the area. The large predators lions (*Panthera leo*), leopards (*P. pardus*) and spotted hyenas (*Crocuta crocuta*) were encountered fairly regularly, as well as black-backed jackals (*Canis mesomelas*).

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CHAPTER 1: THE ABUNDANCE AND NUTRITIONAL VALUE OF POTENTIAL FOOD

Defining potential food abundance

As discussed previously the objectives in measuring potential food abundance were firstly to provide an indication of habitat con=ditions that could be related to kudu population dynamics, and secondly to estimate the relative availability of the different plant species. It was therefore necessary to measure the abun=dance of vegetation components that would give a satisfactory indication of these aspects. It was also necessary that the procedures be clearly standardized so that comparable measure=ments could be obtained in future studies.

As defined by Owen-Smith (1979) potential food comprises all the vegetation components that the kudus may at some time include in their diet, and since they do occasionally eat grass this may be regarded as potential food. However, as noted, grass makes up an insignificant proportion of the kudus' diet but a substantial pro=portion of vegetation biomass, and including it in the estimates of potential food abundance would give a false impression of habi=tat quality for kudus. Estimates of potential food abundance were therefore restricted to woody plants and forbs (the term forbs is used here to include non-graminaceous herbs, creepers and dwarf shrubs).

All species of woody plants and forbs present in the study area were regarded as potential food. It is conceivable that some plants were never eaten by kudus, for example because of excessive concentrations of toxic compounds (Freeland and Janzen 1974), but no such plants were identified. Although there were some woody plants that were seldom eaten, all but the most rare species were seen to be browsed by kudus at some time during the study period. For forbs however, the question remains open because it was not possible to determine differences in acceptance among plants in the herb layer.

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Kudus accept leaves as well as shoot ends, but select mainly for the former, including shoots only incidentally with groups of leaves. Leaves are an easily identifiable component of potential food, but it was not possible to clearly determine the quantity of shoot ends that could be regarded as potential food. Newly emerging shoots are soft, but thicken and harden with age. Hardening proceeds gradually from the proximal to the distal end of the growing shoot, and there was insufficient evidence on which to define the maximum length of shoot end that could be accepted by kudus. In view of this uncertainty potential food abundance was measured in terms of leaves only. Thus an absolute measure of potential food abundance could not be obtained, but as a relative measure the abundance of leaves should be satisfactory since the leaves are the component that is favoured by the kudus.

For the purpose of sampling,potential food was divided into two main categories:

(i) Components in the tree-shrub layer, including all leaves within the maximum height reach of kudus but excluding those protected deep within thorny canopies (the estimates of maximum browsing depth and height reach are discussed below).

(ii) Components in the herb layer, further subdivided into:

  (a) the leaves of woody plant seedlings (defined as young trees and shrubs under 0,5 m tall), and
  (b) the leaves of herbaceous forbs, creepers and dwarf shrubs (together referred to as forbs).

Nutritional value

To assess habitat quality an overall indication of nutritional value of food plants was required. For ruminants the nutritional value of a forage depends largely on its ratio of cell sap to cell wall. The cell sap is potentially digestible by all animals, whereas part of the cell wall is digestible only by symbiont micro-organisms in the digestive tract of herbivores, and part is

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resistant to digestion (Van Soest 1967). In ruminants the rate of digestion is closely related to the proportion of cell wall as opposed to cell sap (Van Soest 1965); the greater the proportion of cell wall the slower the turnover rate of rumen contents. Voluntary intake of food depends on the digestion rate, so that if the diet has a high proportion of cell wall it digests slowly and appetite is depressed (Blaxter, Wainman and Wilson 1961). The concentration of protein in the forage is negatively correlated with the amount of cell wall. In young plant material the proportion of cell wall is low and the protein content high, but with increasing maturity the amount of cell wall increases and the protein content declines. Thus because of its negative relationship with cell wall, protein provides an overall index of nutritional value. A high protein content indicates a potentially rapid digestion rate and hence high food value, not only in terms of protein directly but also in the availability of energy and other nutrients (see also Owen-Smith and Novellie 1982).

Important food plants in the study area were therefore analysed for crude protein content, and also phosphorus, calcium and moisture contents.

Methods for sampling available browse on trees and shrubs are quite different to those used for plants in the herb layer, so the two categories are dealt with separately below.

PLANTS IN THE HERB LAYER

METHODS

The unit of sampling chosen for plants in the herb layer was a 1 m^2 quadrat. A 1 m^2 wooden frame was about the maximum size which could be carried comfortably in the field. The largest convenient quadrat size was preferred because the statistical distribution of samples would be more likely to follow the normal distribution required for application of parametric tests.

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If a smaller quadrat were used a larger proportion of plots would include no forbs and the distribution would be skew.

Preliminary non-destructive surveys were made in the hill base ecotone to see if there was a gradient in forb density, aerial cover and species composition from the hill slopes down to the base and out across the pediment (see Study area). Two transect lines were laid out, each extending 60 m up the slopes of Little Nwamuriwa and 240 m out from its base. Their positions were marked so that they could subsequently be relocated (transects 11 and 13, Fig. 3). A transect was located in the following way: I arbitrarily chose a starting point next to the road (Fig. 3), then chose a number at random from a pack of numbered cards and walked that number of paces down the road. The transect was then aligned so that it ran through this point at right angles to the hill base. The general areas to be surveyed were selected simply because kudus had frequently been seen foraging there.

The quadrats were spaced at 10 m intervals along the transect. The number of individual forbs rooted within each quadrat was counted. The aerial cover of forbs was estimated according to the following six point scale:

Score	Cover
+	0-5%
1	5-20%
2	20-40%
3	40-60%
4	60-80%
5	80-100%

The species within each quadrat were identified if possible (imma=ture forbs without reproductive parts could not always be identi=fied).

The southern transect (No. 11, Fig. 3) was first surveyed in November 1975 and the northern one (No. 13) in February 1976.

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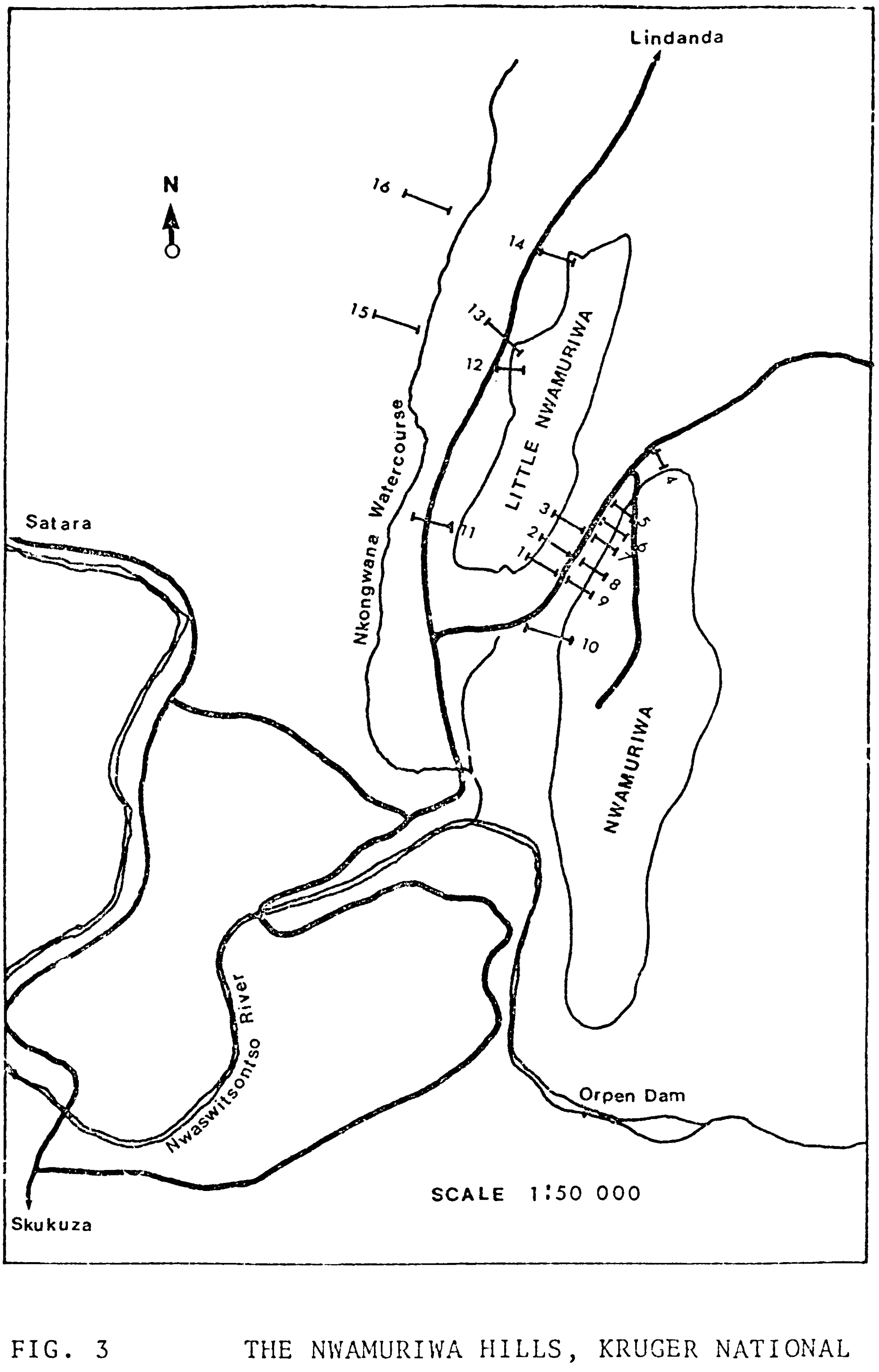

FIG. 3 THE NWAMURIWA HILLS, KRUGER NATIONAL PARK, SHOWING THE LOCATIONS OF 16 BELT TRANSECTS FOR THE SURVEY OF WOODY PLANTS. THE OUTLINE OF THE HILLS IS INDICATED BY THE 310 m CONTOUR LINES

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Both were surveyed at intervals up to February 1977 in order to check whether the pattern of seasonal changes in forb density and cover was the same over all parts of the gradient.

Sampling for estimation of forb abundance in terms of weight per unit area began in July 1976 and ended in August 1977. The unit of sampling was again the 1 m^2 quadrat from which all rooted forbs and woody plant seedlings were clipped at ground level. Clipping and sorting of plants in the herb layer was laborious and detailed estimations of differences over the slope-pediment gradient could not be undertaken. On the basis of the results from the two transects referred to above the hill base ecotone was regarded as comprising only two subdivisions; the pediment (areas of almost flat ground 20 to 300 m from the hill base) and the slopes (from 20 m out from the base to 80 m up hill).

Samples were collected monthly. From July to December 1976 each monthly sample included 20 quadrats from the pediment and 20 from the slopes. In mid-January 1977 Nwamuriwa Hill and surrounding savanna were burnt (Fig. 1) and sampling had to be extended to investigate differences between burnt and unburnt areas. From then until August 1977 monthly samples included 15 quadrats each from the unburnt slopes and pediment, and 10 each from the burnt slopes and pediment, except for April when only the unburnt areas were sampled. Ten quadrats were sampled from the knobthorn savanna during each of the months January, March, July and August 1977.

To assess acceptance, the frequency of the various vegetation com=ponents in the kudus' diet were to be compared with their relative abundance in the habitat. The vegetation samples therefore had to reflect availability as experienced by the kudus. The areas from which any monthly sample was clipped were thus selected to repre=sent the areas from which I had obtained records of foraging (see Chapter 2) during that month. The quadrat locations in the hill base ecotone were determined as follows. I chose a point arbitra=rily in the selected area, and from there walked ten paces in the direction of the hill base. This marked the starting point of a transect line running at right angles to the hill base. From one to five quadrats were placed at ten pace intervals along the transect. The procedure was repeated in other selected areas of the hill base ecotone until the required monthly sample size for each habitat subdivision was obtained. The orientation of the transect line in relation to the hill base was simply to standardise the procedure, and samples were recorded only as pediment or slope. If no kudus had been observed feeding in one of the habitat subdivisions of the hill base ecotone during the previous month the sampling areas were selected arbitrarily. The same procedure was followed in the knobthorn savanna except that transect lines were orientated at right angles to the Nkongwana drainage line (Fig. 3).

Diet composition was estimated from direct observations on foraging animals (see Chapter 2). Plants selected by kudus from the herb layer could not be seen and so the forb species composition of the diet could not be determined. Because of this limitation separation of clipped forbs by species was not undertaken. The five most abundant forb species were simply noted as being either present or absent in each quadrat. The forbs harvested from each quadrat were sorted into the following parts: (i) reproductive parts, flowers and fruits (ii) leaves (iii) terminal stems and (iv) main stems. A terminal stem was defined as the length of stem from the terminal tip to the point where it branched from a main stem. Main stems were those which remained after the terminal stems had been removed (Fig. 4).

Before December 1976 lack of facilities in the field prevented weighing of the material from each quadrat separately, so monthly samples were pooled and dried before sorting. Thus for the months July to November mean dry weight per quadrat was calculated without measures of variability.

From December 1976 to August 1977 the material clipped from each quadrat was sealed in separate polythene bags. The bags with contents were weighed to the nearest 0,1 g as soon as possible after clipping, and the contents were then sorted. Immediately after sorting the empty bag and each plant part category except leaves were weighed. The weight of the forb leaves was then obtained by subtraction. This assumed that all the moisture lost during sorting came from the forb leaves.

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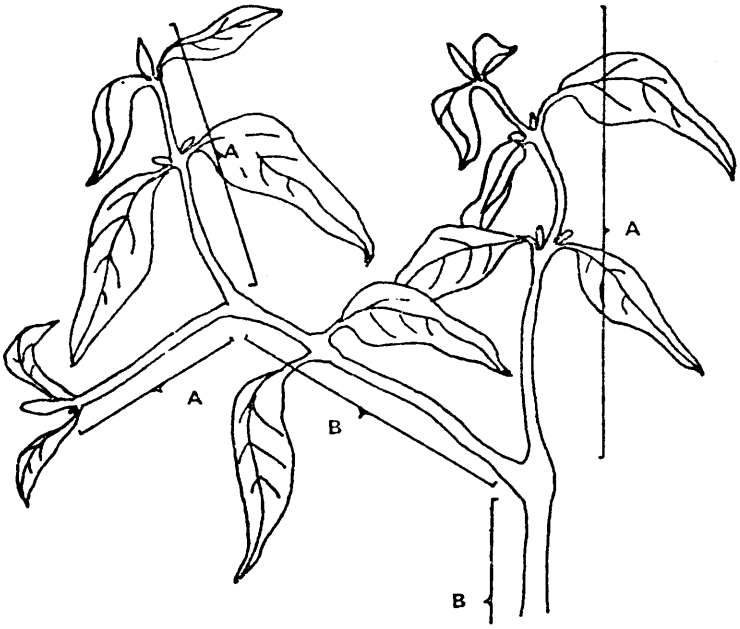

FIG. 4 SKETCH OF A FORB TO ILLUSTRATE THE SEPARATION INTO A, TERMINAL STEMS AND B, MAIN STEMS

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Lack of space made it difficult to dry the material from each quadrat separately. Quadrats from each habitat subdivision were pooled, placed in cardboard cartons and air dried for up to one week. Thereafter they were dried to constant weight in a forced-draught oven at about $100^{o}C$. The wet mass values for each quadrat were converted to dry using the per cent moisture of the pooled samples.

The total sample of dried forb leaves from each habitat subdivi= sion was then milled, thoroughly mixed, and a 500 mg subsample taken for analysis of crude protein (nitrogen content x 6,25), phosphorus and calcium. The analyses were done using an H_2SO_4 - H_2O_2 ashing procedure and the Auto-Analyzer system (Thomas, Sheard and Moyer, 1967) at the National Food Research Institute, CSIR, Pretoria.

RESULTS

The gradient in density and cover of forbs with increasing distance from the hill base

The densities (individual plants per m^2) and cover scores of forbs along the two transects are shown in Fig. 5. The values shown are for the mid-wet season (February), the time of highest forb abun= dance, and the late dry season (August), when forb abundance was low. Neither transect showed a marked trend over the gradient in the density of forbs, although there is an indication that density was lower on the pediment more than about 150 m from the hill base. For the cover score, however, both transects showed an obvious decline further than 100 to 150 m from the hill base.

Apart from this feature the pattern was variable. Transect I had generally higher cover scores at the hill base than on the upper slopes and pediment but transect II showed no particular trend over the zone from 60 m up the slope to 100 m out from the base.

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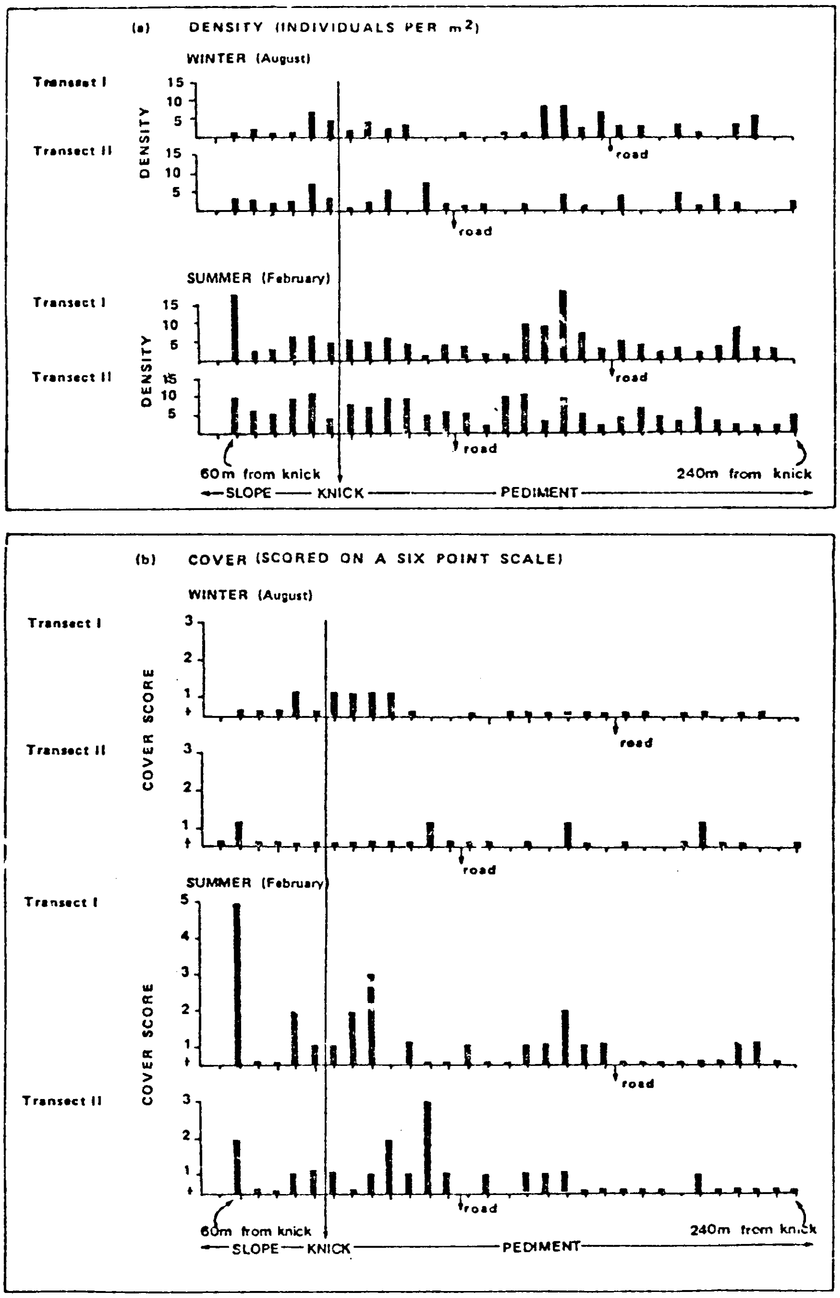

FIG. 5 GRADIENTS IN DENSITY AND COVER OF FORBS ON THE NWAMURIWA HILLS AS ESTIMATED IN 1 m^2 QUADRATS SPACED 10 m APART ALONG TWO TRANSECT LINES. EACH TRANSECT RAN 60 m FROM THE KNICK UP THE HILL SLOPES AND 240 m OUT FROM THE KNICK ACROSS THE PEDIMENT

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The results thus suggest that there was a gradual decline in the abundance of forbs with increasing distance from the pediment into the knobthorn savanna, but a larger number of transects would have been required to establish whether there was any variation in forb abundance closer to the hill base. It seems from the difference between transects I and II that the pattern was variable.

As noted under Methods the two transects were surveyed several times over the seasonal cycle. There was a pronounced seasonal cycle in both the density and cover of forbs (compare the February and August values in Fig. 5) but the pattern of seasonal variation seemed to be approximately the same over all sections of the gradient. The seasonal cycle in forb abundance is dealt with further in the following sections and therefore only the February and August values are shown in Fig. 5.

The dominant forb species in the hill base ecotone

Forbs were treated as a single component of the vegetation without distinguishing between species. However the percentage frequencies of the five species estimated to be dominant in terms of biomass were recorded (Table 1). The results show pronounced differences between the slopes and the pediment. _Solanum panduraeforme_ (Solanaceae) was the dominant forb throughout the pediment, but its distribution stopped at the knick, although isolated individuals were found on the lower slopes below about 30 m. _Aspilia mossambicensis_ (Compositae) and _Barleria lancifolia_ (Acanthaceae) on the other hand, were virtually confined to the slopes. The former, by virtue of its large size, was probably the dominant species on the slopes in terms of biomass. The other two species, _Justicia flava_ (Acanthaceae) and _Hibiscus micranthus_ (Malvaceae) were widespread on both slopes and pediment, although _H. micranthus_ tended to be more common on the slopes. Throughout the study area _Acacia nigrescens_ was by far the most abundant woody plant seedling (Table 1).

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TABLE 1 : FREQUENCY (PER CENT OF 1m² QUADRATS) OF THE DOMINANT FORB SPECIES AND WOODY PLANT SEEDLINGS IN THE HILL BASE ECOTONE. (BASED ON SAMPLES CLIPPED FOR BIOMASS ESTIMATION OVER THE WHOLE STUDY PERIOD.)

Species	Slopes N = 260 Quadrats	Pediment N = 270 Quadrats
Acacia nigrescens seedlings	10,8%	14,8%
Other seedlings	3,5%*	3,0%+
Justicia flava	35,8%	30,7%
Hibiscus micranthus	19,2%	10,0%
Solanum panduraeforme	8,5%	54,1%
Barleria lancifolia	22,7%	0,0%
Aspilia mossambicensis	20,0%	0,4%

*Combretum apiculatum
Sclerocarya caffra
Lannea stuhlmannii
Acacia tortilis
Acacia exuvialis
Maerua parvifolia

+Ehretia rigida
Ehretia amoena
Acacia gerrardii
Ormocarpum trichocarpum
Maerua parvifolia
Combretum imberbe

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There were a large number of forb species in the study area apart from the ones listed above. A total of 78 species were identified during this study from the slopes, pediment and knobthorn savanna combined, and an additional 24 were listed from the hill top by Coetzee (1977). The species are listed in Appendix I, and even this list is probably incomplete.

THE BIOMASS OF PLANTS IN THE HERB LAYER

The transects described above showed no consistent pattern of variation in forb abundance over the slopes-pediment gradient. Therefore no distinction was made between different subzones of the gradient in taking samples for biomass estimation. However because of the difference in species composition between the slopes and pediment I decided to divide the gradient into the two categories 'slopes' and 'pediment', as discussed above.

Statistical analysis

Since no measure of variation was made for samples clipped between July and November 1976 only means for these months could be calculated. For the period December to August the means are presented with 75% error bound confidence limits. These limits were chosen in preference to the conventional confidence interval because the latter assumes the population to be normally distributed. The distribution of mass per quadrat was skew, i.e. most quadrats included a small quantity but a few had very large quantities. The conventional confidence limits calculated for non-normal data can be in error (Fowler and Hauke 1979). The error bound method puts a lower bound on the confidence coefficient irrespective of the population distribution (for these data the lower bound is selected at 75%) and at the same time provides a specific value to the confidence coefficient if the distribution is in fact normal (in this case 95%, see Fowler and Hauke 1979).

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The recommended procedure for non-normal distributions is to apply a transformation and to calculate mean and confidence limits for the transformed variates (Sokal and Rohlf 1969). This procedure was not followed here because the means would not have been comparable with the July to November means which were calculated without measures of variation.

The significance of differences in forb abundance due to the three factors season, fire and gradient subdivisions were tested by three-way analysis of variance. The samples analysed were those from January to August 1977, excluding April as no samples were taken from the burnt veld during this month.

In performing the analysis of variance it is assumed that the variates are independent and randomly selected. The sampling procedure used (see Methods) does not strictly fulfill these requirements (quadrats from the same transect line may not be independent) but there is no reason to suspect that results would be seriously affected.

The analysis of variance also assumes that the variates are normally distributed and that the variance is homogeneous. As noted the distribution is skew and the means and variance tend to be positively correlated (variance is higher in summer than the dry season). The logarithmic transformation was therefore applied (Sokal and Rohlf 1969).

The analyses were performed by computer using the program <u>Rummage</u> (Scott, Bryce and Carter, 1977). The program output gives an indication of whether the variates are normally distributed and whether the variance is homogeneous. The results indicated that the logarithmic transformation was not completely successful in producing homogeneity of variance but the consequences of moderate heterogeneity of variance is not serious for the overall test of significance (Sokal and Rohlf 1969).

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The biomass of forbs in the hill base ecotone

Forb leaves

The mean weight of forb leaves per unit area (Fig. 6) followed a clear seasonal trend. Values declined from July to October 1976, and then, after the arrival of the first good rains in November, increased to peak levels in the mid-wet season (February to May), thereafter to decline once more through the 1977 dry season to a low point in August.

The analysis of variance of the samples from January to August (Table 2) showed highly significant variation between months. The overall differences between slopes and pediment and between burnt and unburnt veld were not significant. However, the significant fire x seasons interaction (Table 2) showed that the relative difference between burnt and unburnt veld was not the same in each month. This is evident from Fig. 6. Forb leaf abundance in the burnt veld was much lower than in the unburnt areas during the months immediately following the fire (January and February). Very heavy rains fell in February (Fig. 2) producing a flush of growth on the burnt veld so that by the time the dry season arrived there was little difference between burnt and unburnt areas in abundance of forb leaves.

Terminal stems

The abundance of terminal stems showed essentially the same features described for the leaves and was therefore not analysed statistically (Fig. 7). The seasonal cycle differed only in that the contrast between peak wet season and lowest dry season values was not as pronounced for the terminal stems as for leaves. As with the leaves the abundance of terminal stems was lower in the burnt veld than in the unburnt veld over the months immediately following the fire but thereafter there was no apparent difference.

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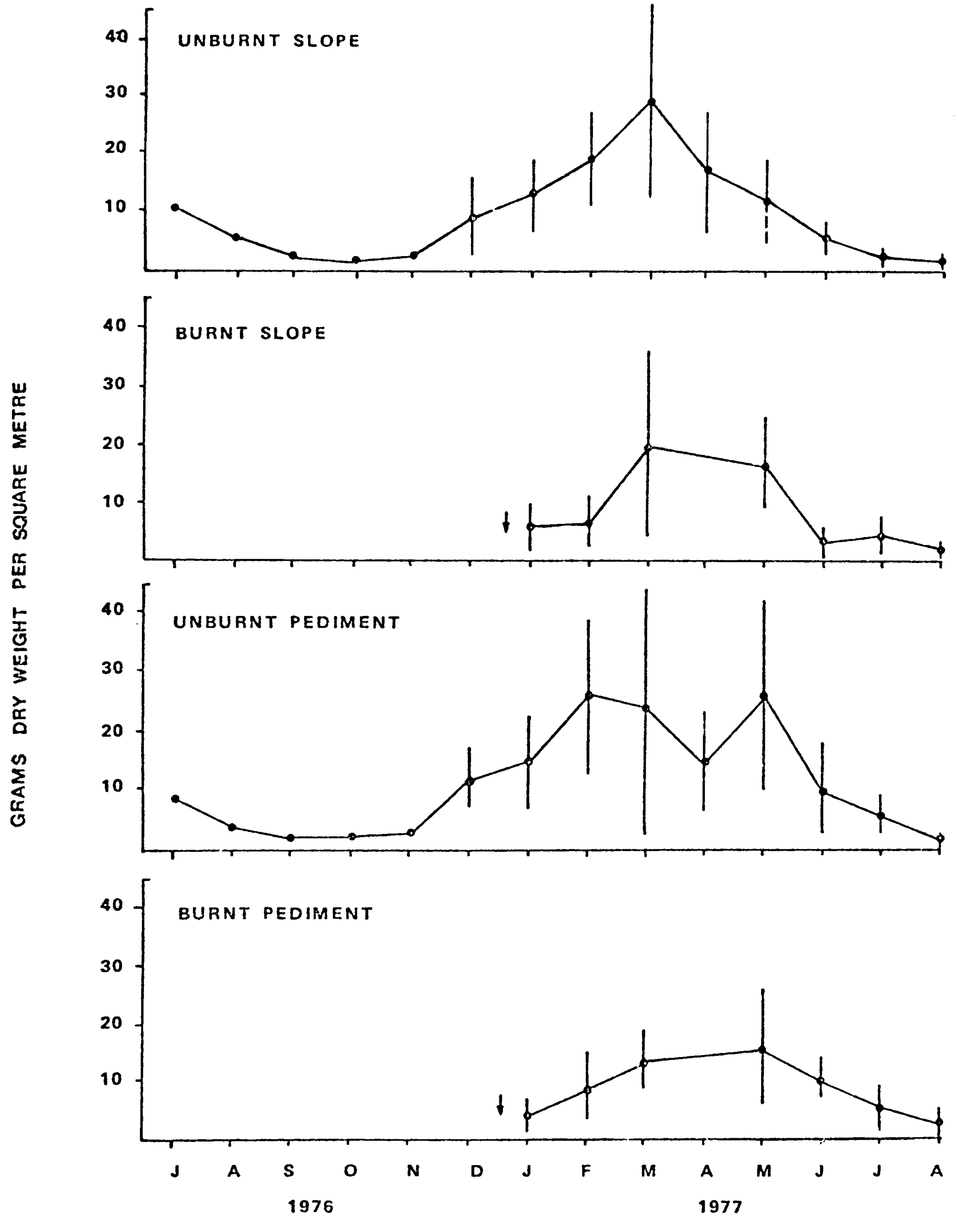

FIG. 6 MONTHLY VARIATION IN BIOMASS OF FORB LEAVES IN THE HILL BASE ECOTONE. VERTICAL LINES INDICATE 75% ERROR BOUND CONFIDENCE LIMITS.

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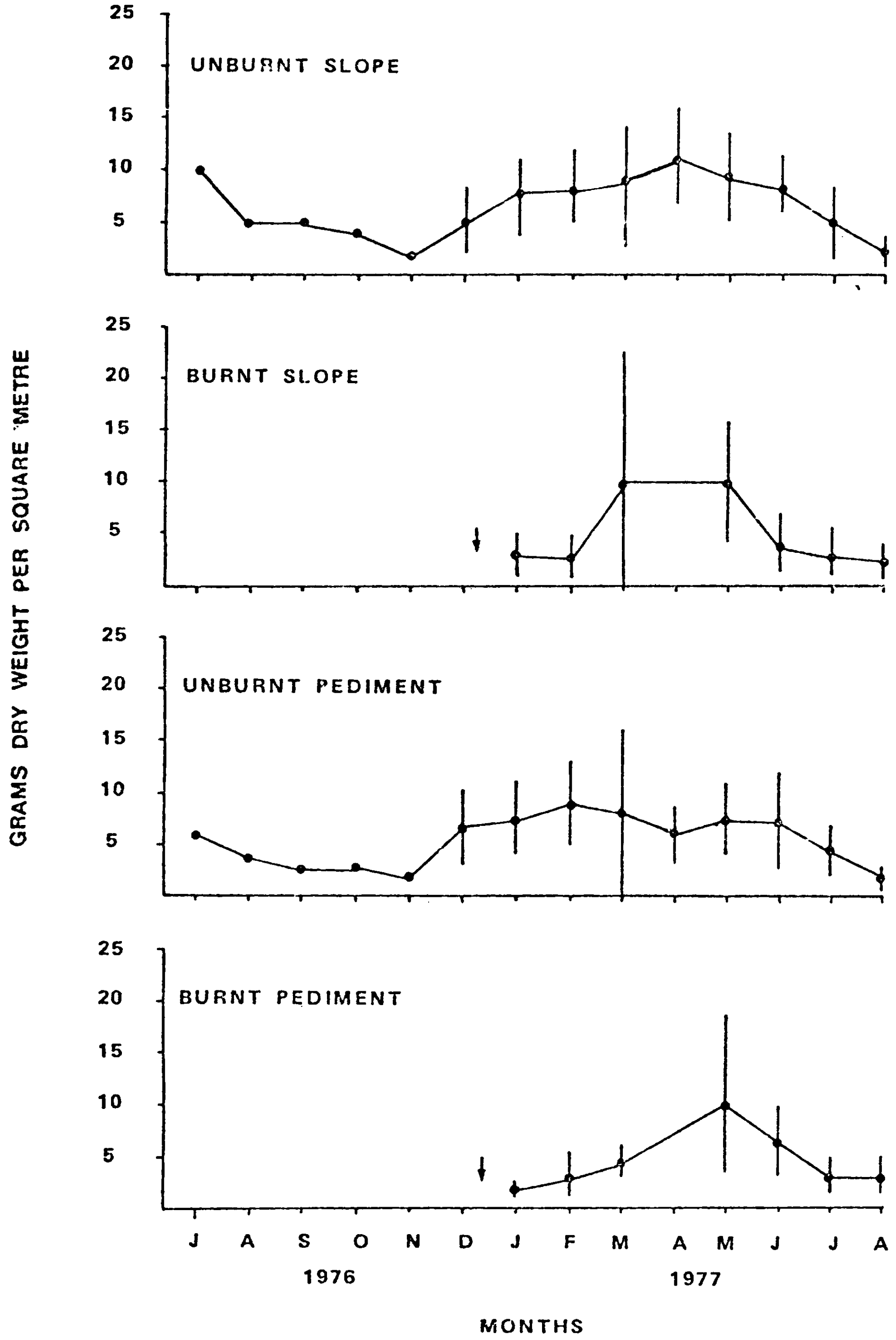

FIG. 7 MONTHLY VARIATION IN BIOMASS OF FORB TERMINAL STEMS IN THE HILL BASE ECOTONE. VERTICAL LINES INDICATE 75% ERROR BOUND CONFIDENCE LIMITS

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TABLE 2 : ANALYSIS OF VARIANCE OF FORB LEAF ABUNDANCE (g/m²) IN THE HILL BASE ECOTONE. VARIATES ARE TRANSFORMED TO LOGARITHMS

Source of variation	df	Mean Square	F ratio	Signifi= cance
Fire	1	0,4761	2,43	ns
Gradient Subdivisions (slopes : pediment)	1	0,3652	1,86	ns
Months (January to August excluding April)	6	3,6269	18,49	P< 0,001
Fire x Gradient Interaction	1	0,1147	0,59	ns
Fire x Months Interaction	6	0,5707	2,91	P< 0,01
Gradients x Months Interaction	6	0,2052	1,05	ns
Fire x Gradients x Months	6	0,2904	1,48	ns
Error	322	0,1962		
Total	349			

TABLE 3 : ANALYSIS OF VARIANCE OF FORB MAIN STEM ABUNDANCE (g/m²) IN THE HILL BASE ECOTONE. VARIATES ARE TRANSFORMED TO LOGARITHMS

Source of variation	df	Mean Square	F ratio	Signifi= cance
Fire (burnt : unburnt)	1	2,9053	7,64	P< 0,01
Gradient Subdivisions (slopes : pediment)	1	1,4240	3,74	P< 0,10
Months (January to August excluding April)	6	0,4947	1,30	ns
Fire x Gradients Interaction	1	0,8786	2,31	ns
Fire x Months Interaction	6	0,1836	0,48	ns
Gradients x Months Interaction	6	0,1004	0,26	ns
Fire x Gradients x Months	6	0,4554	1,20	ns
Error	322	0,3804		
Total	349			

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Main stems

The abundance of main stems (Fig. 8) did not follow as clear a seasonal trend as that of the leaves and terminal stems. There appeared to be a decline in main stem abundance from July to November 1976, followed by an increase to higher levels in May to July 1977. However, the trend was not pronounced and the analysis of variance of the samples from January to August (Table 3) showed no significant difference between months. Main stem abundance was generally higher on the pediment than on the slopes but the difference was significant only at the ten per cent level. The difference was probably due to the presence on the pediment of Solanum panduraeforme which has thick woody stems. The overall difference between the burnt and unburnt veld in abundance of main stems was highly significant. Unlike the leaves and terminal stems the abundance of main stems on the burnt veld remained lower than the unburnt veld over the dry season following the fire. This would be expected because the recovering forbs on the burn would have been at a less mature stage of growth when the dry season set in, and main stems would not have been so thick as those of the undamaged forbs on the unburnt areas.

Forb biomass in the knobthorn savanna

The abundance of forbs in the knobthorn savanna (Table 4) also showed pronounced seasonal changes, with high values in the wet season (January and March) and low values in the dry season (July and August). Analysis of variance (after transformation of the variates to logarithms) showed leaf biomass in the knobthorn savanna (overall mean 5,9 g/m^2) to be significantly lower than on the unburnt pediment (overall mean 11,7 g/m^2) ($F = 6,71$, df 1, 92, $P < 0,05$). Abundance of both terminal and main stems were also lower in the knobthorn savanna than the hill base ecotone. This result accords with that found from the two transect lines discussed above.

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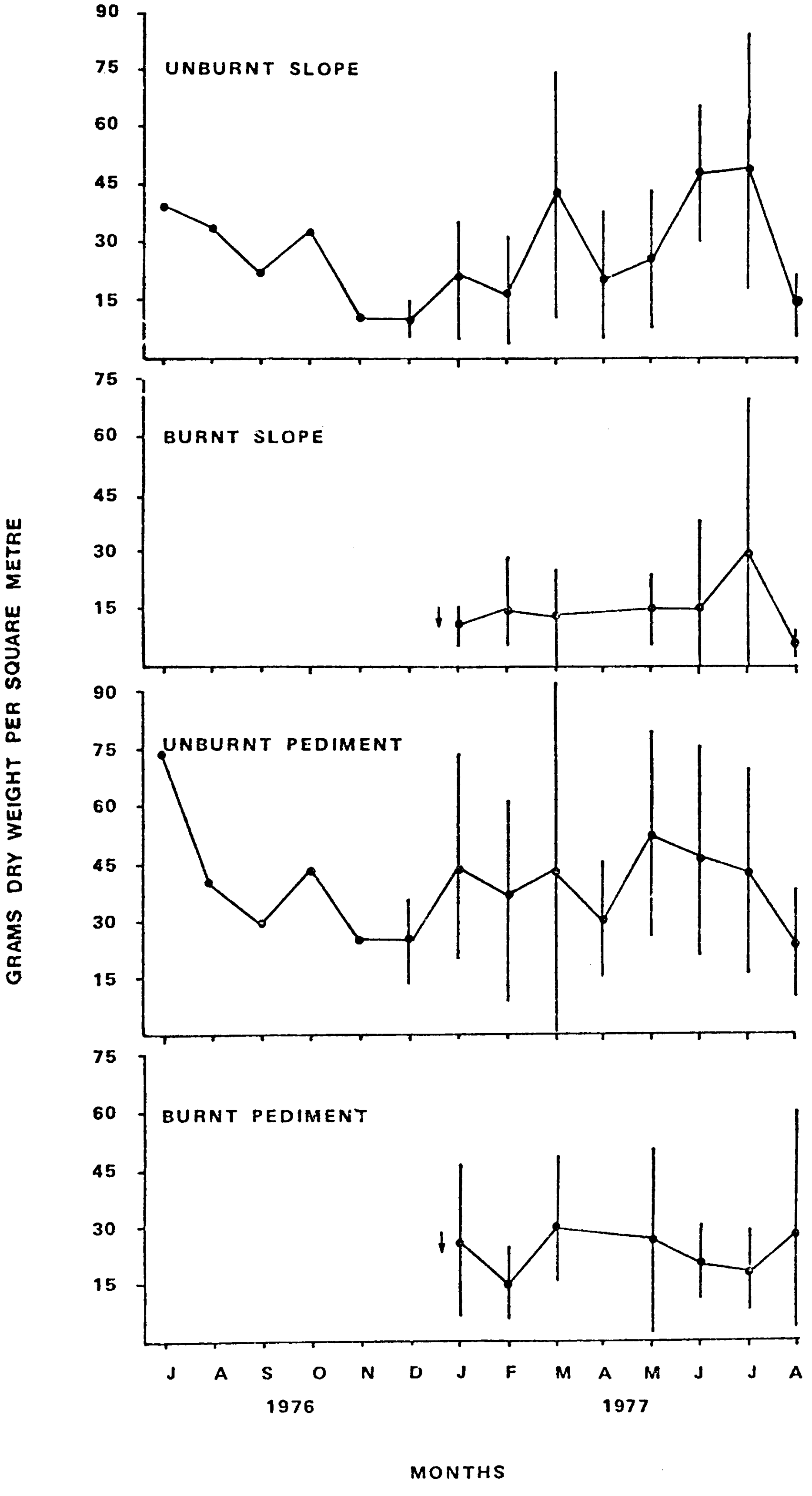

FIG. 8 MONTHLY VARIATION IN BIOMASS OF FORB MAIN STEMS IN THE HILL BASE ECOTONE. VERTICAL LINES INDICATE 75% ERROR BOUND CONFIDENCE LIMITS

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TABLE 4 : MEAN DRY WEIGHT (GRAMS PER SQUARE METRE) OF FORB LEAVES, TERMINAL STEMS AND MAIN STEMS IN THE KNOBTHORN SAVANNA

	MONTHS			
Plant part	January	March	July	August
Forb leaves	5,30g	17,10g	0,94g	0,40g
Terminal Stems	2,34g	6,82g	0,89g	0,28g
Main Stems	16,25g	18,60g	3,61g	0,70g

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The abundance of forb reproductive parts

The weight per unit area of reproductive parts was made up largely of fruits, with only a small proportion of flowers. Several forb species in the study area produced relatively large fruits which were eaten by kudus. By far the most abundant of these were the round yellow fruits of _Solanum panduraeforme_. Other frequently utilized fruits were those of the creepers, _Cucumis africanus_ and _Cucumis metuliferus_.

Compared with the other plant part categories fruits were scarce and tended to be clumped in distribution, so that they were absent from most quadrats and present in only a few. This distribution pattern makes statistical analysis difficult and a larger monthly sample would have been necessary for reliable estimates of abundance. However, the monthly means (Table 5) give an overall indication of seasonal trend and differences between habitat subdivisions.

Reproductive parts were generally more abundant on the pediment than the slopes because of the predominance of _Solanum panduraeforme_ in the former area. On the unburnt pediment fruits reached maximum abundance in the late wet - early dry season (March to May). In the other habitat subdivisions no seasonal differences were evident. There was some indication that fruit abundance was higher on the unburnt veld than on the burns.

Woody plant seedlings

As with fruit the relative scarcity of seedlings makes statistical analysis difficult. Monthly weights per m^2 of whole seedlings above ground are shown in Table 6. There was little difference between the slopes and the pediment, but abundance appeared to be higher on unburnt than on burnt veld. The monthly seedling samples were not sorted into plant parts in their entirety, but, based on subsamples, the leaves were estimated to comprise 40% of the total dry mass in the wet season (November to April) and 20% in the dry season (May to October). Leaf abundance of woody plant

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TABLE 5 : MEAN DRY WEIGHT (GRAMS) OF FORB REPRODUCTIVE PARTS PER SQUARE METRE

Habitat Subdivision	1976				1977							
	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.
Hill Base Ecotone, Unburnt Pediment	0,4g	0,2g	0,3g	0,5g	0,3g	0,7g	1,9g	1,7g	3,1g	1,2g	0,6g	0,0g
Hill Base Ecotone, Unburnt Slopes	0,8g	0,0g	0,0g	0,7g	0,0g	0,0g	0,3g	0,1g	0,2g	0,1g	0,2g	0,0g
Hill Base Ecotone, Burnt Pediment	-	-	-	-	0,0g	0,0g	0,4g	-	1,2g	0,3g	0,0g	0,2g
Hill Base Ecotone, Burnt Slopes	-	-	-	-	0,0g	0,0g	0,0g	-	0,5g	0,1g	0,1g	0,0g
Knobthorn Savanna	-	-	-	-	0,0g	-	0,0g	-	-	-	0,1g	0,0g

- Signifies no samples taken

TABLE 6: MEAN DRY WEIGHT (GRAMS) OF WOODY PLANT SEEDLINGS PER SQUARE METRE. THE VALUES ARE FOR ALL ABOVE GROUND PARTS*

Habitat Subdivision	1976				1977							
	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.
Hill Base Ecotone, Unburnt Pediment	1,0g	0,7g	1,0g	2,6g	1,6g	0,0g	0,9g	1,9g	5,7g	1,4g	1,0g	0,6g
Hill Base Ecotone, Unburnt Slopes	0,2g	0,3g	1,4g	4,8g	5,1g	1,8g	0,7g	1,8g	0,0g	0,7g	0,7g	0,9g
Hill Base Ecotone, Burnt Pediment	-	-	-	-	0,5g	0,4g	0,1g	-	0,9g	0,1g	0,5g	0,0g
Hill Base Ecotone, Burnt Slopes	-	-	-	-	0,0g	0,0g	1,0g	-	1,9g	0,0g	0,0g	0,0g
Knobthorn Savanna	-	-	-	-	0,0g	-	0,2g	-	-	-	1,0g	8,2g

- Signifies no samples taken

*For estimates of seedling leaf biomass see text

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seedlings in the unburnt hill base ecotone can thus be estimated as 0,8 gm^{-2} in the wet season and 0,2 gm^{-2} in the dry season.

THE NUTRIENT CONTENT OF FORB LEAVES

Statistical analysis

The differences in nutrient content of forb leaves due to the seasons, the fire and the gradient subdivisions were tested by three-factor analysis of variance. These analyses were also done on the monthly samples from January to August 1977 excluding April. The measurements of nutrient content were done without replication and so the second-order interaction mean square is used as the error variance on the assumption that the seasons x fire x gradient subdivision interaction is zero (Sokal and Rohlf 1969).

Moisture content of forb leaves

The moisture content of unburnt forb leaves declined from highest levels in December 1976 to lowest levels in August 1977 (Fig. 9). The relatively low moisture content of forb leaves on the unburnt areas in January was the result of the mid-summer drought in December-January 1976-77 when forbs and grass showed signs of wilting throughout the study area.

The analysis of variance showed a highly significant interaction between the effects of fire and the months (Table 7) which indicates that the seasonal trend in leaf moisture content differed significantly between burnt and unburnt areas. On the burns the moisture content was naturally much lower than on the unburnt areas after the fire in January (Fig. 9). After the good rains in February the burnt forbs recovered so that their leaf moisture

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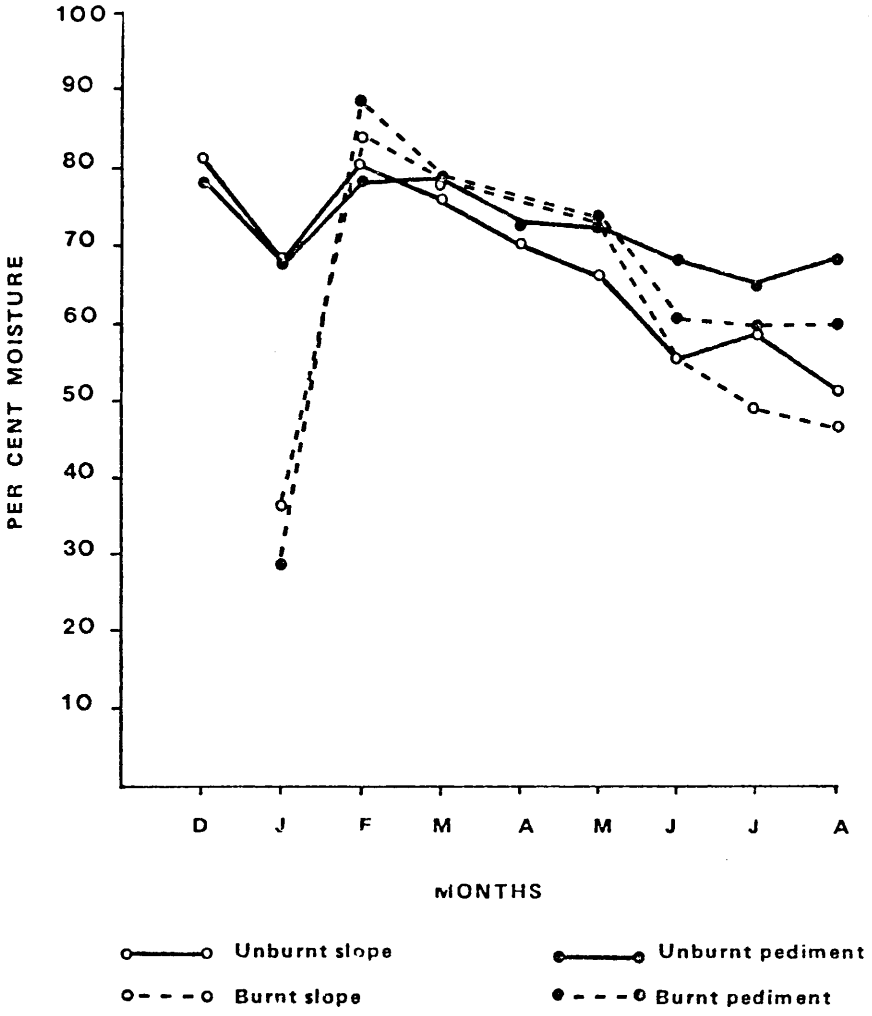

FIG. 9 MOISTURE CONTENT OF FORB LEAVES IN THE HILL BASE ECOTONE

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TABLE 7 : ANALYSIS OF VARIANCE OF MOISTURE CONTENT OF FORB LEAVES

Source of variation	df	Mean Square	F ratio	Signifi=cance
Fire (burnt : unburnt)	1	234,32	42,30	P< 0,005
Gradient Subdivisions (slopes : pediment)	1	190,32	34,35	P< 0,005
Months (January to August excluding April)	6	603,49	108,93	P< 0,005
Fire x Gradients Interaction	1	8,04	1,45	ns
Fire x Months Interaction	6	201,32	36,34	P< 0,005
Gradient x Months Interaction	6	38,32	6,92	P< 0,05
Fire x Months x Gradients*	6	5,54		
Total	27			

TABLE 8 : ANALYSIS OF VARIANCE OF MOISTURE CONTENT OF FORB TERMINAL STEMS

Source of variation	df	Mean Square	F ratio	Signifi=cance
Fire (burnt : unburnt)	1	0,57	0,01	ns
Gradient Subdivisions (slopes : pediment)	1	17,28	0,29	ns
Months (January to August excluding April)	6	1123,62	18,60	P< 0,005
Fire x Gradients Interaction	1	3,57	0,06	ns
Fire x Months Interaction	6	333,91	5,53	P< 0,05
Gradient x Months Interaction	6	60,12	1,00	ns
Fire x Months x Gradients*	6	60,41		
Total	27			

*The moisture contents were measured without replication and therefore the mean squares are all tested over the second order interaction mean square on the assumption that the fire x months x gradients interaction is zero.

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content then equalled that of the unburnt forbs. However, in the dry season following the fire leaf moisture content on the burnt areas declined to lower levels than on the unburnt veld (Fig. 9).

The significant interaction between gradient subdivisions and months (Table 7) shows that the trend of seasonal variation in forb leaf moisture content was not the same on the slope and the pediment. The contrast between peak wet season and lowest dry season values was more marked for forbs on the slopes than those on the pediment. Thus there was little difference in leaf moisture content between forbs on the slopes and those on the pediment during the wet season. In the dry season, however, leaf moisture content on the slopes was lower than on the pediment. This is possibly due to a difference between the slopes and pediment in soil moisture content in the dry season, a point further discussed below.

Moisture content of terminal stems

The seasonal trend in moisture content of terminal stems was essentially the same as that of the leaves (Fig. 10). The significant fire x months interaction (Table 8) shows that the relative differences between burnt and unburnt areas were not the same over all months. Once again this is because there was a marked difference in moisture content between burnt and unburnt forbs immediately after the fire, but no difference existed after the February rains had brought about a recovery of the burnt forbs.

Unlike the leaves the moisture content of the terminal stems did not differ significantly between the gradient subdivisions (Table 8), and since there is no significant months x gradients interaction there is no reason to suspect that the seasonal trend in terminal stem moisture differed between slopes and pediment.

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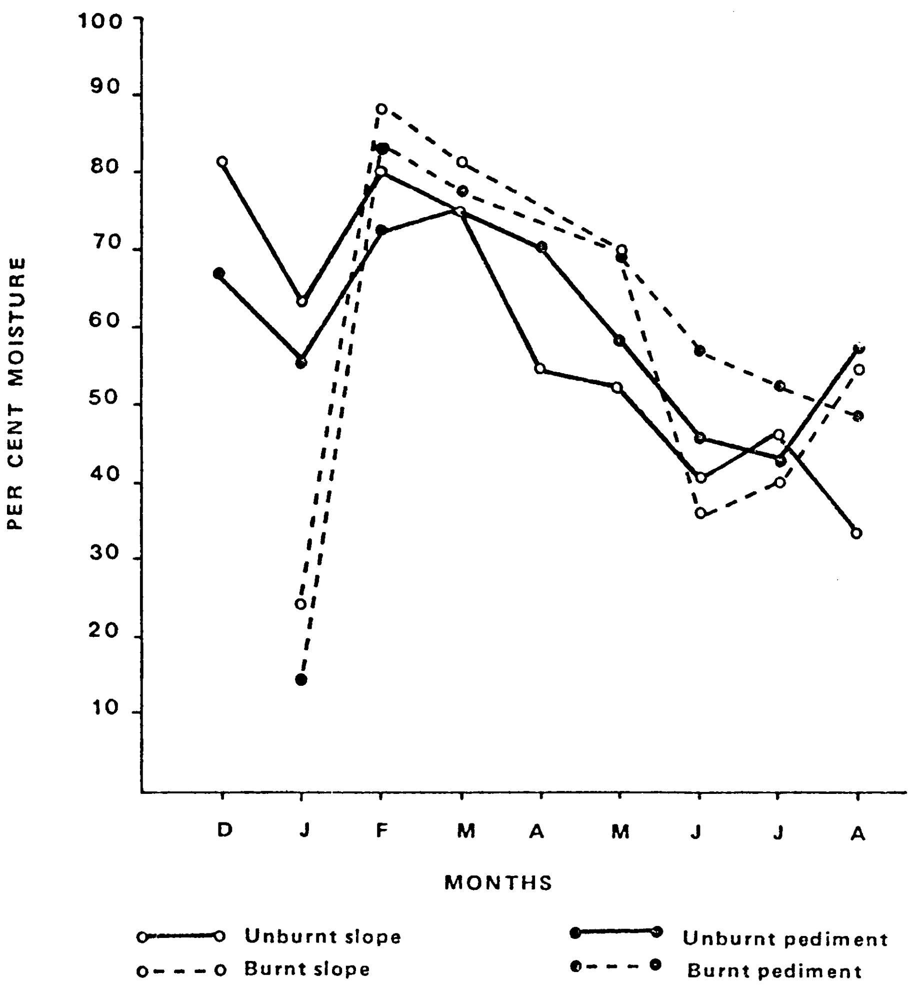

FIG. 10 MOISTURE CONTENT OF FORB TERMINAL STEMS IN THE HILL BASE ECOTONE

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Crude protein content of forb leaves

Monthly leaf samples analysed for crude protein concentrations were taken from July 1976 to August 1977, thus covering a longer period than the analyses of moisture content. The seasonal trends on unburnt veld were as follows: Protein content was low during the dry period from July to October 1976, then increased to peak levels with the arrival of the spring rains in November. Thereafter protein content declined over the summer months, December to February, and then declined to yet lower levels during the dry season from May to August 1977 (Fig. 11). Unlike moisture the protein content of forb leaves on the unburnt areas did not decline during the January drought.

The analysis of variance (Table 9) concerns only the period after the summer fire, i.e. January to August 1977. The analysis showed significant main effect differences between seasons, between burnt and unburnt areas and between slopes and pediment. Thus over the period considered in the analysis the protein content of forb leaves on the pediment was higher than those on the slopes, and higher for the unburnt forbs than for the burnt ones.

The analysis of variance shows no significant interactions between any of the factors (Table 9) so there were apparently no differences between the habitat subdivisions in the seasonal trend between January and August 1977. However if the whole study period is considered (Fig. 11) it is evident that the protein content of forbs on the slopes was lower than those on the pediment only in the dry seasons (in both 1976 and 1977). In the wet season, November to February, forbs on the slopes had as high or higher protein content than those on the pediment. This is in fact the same effect revealed by the analysis of the forb leaf moisture contents.

Phosphorus content of forb leaves

On the unburnt veld the phosphorus content of forb leaves rose from low levels in the 1976 dry season to a peak in November when

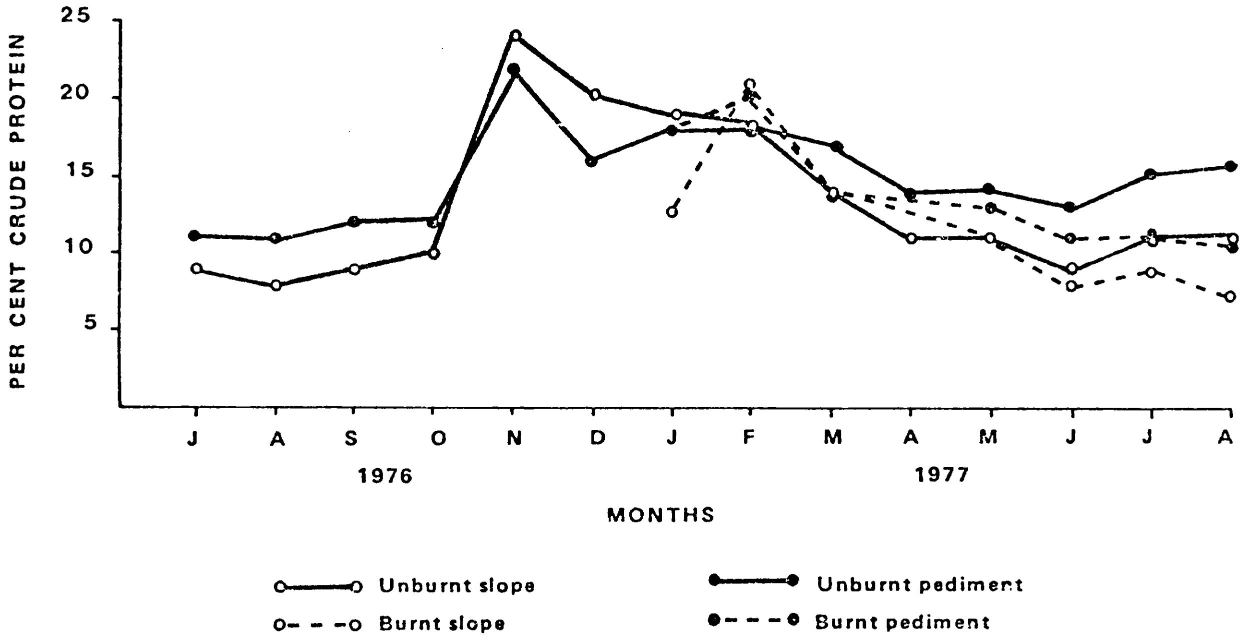

FIG. 11 CRUDE PROTEIN CONTENT OF FORB LEAVES (EXPRESSED AS A PERCENTAGE OF DRY WEIGHT) IN THE HILL BASE ECOTONE

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TABLE 9 : ANALYSIS OF VARIANCE OF THE CRUDE PROTEIN CONTENT OF FORB LEAVES

Source of variation	df	Mean Square	F ratio	Signifi= cance
Fire (burnt : unburnt)	1	20,23	7,40	P< 0,05
Gradient Subdivisions (slopes : pediment)	1	36,57	13,38	P< 0,05
Months (January to August excluding April)	6	47,46	17,36	P< 0,005
Fire x Gradients Interaction	1	0,82	0,30	ns
Fire x Months Interaction	6	5,91	2,16	ns
Gradients x Months Interaction	6	1,26	0,45	ns
Fire x Months x Gradients*	6			
Total	27			

TABLE 10 : ANALYSIS OF VARIANCE OF THE PHOSPHORUS CONTENT OF FORB LEAVES

Source of variation	df	Mean Square	F ratio	Signifi= cance
Fire (burnt : unburnt)	1	0,006	1,33	P< 0,10
Gradient Subdivisions (slopes : pediment)	1	0,125	27,76	P< 0,005
Months (January to August excluding April)	6	0,018	4,07	ns
Fire x Gradients Interaction	1	0,008	1,76	ns
Fire x Months Interaction	6	0,004	0,87	ns
Gradient x Months Interaction	6	0,002	0,38	ns
Fire x Gradients x Months*	6	0,005		
Total	27			

*The contents of protein and phosphorus were measured without replication and therefore the mean squares are all tested over the second order interaction mean square on the assumption that the fire x months x gradient interaction is zero.

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the spring rains commenced. It then declined to a low point in January (possibly as a result of the drought at this time), increased again in February, then declined during the 1977 dry season (Fig. 12). However the phosphorus content of leaves was more variable between months than the protein content, and the difference between the months January to August is significant only at the ten per cent level (Table 10). Forb leaves from the pediment tended to be much higher in phosphorus content than those from the slopes and the difference is highly significant (Table 10). The reason for the difference is unknown. The differences between burnt and unburnt areas in the phosphorus content of forb leaves are not significant.

The calcium content of forb leaves, and the calcium : phosphorus ratio are discussed below.

Moisture, protein and phosphorus content of forb leaves in the knobthorn savanna

The nutrient content of forb leaves in the knobthorn savanna are shown in Table 11. A comparison of these values with those of the unburnt pediment shows the following differences:

(i) protein content was higher in forb leaves on the pediment than in the knobthorn savanna for all samples;

(ii) moisture content of forb leaves was higher in the knobthorn savanna than on the pediment in the wet season samples but lower for the dry season samples;

(iii) phosphorus contents of forb leaves tended to be lower in the knobthorn savanna than on the pediment.

There was no consistent difference between the two areas in the moisture content of terminal stems. However, in view of the small number of samples taken from the knobthorn savanna these conclusions must be regarded as tentative.

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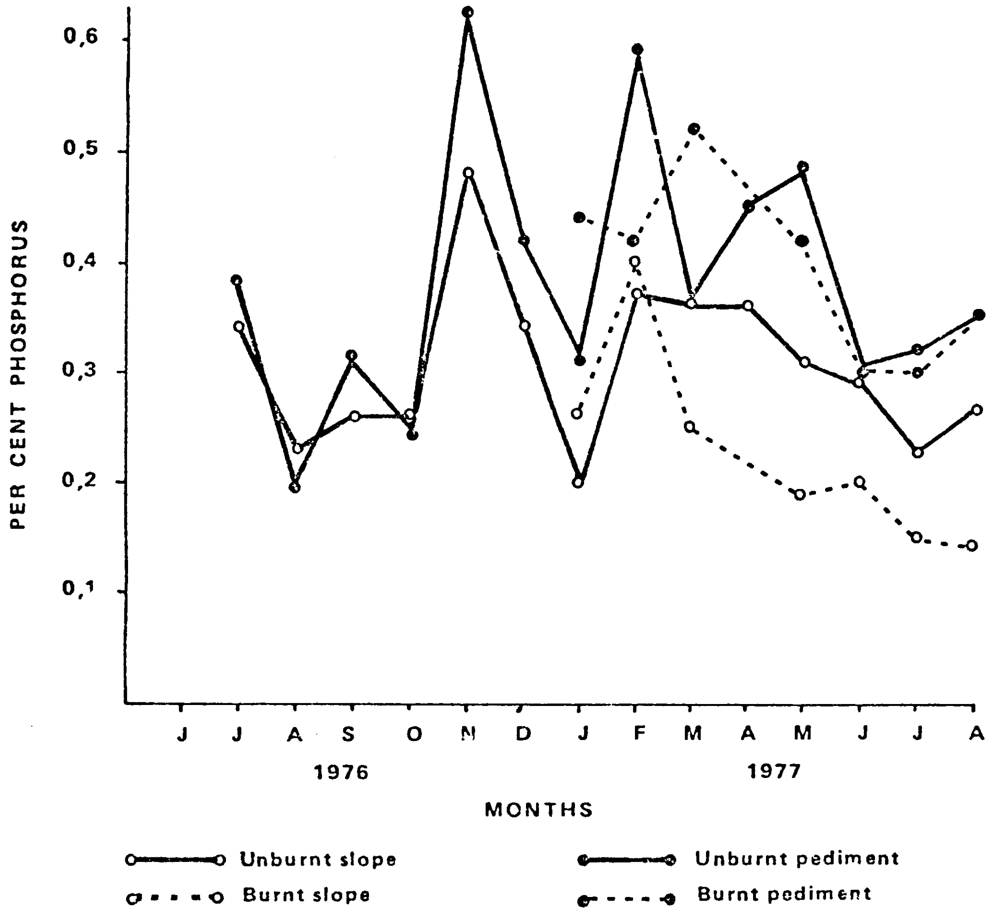

FIG. 12 PHOSPHORUS CONTENT OF FORB LEAVES (EXPRESSED AS A PERCENTAGE OF DRY WEIGHT) IN THE HILL BASE ECOTONE

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TABLE 11 : MOISTURE, PROTEIN AND PHOSPHORUS CONTENT OF FORBS IN THE KNOBTHORN SAVANNA (PROTEIN AND PHOSPHORUS EXPRESSED AS A PERCENTAGE OF DRY WEIGHT)

	MONTHS (1977)			
	Jan.	Mar.	Jul.	Aug.
Per cent Moisture in Leaves	71	83	61	13
Per cent Moisture in Terminal Stems	64	70	50	28
Per cent Protein in Leaves	-	15,1	8,3	9,1
Per cent Phosphorus in Leaves	-	0,24	0,31	0,23

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WOODY PLANTS

METHODS

To determine the abundance of woody plant leaves in dry weight per unit ground area two separate estimates were made, one of the canopy volume per unit area, and another of the weight of leaves per unit canopy volume (referred to as canopy leaf density). The product of the two estimates provides the measure of leaf weight per unit area.

Estimation of canopy volume per unit area

The method adopted is similar to that of Anderson and Walker (1974) and Walker (1976). Species composition, density and canopy volumes of woody plants were estimated from 4 m wide belt transects. In the hill base ecotone the transects ran from the knick at the hill base to 80 m up the slopes (or as far as the crest of the hill if this was lower than 80 m from the base) and varying distances out from the base across the pediment. The transects were aligned so that they ran at right angles to the hill base (following the procedure described for the herb layer transects above) so that variation along the slopes-pediment gradient could be assessed.

The midline of the transect was marked by stretching a tape measure along the ground, and any woody plant over 0,5 m tall, rooted within 2 m on either side of the tape was considered 'in'. For each woody plant within the belt transect the following information was recorded:

(a) The species
(b) Its distance from the start of the transect

(c) Its height (measured to the nearest 0,1 m for those below 3 m in height, and estimated to the nearest metre for taller ones)

(d) Phenology (scored as new leaf, new shoot, mature leaf, leaf fall, flowers or fruit)

(e) Measurements for the calculation of canopy volume below 2,5 m. These measurements (from Anderson and Walker 1974, Walker 1976) are:

   (i) Canopy depth (CD), from the lowest foliage up to 2,5 m, or to the uppermost foliage for plants below 2,5 m in height. (This value could be zero for large trees with no part of the canopy within the browse range.)

   (ii) The longest diameter (D_1) of the canopy within the browse range.

   (iii) The diameter (D_2) at right angles to D_1.

For calculation of volume the canopy is regarded as a cylinder with height equal to CD and radius equal to $(D_1 + D_2)/4$ (half the mean of the two diameters). The value of 2,5 m for the upper limit of the browse range of kudu has been used in other studies (Goodman 1975, Dayton 1978). I made four measurements of the maximum height reached by foraging kudus, three of females and one of a male. In all cases the animals kept all four feet on the ground and stretched upwards to reach a high shoot. The highest of the three females was 2,1 m while the male reached 2,3 m. These animals may not have stretched to their utmost but it seemed unlikely that they could have reached 2,5 m unless they reared up on their hindlegs or the bull used his horns to break branches. (Only one bull was seen doing this during the two year study period.) The estimate of 2,5 m above ground should therefore be regarded as the absolute maximum browse height of kudu, except for males breaking down branches.

Locating the transects

As noted, one aim of the study was to compare the botanical compo=sition of the kudus' diet with that of the available vegetation. Owing to limitations of topography and visibility observations on plants eaten could be made only in certain regions of the kudus' home range (see Chapter 2). To assess diet composition in rela=tion to availability it was desirable that estimates of food abundance should reflect these areas. Most of the belt transects in the hill base ecotone were surveyed towards the end of the study. They were placed so as to cover the general region in which observations on foraging kudus had been made over the study period. The numbers of transects were apportioned between regions roughly in accordance with the amount of foraging data gathered in each region. Thus most observations were made on the saddle be=tween Nwamuriwa and Little Nwamuriwa, particularly on the south-west (Nwamuriwa) side, so most transects were placed in this region (the positions of the transects are shown in Fig. 3).

Because of the difficulty of locating kudu in the knobthorn savanna few observations were made there, and so this area was not sur=veyed extensively. Early in the study period two transects were laid out west of the Nkongwana drainage line (transects 15 and 16, Fig. 3). They were positioned to pass through regions where data on food selection had been collected. These transects were sur=veyed to estimate density and species composition but measurements were not taken for estimation of canopy volume. In total the transects in the hill base ecotone covered an area of 1,21 ha and those in the knobthorn savanna 0,28 ha.

Measuring canopy leaf density

The sampling unit for estimating canopy leaf density was an open-sided cubic frame, 0,1 m^3 in volume (dimensions 40 x 50 x 50 cm). The frame was pushed into the canopy until the outermost shoots within it were flush with its outer edge. Twigs which obstructed the entry of the frame were cut at the point where they touched the edge. All leaf bearing twigs within the frame were clipped off and sealed in polythene bags.

Samples were taken monthly. There was insufficient time to sample all the species present in the study area in each month. The four species found by Owen-Smith (1979) to feature most prominently in the kudus' diet were Acacia nigrescens, Combretum apiculatum, Combretum hereroense and Securinega virosa, and these were selected for regular monthly sampling. Monthly samples included ten frames each from the two most common species, Acacia nigrescens and Combretum apiculatum, and five each from the less common C. hereroense and Securinega virosa. An additional three to five frame samples were taken from each of the other woody species which had featured prominently in the kudus' diet during the month of sampling.

The plants from which samples were clipped were located by starting from an arbitrarily selected point, then walking along a transect which for the sake of standardization always ran at right angles to the hill base. Any plant of the required species located within an estimated 5 m from the line was sampled. The starting point of the line was usually selected so that the line would pass through an area seen to be utilized by kudus during the month of sampling. However if samples from uncommon or localized species were required the starting point was chosen so that the line passed through an area where these species were known to occur. Usually no more than three or four individual plants of a particular species were sampled from any one transect. Four to six such transects were sampled in each month.

The frame was always inserted on the side facing the start of the transect, usually with the lower edge of the frame about 1 m from the ground, although the height of sampling sometimes had to be modified to suit the height of the plant. Only one sample was taken from each plant. Descriptive notes on the phenology of sampled plants were also made.

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As noted above, sampling variation was not measured between June and November 1976; monthly leaf samples from each species were pooled and dried without weighing the material from each frame. From December to August 1977 the bags containing each frame sample were weighed as soon as possible after collection and the leaves then separated from the twigs. The wet weight of leaves in each frame was obtained by subtracting the weight of the bag plus twigs from the total weight. The procedures for drying and analysis of nutritional value were as described for forb leaves above.

Checks on the validity of the leaf biomass estimates

As noted, the product of the mean leaf density of a species and its canopy volume per unit area provided an estimate of leaf weight per unit area. Checks on the validity of this estimate were made for the two dominant species *Acacia nigrescens* and *Combretum apiculatum*. Fifteen specimens of the former and 20 of the latter were selected to provide a range of sizes from small to large. Each tree was measured as described above for calculation of canopy volume below 2,5 m, and a frame clipping was then taken. All remaining leaves below 2,5 m were removed from the tree and weighed. The mean leaf weight per frame volume of the sample multiplied by the canopy volume of each tree yielded an estimate of leaf weight, which was then checked against true leaf weight.

Subdivisions of the hill base ecotone

The areas covered by the belt transects in the hill base ecotone were not uniform in terms of floristic composition. The variation in species composition of woody plants over the slopes-pediment gradient, and the differences between east and west facing slopes have been mentioned. The relative proportions of foraging time spent by the kudus in the various parts of the hill base ecotone also varied over the study period, for example in

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the early to mid-dry seasons they spent relatively more time on the upper slopes whereas in the late dry seasons they favoured the pediment (see Chapter 2). The composition of the vegetation available to them would thus vary in accordance with foraging time apportioned to different vegetation communities within the hill base ecotone.

It was therefore necessary to divide the hill base ecotone into subzones or communities according to floristic composition. The relative availability of the various woody species as encountered by the kudus could then be assessed according to the proportion of time spent foraging in the different subzones (see Chapter 2).

The vegetation surveys done in this study were not sufficient to make a detailed phytosociological analysis of the plant communities in the study area, or even to adequately identify them. Nevertheless certain broad subdivisions can be recognized. The most obvious source of variation in species composition is that along the slope-pediment gradient, so the gradient was divided into separate zones. Any subdivision of a gradient into discrete zones is likely to be arbitrary. However the kudus particularly favoured the zone just above and below the knick at the hill base, and thus the gradient was subdivided as follows:

(i) the upper slopes, higher than 20 m from the knick
(ii) the hill base, the zone 20 m up and 20 m out from the knick
(iii) the pediment, the flat ground more than 20 m out from the knick.

The hill base ecotone was further subdivided into three regions:

(i) the Little Nwamuriwa side of the saddle (east-facing)
(ii) the Nwamuriwa side of the saddle (northwest-facing)
(iii) the west side of Little Nwamuriwa.

The three regions are referred to as LNE, NW and LNW respectively. The difference between the east and west facing slopes in plant species composition was discussed in the Introduction. Although there are differences in species composition between the west-

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facing slopes of Nwamuriwa and Little Nwamuriwa these are not as marked as in the case of the other subdivisions. However the division between these two regions is convenient to separate burnt and unburnt areas (see Fig. 1).

The first region (LNE) is covered by transects 1 to 3, the second (NW) by transects 4 to 10, and the third (LNW) by transect 11 to 14 (see Fig. 3).

The densities and canopy volumes per unit area of woody plants were estimated for each of these nine subdivisions separately.

RESULTS

Density and canopy volume per unit area in the hill base ecotone

Estimates of the density (individuals per unit area) and canopy volumes of woody plants, based on the combined data of all four=teen transects, are given in Table 12. A total of 49 species were encountered within the transects. A further 11 rare or loca=lized species are known to occur in the hill base ecotone but were not contacted in the surveys. These were Galpinia transvaalica, Ficus soldanella, Acacia xanthophloea, Acacia borleae, Gardenia spatulifolia, Maytenus senegalensis, Berchemia zeyheri, Manilkara mochisia, Ozoroa engleri, Pappea capensis and Sterculia rogersii.

Table 13 shows the densities and canopy volumes of woody plants in each of the nine habitat subdivisions of the hill base ecotone. Only those species with an overall density of more than 15 ha^{-1} are shown; remaining species are pooled as one category, 'other species'. Two smaller shrub species, Combretum mossambicense and Maerua parvifolia, were included in the 'other species' category despite their having densities higher than 15 ha^{-1}.

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TABLE 12 : DENSITY AND CANOPY VOLUMES PER UNIT AREA OF WOODY PLANTS IN THE HILL BASE ECOTONE, ESTIMATED FROM FOURTEEN BELT TRANSECTS. THE HILL BASE ECOTONE EXTENDS 80 m UPSLOPE FROM THE HILL BASE AND 400 m OUT FROM THE BASE ACROSS THE PEDIMENT

Species	Density (Individual plants per ha)	Canopy Volume (Cubic metres per ha)
Acacia nigrescens	319	394
Combretum apiculatum	85	144
Combretum hereroense	28	60
Securinega virosa	19	41
Ziziphus mucronata	25	100
Dichrostachys cinerea	42	85
Maytenus heterophylla	21	19
Dalbergia melanoxylon	63	44
Acacia gerrardii	39	69
Ehretia amoena	19	10
Acacia tortilis	37	94
Cissus lonicerifolia	23	39
Dombeya rotundifolia	22	23
Pterocarpus rotundifolius	56	62
Euclea divinorum	39	127
Grewia monticola	39	101
Lonchocarpus capassa	22	29
Commiphora mollis	10	7
Maerua parvifolia	18	2
Cassia abbreviata	2	0,3
Diospyros mespiliformis	5	8
Grewia flavescens	2	3
Grewia hexamita	8	63
Grewia bicolor	1	28
Lannea stuhlmannii	9	9
Acacia nilotica	4	33
Combretum mossambicense	25	37
Spirostachys africana	4	12
Commiphora africana	4	3
Mundulea sericea	4	15
Peltophorum africanum	13	165
Sclerocarya caffra	15	7
Bridelia micrantha	1	0,1
Phyllanthus reticulatus	11	5
Acacia senegal	1	0,1
Albizzia harveyi	5	5
Ficus ingens	1	1
Schotia brachypetala	2	6
Strychnos madagascariensis	5	1
Ehretia rigida	7	0,4
Acacia caffra	2	1
Acacia exuvialis	5	6
Acacia erubescens	2	12
Combretum imberbe	6	14
Ximenia caffra	2	12
Balanites maughamii	2	27
Terminalia phanerophlebia	2	3
Ormocarpum trichocarpum	1	0,4
Ximenia americana	3	6
Unidentified	9	18

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TABLE 13 : DENSITY AND CANOPY VOLUMES PER UNIT AREA FOR THE COMMON WOODY PLANTS IN NINE SUBDIVISIONS OF THE HILL BASE ECOTONE

GRADIENT SUBDIVISIONS	SPECIES	REGIONS					
		LITTLE NWAMURIWA WEST SLOPES		LITTLE NWAMURIWA EAST SLOPES		NWAMURIWA WEST SLOPES	
		Density (Individuals per ha)	Canopy Volume (Cubic metres per ha)	Density (Individuals per ha)	Canopy Volume (Cubic metres per ha)	Density (Individuals per ha)	Canopy Volume (Cubic metres per ha)
UPPER SLOPES	Acacia nigrescens	625	412	28	4	147	265
	Combretum apiculatum	411	1361	25	886	237	101
	Combretum hereroense	16	316	28	29	6	44
	Securinega virosa	66	136	0	0	0	0
	Ziziphus mucronata	16	9	14	11	58	526
	Dichrostachys cinerea	33	15	42	29	45	59
	Maytenus heterophylla	99	181	0	0	39	16
	Dalbergia melanoxylon	82	9	28	4	77	125
	Acacia gerrardii	0	0	0	0	19	108
	Ehretia amoena	0	0	0	0	32	27
	Acacia tortilis	16	13	14	8	0	0
	Cissus lonicerifolia	99	210	28	20	64	113
	Dombeya rotundifolia	0	0	69	127	0	0
	Pterocarpus rotundifolius	0	0	764	913	0	0
	Euclea divinorum	0	0	0	0	0	0
	Grewia monticola	0	0	14	0	90	441
	Lonchocarpus capassa	0	0	0	0	0	0
	Other Species	576	858	292	283	269	538
	TOTAL	2039	3520	1446	2314	1083	2363
HILL BASE	Acacia nigrescens	766	942	375	151	357	325
	Combretum apiculatum	281	78	62	12	71	47
	Combretum hereroense	47	51	125	49	45	33
	Securinega virosa	94	505	21	0	80	38
	Ziziphus mucronata	16	2	83	58	18	29
	Dichrostachys cinerea	94	33	83	187	62	107
	Maytenus heterophylla	16	43	0	0	18	1
	Dalbergia melanoxylon	47	24	375	347	107	32
	Acacia gerrardii	16	21	208	431	98	202
	Ehretia amoena	0	0	21	11	18	9
	Acacia tortilis	141	145	21	15	18	23
	Cissus lonicerifolia	31	73	0	0	36	62
	Dombeya rotundifolia	0	0	229	267	9	2
	Pterocarpus rotundifolius	0	0	250	183	0	0
	Euclea divinorum	31	146	0	0	98	251
	Grewia monticola	16	130	21	89	143	231
	Lonchocarpus capassa	0	0	42	140	9	13
	Other Species	500	1889	250	1806	225	729
	TOTAL	2096	4082	2166	3746	1412	2134
PEDIMENT	Acacia nigrescens	77	267	359	337	521	584
	Combretum apiculatum	4	0	5	1	0	0
	Combretum hereroense	4	8	42	49	29	95
	Securinega virosa	12	18	0	0	0	0
	Ziziphus mucronata	15	47	10	12	25	68
	Dichrostachys cinerea	42	175	36	45	17	55
	Maytenus heterophylla	8	9	16	5	21	13
	Dalbergia melanoxylon	4	16	57	16	50	17
	Acacia gerrardii	0	0	88	35	21	61
	Ehretia amoena	4	2	57	21	12	8
	Acacia tortilis	54	156	5	1	66	244
	Cissus lonicerifolia	8	10	0	0	8	6
	Dombeya rotundifolia	0	0	42	30	4	1
	Pterocarpus rotundifolius	0	0	5	2	0	0
	Euclea divinorum	0	0	104	335	59	211
	Grewia monticola	4	2	21	13	37	49
	Lonchocarpus capassa	4	12	83	67	25	46
	Other Species	35	13	229	694	33	169
	TOTAL	266	735	1159	1663	937	1627

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This is because they could not always be seen above the herb layer and consequently estimates of their utilization by kudus could be biased.

In all three regions total woody plant density and canopy volume were highest at the hill base, lower on the upper slopes and lowest on the pediment. The pediments in the saddle had a higher total density and canopy volume of woody plants than that west of Little Nwamuriwa.

Acacia nigrescens occurred throughout the gradient but was less dense on the upper slopes. Combretum apiculatum was most common on the upper slopes, less common at the base and virtually absent from the pediment. Two other common species which were associated with the base and upper slopes are Pterocarpus rotundifolius and Cissus lonicerifolia. The three species Acacia tortilis, Lonchocarpus capassa and Euclea divinorum on the other hand, were more common on the pediment and hill base than on the upper slopes. Combretum hereroense, Ziziphus mucronata, Dalbergia melanoxylon and Maytenus heterophylla were widespread throughout the gradient. As noted the characteristic feature of the east-facing slopes was the patches of Pterocarpus rotundifolius growing as a multi-stemmed shrub. In parts of the east-facing upper slopes it replaced Acacia nigrescens and Combretum apiculatum as the dominant woody plant. P. rotundifolius also occurred at the hill base and to a lesser extent on the pediment of east-facing slopes, but was absent from west-facing slopes and pediment.

Within these subdivisions further sub-communities could be recog= nized, but the surveys were insufficient to properly characterise them. Thus in several places in the hill base ecotone the ever= green shrub, Euclea divinorum, grew in dense patches which excluded almost all other woody species. To the south-west the study area bordered on Acacia tortilis savanna. There was no distinct dividing line between the two areas, and Acacia tortilis tended to be more common in the south-western half of the hill base ecotone.

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Density and canopy volumes in the knobthorn savanna

The area surveyed in the knobthorn savanna was small (0,28 ha) but the results nevertheless give an overall impression of the species composition in this area (Table 14). Measurements for estimation of canopy volumes were not taken during the knobthorn savanna surveys. However for some species canopy volume per unit area could be estimated using the average canopy volume per individual calculated from the hill base ecotone surveys. This of course assumes that tree size did not differ greatly between the hill base ecotone and the knobthorn savanna. From visual inspection this seemed a reasonable assumption for most species except Ehretia rigida, which was obviously smaller in the hill base ecotone. For this species, and also those which were rare or absent in the hill base ecotone, no estimates of canopy volumes were made.

The overall density of woody plants was lower in the knobthorn savanna than in the hill base ecotone (Tables 13 & 14). Species composition also differed between the two areas. Species which were relatively common on the pediment but rare in the knobthorn savanna are Peltophorum africanum, Combretum hereroense, Euclea divinorum and Dombeya rotundifolia. Ormocarpum trichocarpum on the other hand, was common in the knobthorn savanna but rare in the hill base ecotone. Securinega virosa was relatively more common in the knobthorn savanna.

As with the hill base ecotone the knobthorn savanna could be divided into various sub-communities. The species composition shown in Table 14 is characteristic of only part of the knobthorn savanna. Over fairly extensive areas Acacia nigrescens saplings form dense thickets in which few other species are present. In other areas Acacia gerrardii replaces Acacia nigrescens as the dominant woody plant. Further surveys would be required to assess the extent of these different communities.

TABLE 14 : DENSITY AND CANOPY VOLUMES PER UNIT AREA OF WOODY PLANTS IN THE KNOBTHORN SAVANNA

Species	Density (Individuals per ha)	Canopy Volume* (Cubic metres per ha)
Acacia nigrescens	132	111
Dichrostachys cinerea	75	151
Ormocarpum trichocarpum	64	-
Securinega virosa	50	73
Acacia gerrardii	39	69
Maytenus senegalensis	32	-
Lonchocarpus capassa	21	28
Ehretia rigida	14	-
Acacia tortilis	11	28
Maytenus heterophylla	11	10
Grewia bicolor	7	-
Dalbergia melanoxylon	4	3
Combretum imberbe	4	10
Acacia nilotica	4	32
Cissus lonicerifolia	4	7
Unknown	4	-
Total	475	-

* Canopy volumes were not measured in the knobthorn savanna, so where possible these were estimated from canopy volumes from the hill base ecotone

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Seasonal variation in leaf density

Like the samples from the herb layer the distribution of the frame samples showed signs of skewness and the variance was not homo= geneous. The methods of statistical analysis were thus the same as for the forbs. Seasonal changes in leaf weight per unit canopy volume for the four species selected for intensive samp= ling (Acacia nigrescens, Combretum apiculatum, Combretum hereroense and Securinega virosa) are shown in Fig. 13. The values for December to August are presented with 75% error bound confidence limits as discussed for forbs.

Two-factor analysis of variance of the December 1976 to August 1977 samples (Table 15) shows significant species x month inter= actions, indicating that the seasonal trend in leaf density varied significantly between species (Fig. 13). The relative dif= ference between peak wet season and lowest dry season values was most pronounced for Securinega virosa and least for Combretum hereroense. Combretum hereroense did not shed its leaves to the same extent as the other species during the dry season, and also tended to flush early in spring. Acacia nigrescens also retained a relatively higher leaf density over the dry season than Combretum apiculatum and Securinega virosa.

The leaf density of Securinega virosa was lower than that of the other species throughout the study period. Combretum apiculatum had a consistently lower leaf density than Acacia nigrescens throughout the 1976 dry season but the two remained essentially equal during the 1977 dry season. However since no measures of variation were made during the 1976 dry season the difference cannot be tested statistically.

Leaf densities of the other woody species were estimated only during those months when they were often seen to be eaten by kudus. These estimates are not presented here, but estimates of mean leaf mass per individual plant and leaf mass per unit ground area for the less intensively sampled species are given in Chapter 2.

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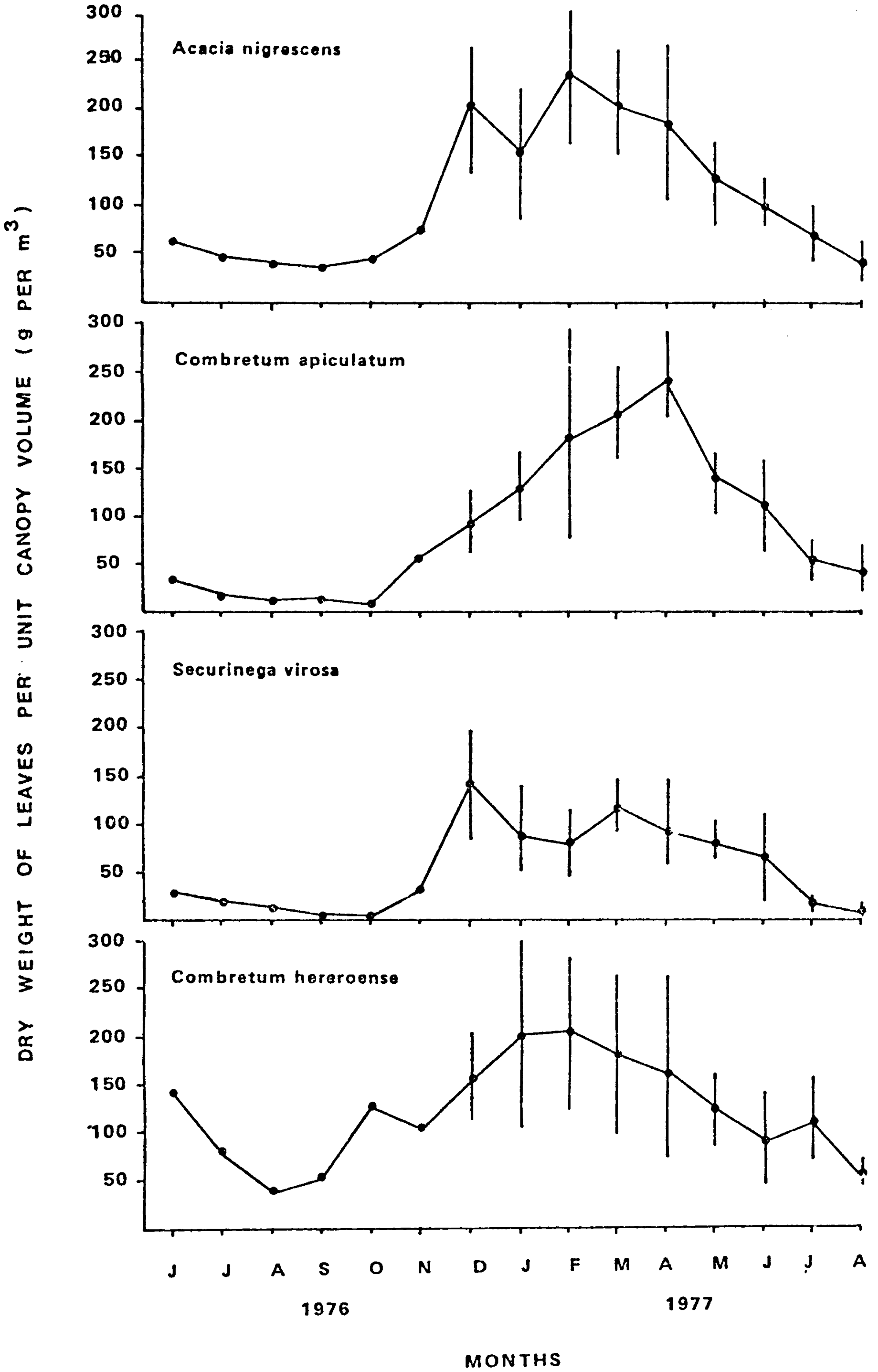

FIG. 13 MEAN LEAF WEIGHT PER UNIT CANOPY VOLUME FOR FOUR WOODY SPECIES. VERTICAL LINES SHOW 75% ERROR BOUND CONFIDENCE LIMITS

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TABLE 15 : TWO FACTOR ANALYSIS OF VARIANCE OF LEAF WEIGHT PER UNIT CANOPY VOLUME (LEAF DENSITY). THE FACTORS ANALYSED ARE (i) DIFFERENCES IN LEAF DENSITY BETWEEN THE FOUR SPECIES ACACIA NIGRESCENS, COMBRETUM APICULATUM, COMBRETUM HEREROENSE AND SECURINEGA VIROSA (ii) DIFFERENCES IN LEAF DENSITY BETWEEN MONTHLY SAMPLES (DECEMBER TO AUGUST) (SEE FIG. 13). VARIATES WERE TRANSFORMED TO LOGARITHMS

Source of variation	df	Mean Square	F ratio	Signifi= cance
Species	3	1,02	16,69	P< 0,005
Months	8	1,71	27,97	P< 0,005
Species x Months Interaction	24	0,10	1,68	P< 0,05
Error	234	0,06		
Total	269			

The significant species x months interaction shows that the pattern of seasonal change in leaf density differed between the four species.

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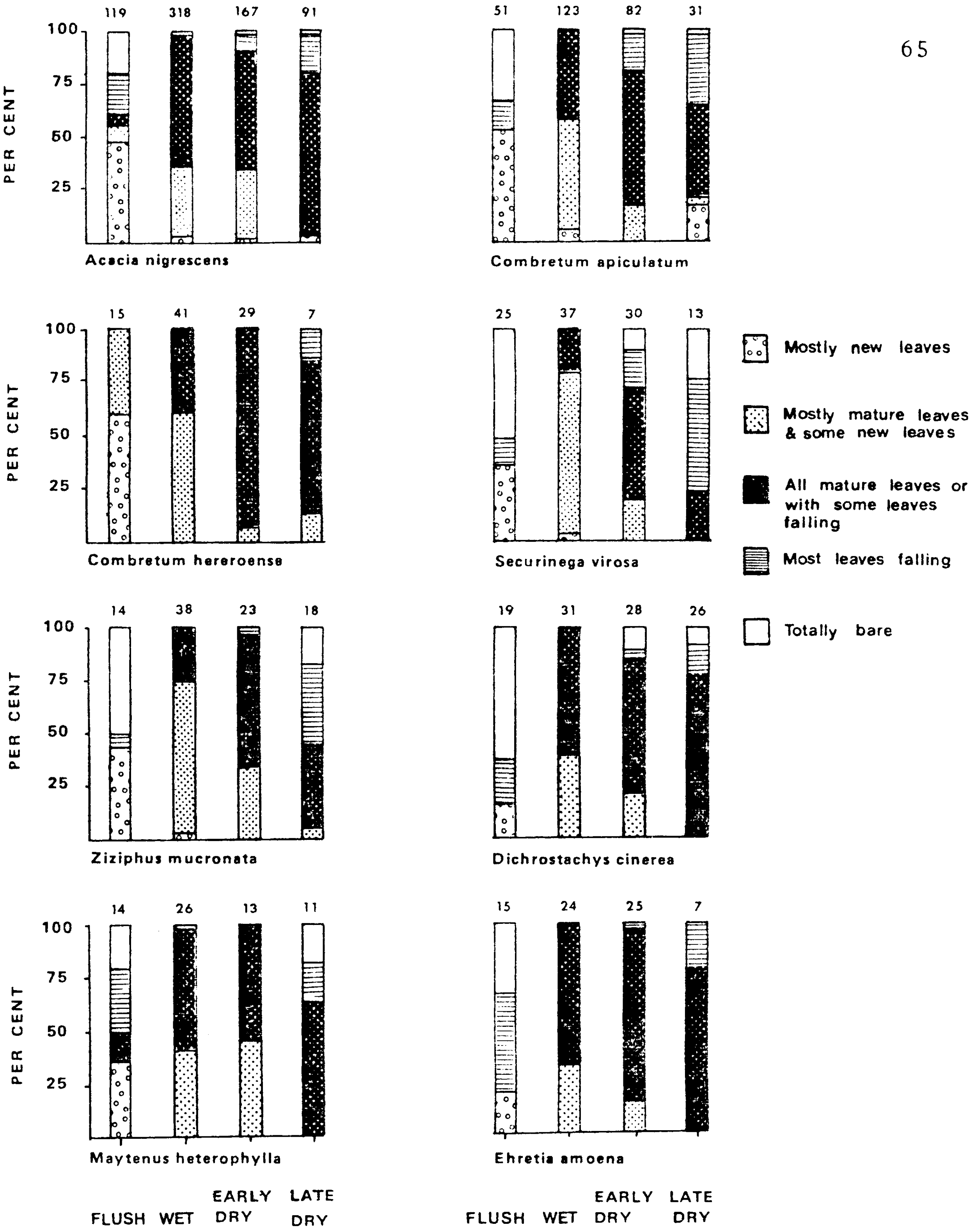
Phenology of woody plants

The timing of leaf production and leaf fall varied not only between species but also between individuals within species. The individuals of any species were never in complete synchrony as regards phenology. In addition the growth stage of leaves on the same individual plant often varied, for example in certain seasons a tree could carry falling leaves, mature leaves as well as new leaves. As will be discussed later these variations are important in interpreting food selection.

Fig. 14 shows variations in phenology between eight woody species that were frequently browsed by kudus. The data are from plants surveyed on the belt transects and those from which frame samples were clipped. Results from both study years 1976 and 1977 combined are grouped into four seasons (Fig. 14).

Although differences between species are evident there are certain basic features common to most. The period mid-September to November (referred to as the pre-rain flush, Fig. 14) was the time when many woody plants began leaf production. Thus in all species the proportion of individual plants carrying predominantly new leaves was higher in the pre-rain flush than in the other seasons. However the timing of the flush varied between individual plants so that at any time between mid-September and mid-November one could find bare as well as flushing individuals of the same species. The pre-rain flush was in fact the time of the year when the number of totally bare plants was highest.

Acacia nigrescens and Combretum hereroense tended to flush early, many individuals starting in mid-September. Those leaves which appeared in September had reached maturity before the end of November. Thus a proportion of plants of these two species carried predominantly mature leaves in November. In contrast Ziziphus mucronata, Dichrostachys cinerea and Securinega virosa did not flush to any extent until November and no specimens with predominantly mature leaves were encountered during the pre-rain flush. Although most Combretum apiculatum plants flushed only in November this varied between areas. In certain localities



SEASONS
- PRE-RAIN FLUSH : Mid-September – end November
- WET SEASON : December – April
- EARLY DRY SEASON : May – July
- LATE DRY SEASON : August – mid-September

FIG. 14 PHENOLOGY OF SOME FREQUENTLY BROWSED WOODY PLANTS. THE HISTOGRAMS SHOW PER CENT OF INDIVIDUAL PLANTS IN EACH CATEGORY. SAMPLE SIZES (NUMBER OF PLANTS) ARE SHOWN ABOVE EACH BAR

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groups of *Combretum apiculatum* trees flushed as early as August and this accounts for the 16% of individuals recorded with pre=dominantly new leaves in the late dry season (Fig. 14).

In the wet season (December to April) almost all plants of all species carried predominantly mature leaves. But production of new leaves did not cease in any of the species studied; through=out the wet season there were always many individuals with a small amount of new leaves available (Fig. 14). Production of small amounts of new leaves continued into the early dry season, although for most species the frequency of this was much reduced. However many *Acacia nigrescens* saplings up to 3 m tall produced an 'autumn flush' in the early dry season, so the proportion of plants with new leaves did not decrease substantially from wet to early dry seasons. It was at this time that falling leaves, mature leaves and new leaves could be seen on the same plant.

Leaf fall in many species began in May but the process was gradual and few plants were recorded as being in an advanced state of leaf fall in the early dry season. During the late dry season most plants did not produce new growth although small numbers of individual *A. nigrescens*, *C. apiculatum*, *C. hereoense* and *Z. mucronata* were observed carrying a few new leaves at this time (Fig. 14). In all species the proportion of plants in an advanced stage of leaf loss increased markedly from the early to the late dry season, but the proportion of totally bare plants remained low until after mid-September.

Within this basic pattern there were many quantitative differences between species. The distinctive phenology of *Combretum hereroense* has been mentioned. At no time were totally bare *Combretum hereroense* plants encountered (Fig. 14); even in the late dry season few were classed as being in advanced leaf fall. Because it tended to retain leaves over the dry season there was a high proportion of plants which carried mature leaves together with new leaves in the early spring.

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Of the four species selected for intensive study *Securinega virosa* showed the greatest frequency of advanced leaf fall and bareness over the dry season (Fig. 14). This accords with the seasonal variation in leaf density discussed above. Peak summer leaf density of *Securinega virosa* is 28 times the lowest dry season value (Fig. 13). The corresponding figures for *Acacia nigrescens*, *Combretum apiculatum* and *C. hereroense* are 6,1 times, 24 times and 5,8 times respectively. Other differences between species in phenology are discussed in Chapter 2.

It is not clear to what extent consumption by kudus and other herbivores influenced the seasonal trends in leaf abundance. Freshly severed shoot ends, indicating browsing by a large herbivore, were noted within only two of the 670 frame samples taken from woody plants during the study period. However, browse damage was not always conspicuous; and light damage, such as missing leaves, would have gone unnoticed, especially in the dry season when the leaves were falling.

Relationships between phenology and tree size

In *Acacia nigrescens* the timing of leaf fall and flush depended upon the size of the tree; bigger trees tended to lose their leaves earlier in the dry seasons than the smaller ones (Fig. 15). Thus in the early dry season 87% of saplings < 1 m showed no sign of leaf fall whereas the corresponding figure for trees > 2 m is 23%. In the late dry season the difference was less pronounced but still considerable. Chi-square contingency tests reject the null hypothesis of independence between leaf fall and plant height (Fig. 15) in both early and late dry seasons. It was my impression in the field that the larger *Acacia nigrescens* trees tended to flush earlier than the smaller ones in spring. The results for the pre-rain flush shown in Fig. 15 are in accord with this impression but the difference between the height classes in the

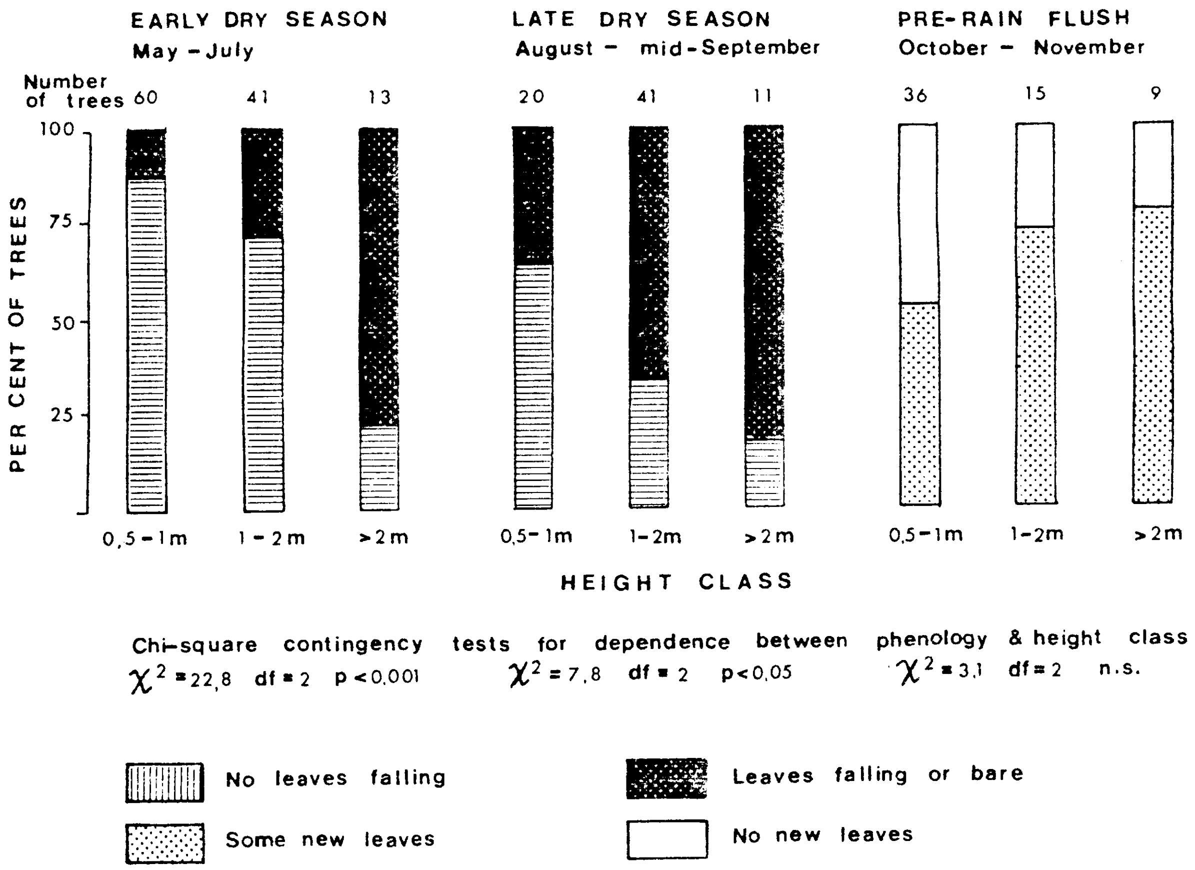

FIG. 15 THE RELATIONSHIP BETWEEN PHENOLOGY AND TREE HEIGHT IN ACACIA NIGRESCENS

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frequency of new leaves is not statistically significant. Further data would be required for definite conclusions.

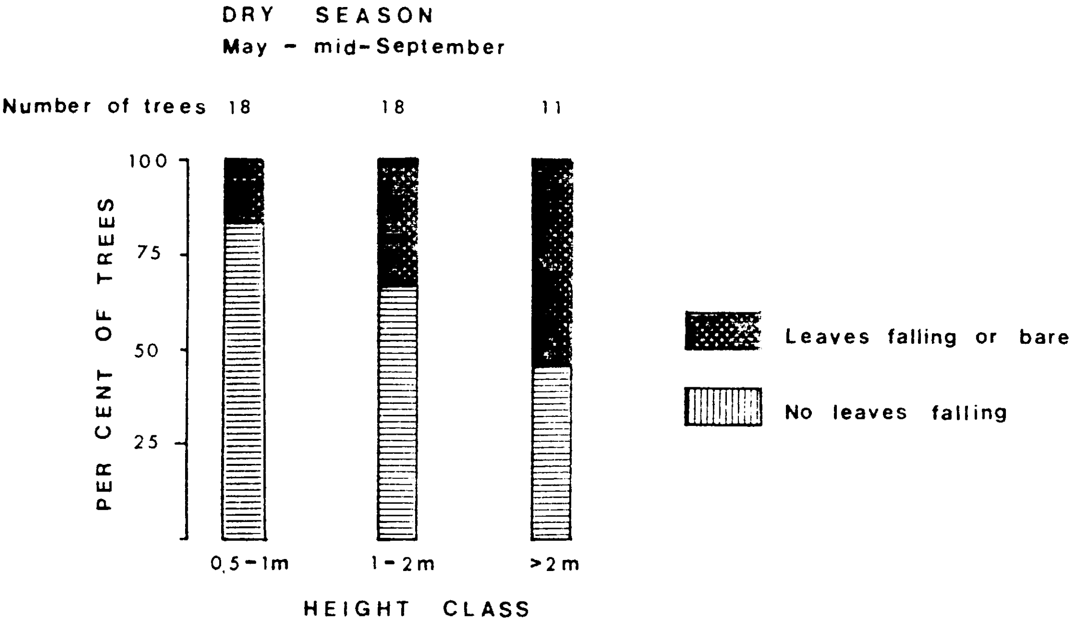
In Combretum apiculatum the timing of leaf fall was also apparently related to tree size. There were insufficient data to examine the early and late dry seasons separately. For the whole dry season (Fig. 16) 83% of saplings < 1 m showed no sign of leaf fall whereas for trees > 2 m this was 45%. However the sample size is small and the difference is not significant at the five per cent level.

For Combretum apiculatum in the pre-rain flush, and for all other species there were too few data to examine relationships between phenology and tree size.

NUTRIENT CONTENT OF WOODY PLANT LEAVES

The seasonal cycle in nutrient content of woody plant leaves was basically similar to that of forb leaves; protein, phosphorus and moisture contents were highest in the spring, lower over the summer and lowest during the dry season (Tables 16, 17 & 18). But there were certain differences between the woody species in the pattern of seasonal variation in nutrient content which reflect differences between them in phenology.

In the early flushing Acacia nigrescens and Combretum hereroense high protein contents were recorded early in September. In con=trast the later flushing Securinega virosa reached peak protein content only in November. Although some Combretum apiculatum plants flushed early (August) most flushed in November so peak protein content was recorded in this month (Table 16). The sea=sonal cycle in protein and moisture contents of Combretum hereroense (Tables 16 & 18) was relatively less pronounced than



Chi-square contingency test for dependence between phenology and height class

$\chi^2 = 4.5$ df = 2 n.s.

FIG. 16 THE RELATIONSHIP BETWEEN PHENOLOGY AND TREE HEIGHT IN COMBRETUM APICULATUM

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TABLE 16 : CRUDE PROTEIN CONTENT (EXPRESSED AS PER CENT OF DRY WEIGHT) OF WOODY PLANT LEAVES IN THE HILL BASE ECOTONE

Species	1976							1977							
	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	Apr.	May	June	July	Aug.
Acacia nigrescens	13,6	13,5	13,4	23,1	20,2	22,9	15,9	16,2	16,2	15,4	15,8	13,6	13,0	12,9	13,0
Combretum apiculatum	8,7	9,2	8,9	13,0	11,8	21,1	13,9	12,3	12,5	10,8	10,7	10,2	8,5	8,6	8,0
Combretum hereroense	9,2	11,4	7,5	14,7	13,8	13,5	11,4	11,6	9,3	11,9	10,1	10,5	11,5	10,6	11,6
Securinega virosa	12,6	14,4	14,9	17,8	17,2	25,4	18.2	18,9	17,3	16,2	16,8	13,0	11,0	10,9	13,4
Ziziphus mucronata	13,6	12,5	12,9	-	-	-	17,2	-	17,5	15,5	-	14,2	-	12,8	15,3
Dichrostachys cinerea	-	-	13,0	-	-	-	-	14,9	-	-	-	13,6	-	13,5	12,3
Maytenus heterophylla	-	6,1	6,7	7,9	10,1	-	8,0	-	-	9,9	-	-	-	6,9	-
Dalbergia melanoxylon	-	-	-	-	-	28,3	-	-	-	-	-	-	-	-	-
Acacia gerrardii	-	-	-	-	16,6	-	-	-	-	-	-	-	-	13,0	-
Ehretia amoena	7,0	6,1	6,1	8,5	-	-	13,2	-	-	11,0	-	-	7,0	-	-
Acacia tortilis	20,6	-	-	-	-	-	-	-	-	-	-	-	-	19,6	-
Pterocarpus rotundifolius	-	-	-	-	-	-	-	-	-	-	-	-	-	16,5	-
Euclea divinorum	-	-	7,0	-	-	-	-	-	-	-	-	-	-	-	7,3
Grewia monticola	-	-	-	-	-	-	-	-	-	-	-	-	-	8,6	-
Lonchocarpus capassa	-	-	-	-	21,9	-	-	14,1	-	-	-	-	-	-	-
Peltophorum africanum	-	-	-	-	12,3	-	-	-	-	-	-	-	-	-	-
Spirostachys africana	-	10,0	-	-	-	-	-	-	-	-	-	-	10,3	-	-
Grewia flavescens	-	-	7,8	-	12,4	-	-	-	13,5	-	-	-	-	-	9,0
Maytenus senegalensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6,7

TABLE 17 : PHOSPHORUS CONTENT (EXPRESSED AS PER CENT OF DRY WEIGHT) OF WOODY PLANT LEAVES IN THE HILL BASE ECOTONE

Species	1976							1977							
	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	Apr.	May	June	July	Aug.
Acacia nigrescens	0,18	0,12	0,12	0,31	0,21	0,33	0,15	0,14	0,16	0,16	0,15	0,13	0,14	0,11	0,10
Combretum apiculatum	0,16	0,16	0,20	0,24	0,16	0,39	0,13	0,11	0,16	0,13	0,12	0,15	0,18	0,17	0,08
Combretum hereroense	0,27	0,23	0,12	0,25	0,18	0,20	0,25	0,27	0,22	0,16	0,12	0,16	0,15	0,12	0,19
Securinega virosa	0,31	0,32	0,33	0,38	0,24	0,51	0,41	0,28	0,36	0,25	0,39	0,46	0,43	0,34	0,16
Ziziphus mucronata	0,15	0,18	0,29	-	-	-	0,16	-	0,25	0,34	-	0,22	-	0,24	0,11
Dichrostachys cinerea	-	-	0,12	-	-	-	-	0,20	-	-	-	0,13	-	0,11	0,10
Maytenus heterophylla	-	0,09	0,18	0,16	0,15	-	0,14	-	-	-	-	-	-	0,14	-
Dalbergia melanoxylon	-	-	-	-	-	0,40	-	-	-	-	-	-	-	-	-
Acacia gerrardii	-	-	-	-	0,24	-	-	-	-	-	-	-	-	0,09	-
Ehretia amoena	0,19	0,28	0,12	0,25	-	-	0,16	-	-	0,25	-	-	0,20	-	-
Acacia tortilis	0,27	-	-	-	-	-	-	-	-	-	-	-	-	0,15	-
Pterocarpus rotundifolius	-	-	-	-	-	-	-	-	-	-	-	-	-	0,10	-
Euclea divinorum	-	-	0,11	-	-	-	-	-	-	-	-	-	-	-	0,08
Grewia monticola	-	-	-	-	-	-	-	-	-	-	-	-	-	0,18	-
Lonchocarpus capassa	-	-	-	-	0,29	-	-	0,13	-	-	-	-	-	-	-
Peltophorum africanum	-	-	-	-	0,16	-	-	-	-	-	-	-	-	-	-
Spirostachys africana	-	0,22	-	-	-	-	-	-	-	-	-	-	0,23	-	-
Grewia flavescens	-	-	0,24	-	0,19	-	-	-	0,28	-	-	-	-	-	0,30
Maytenus senegalensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0,16

TABLE 18 : MOISTURE CONTENT (PER CENT) OF WOODY PLANT LEAVES IN THE HILL BASE ECOTONE

	1976		1977							
	Nov.	Dec.	Jan.	Feb.	March	Apr.	May	June	July	Aug.
Acacia nigrescens	70	55	58	60	55	54	51	46	47	48
Combretum apiculatum	71	54	54	60	56	53	44	37	35	38
Combretum hereroense	62	55	51	57	56	47	49	48	49	47
Securinega virosa	77	63	62	70	46	68	55	49	61	28
Ziziphus mucronata		58		63	57		58		54	47
Dichrostachys cinerea			55				51		35	49
Maytenus heterophylla		65			71				59	
Dalbergia melanoxylon	72									
Acacia gerrardii									43	
Ehretia amoena		64			64			48		
Acacia tortilis									56	
Pterocarpus rotundifolius									45	
Euclea divinorum										46
Grewia monticola									42	
Lonchocarpus capassa			60							
Grewia flavescens				64						35
Maytenus senegalensis										56

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in the other species. This would be expected in view of its less pronounced leaf fall in the dry season.

The calcium contents of woody plant and forb leaves are shown in Table 19. Relatively few analyses for calcium content were done and so the values are grouped into three seasons. The value for each season is the mean of the monthly samples within that season. Unlike the other nutrients analysed calcium content did not show pronounced seasonal variation. Values in spring tended to be slightly lower than in the dry season, again in contrast to the other nutrients. The ratio of calcium to phosphorus in the diet affects the extent to which these two minerals can be uti=lized by an animal (McDonald, Edwards & Greenhalg, 1973). The calcium:phosphorous ratios in forb and woody plant leaves (Table 19) vary from 5:1 to 28:1.

Monthly variation in crude protein content compared between woody plants and forbs

Average crude protein contents of woody plant and forb leaves are compared in Fig. 17. The values for woody plants are the average of all species analysed in each month, while those for forb leaves are the average of unburnt slopes and pediment.

ESTIMATION OF WOODY PLANT LEAF BIOMASS

The product of the mean leaf density of a species and its canopy volume per unit area gives the estimate of leaf abundance. The accuracy of this estimate depends on whether leaf weight per unit volume of the frame is a reliable estimate of leaf weight per unit canopy volume. As described above the validity of this estimate was checked for a sample of *Acacia nigrescens* and *Combretum apiculatum* trees. The trees were all sampled in the

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TABLE 19 : CALCIUM CONTENT OF SOME FORB AND WOODY PLANT LEAVES (PER CENT OF DRY MATTER) AND THE CALCIUM:PHOSPHORUS RATIO (UPPER FIGURE IS % CALCIUM AND LOWER FIGURE IN PARENTHESES IS Ca:P RATIO)

	Dry Season (July - August)	Pre-rain Flush (October - November)	Wet Season (December - January)
Forb Leaves Slopes	2,8 (10:1)	2,1 (6:1)	2,4 (9:1)
Forb Leaves Pediment	3,0 (10:1)	2,5 (6:1)	2,3 (6:1)
Acacia nigrescens	2,8 (23:1)	1,4 (5:1)	2,1 (14:1)
Combretum apiculatum	1,5 (8:1)	1,3 (5:1)	1,6 (13:1)
Combretum hereroense	2,1 (12:1)	1,4 (7:1)	1,3 (5:1)
Securinega virosa	2,2 (7:1)	1,9 (5:1)	2,0 (6:1)
Ziziphus mucronata	2,5 (11:1)		
Ehretia amoena	3,8 (19:1)		
Maytenus heterophylla	3,8 (28:1)		

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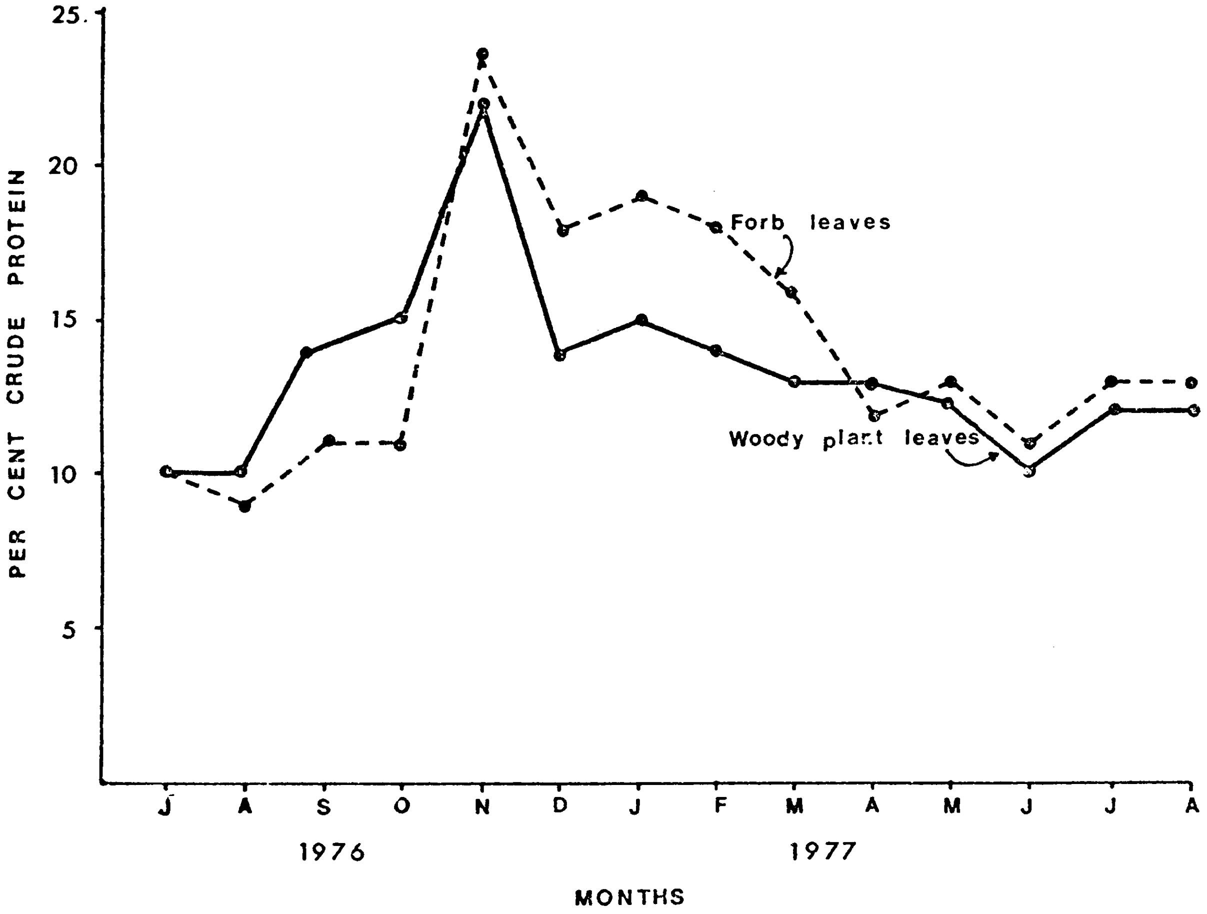

FIG. 17 MONTHLY VARIATION IN CRUDE PROTEIN CONTENT OF WOODY PLANT AND FORB LEAVES AVAILABLE TO KUDUS IN THE HILL BASE ECOTONE

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dry season of 1977. For each species the mean leaf weight per frame was multiplied by the canopy volume of each tree to estimate its leaf weight. Estimated leaf weight was then compared with actual leaf weight.

The total leaf weight of the 15 sampled Acacia nigrescens trees was 5 247 g. The sum of the estimated values was 6 099 g, a 17% overestimate. However seven trees were underestimated and eight overestimated, and the large total overestimate was due to the very substantial overestimate of one tree in the sample. Actual and estimated values did not differ significantly (Wilcoxon test for matched pairs, Siegel 1956). Thus although estimates of the leaf weight of individual trees may be in error there was no evidence of a consistent bias towards overestimation.

For Combretum apiculatum, however, the sum of the estimates of the 20 trees was 17 319 g, compared with a true total of 10 535 g, a 64% overestimate. The degree of error was dependent upon size, the leaf weight of the larger trees was grossly overestimated while the smallest ones were slightly underestimated. Thus there was a significant correlation between the ratio of true : estimated weight and canopy volume ($r = -0{,}5$ $P < 0{,}05$). In contrast there was no significant relationship between the error of estimation and tree size in Acacia nigrescens.

There are a number of factors that could account for the tendency to overestimate the leaf weight of the larger Combretum apiculatum trees. The first of these is the pattern of growth. The smaller Combretum saplings have a rounded or cylindrical crown with fairly evenly distributed leaves. The canopy volume calculated from the measurements of canopy depth and diameter (see Methods) assumes the canopy shape to be a cylinder, and for the smaller plants this is a reasonable approximation. But as the tree grows it typically spreads, so that while parts of the canopy may be densely filled with leaves there are many leafless gaps in between. The cylinder calculated to represent the canopy of larger trees tends to include the gaps. Because of this one would expect a negative correlation between canopy volume and leaf density. The mean weight of leaves per unit frame volume used to estimate biomass was derived from trees of various sizes. This mean would tend to be too high for the large trees and too low for the smaller ones, and this is one likely factor accounting for the underestimation of the smaller individuals and the overestimation of the larger ones. Another problem was that the procedure used in sampling with the frame was rather insensitive to gaps in the canopy. The frame was inserted until the outermost leaves within it were flush with its outer edge. This meant that if there were any shoots between the point of entry of the frame and the trunk they would be included in the frame, and the leaf density would be overestimated. This effect would magnify the overestimation of larger spreading Combretum apiculatum trees.

A third point is that big trees tend to have a lower leaf density in the center of the canopy, partly because the center is occupied by the trunk and partly because of reduced availability of light. Frame samples tended to come from the outer canopy, and this would also lead to overestimation of the leaf density of the larger trees.

Acacia nigrescens also spreads as it matures, but in contrast to Combretum apiculatum this only occurs when the tree is above maximum kudu browse height. Below 2,5 m the crowns of Acacia nigrescens are usually fairly evenly distributed with leaves and the shape of most specimens is approximately cylindrical. Because of its growth pattern one would expect that leaf density of Acacia nigrescens would not decrease with increasing volume to the same extent as is the case with Combretum apiculatum.

For the sample of Combretum apiculatum trees harvested in the late dry season there is, as expected, a negative relationship between canopy volume and the actual leaf density (true leaf weight per unit canopy volume). The linear regression equation relating canopy volume to leaf density is:

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$Y = 194 - 7{,}5X$, where Y is leaf density (g/m^3) and
X is canopy volume (m^3).

For the sample of Acacia nigrescens harvested at the same time the regression equation is:

$Y = 128 - 3X$, where X and Y are as above.

The result is as expected on the basis of the factors discussed above. Both species show evidence of declining leaf density with increasing size but the slope of the regression line is higher for Combretum apiculatum indicating that the negative relationship is more pronounced than is the case for Acacia nigrescens. This is probably largely because of the spreading growth form of the former species.

For Combretum apiculatum it was necessary to apply a correction factor to the leaf abundance estimates. A regression was computed relating the ratio of real : estimated leaf mass to canopy volume:

$\log T/E = -0{,}062 - 0{,}282 \log CV$, where T = true mass,
E = estimated mass, and CV = canopy volume.

The value T/E was used as a correction factor to correct the estimated leaf masses of the 20 sampled trees. The sum of cor= rected estimates was then 9 671 g which is within ten per cent of the observed total mass. The regression equation was then used to adjust the canopy volume of each Combretum apiculatum contacted in the belt transects so as to derive a corrected biomass estimate.

Although the total leaf mass of the sample of Acacia nigrescens trees was overestimated the error was not significantly related to tree size, and therefore a corrective equation was not calcu= lated. The canopy of Acacia nigrescens is usually dense and well protected with sharp thorns, so that much of the inner canopy is inaccessible to kudus. A more realistic correction for available leaf biomass is to assume that kudus can feed only to a depth of 40 cm (which seems to reasonable estimate from observations on foraging kudus). Two other species favoured by the kudus,

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Securinega virosa and Ziziphus mucronata also tend to have thorny or spiny impenetrable crowns and they were adjusted in the same way as Acacia nigrescens.

Combretum hereroense has a growth form similar to C. apiculatum and the regression equation given above was used as a correction factor for C. hereroense as well.

The remaining species for which estimates of leaf density were made have small to medium, fairly accessible crowns. The estimates based on the frame samples are thus not likely to be grossly in error and in the absence of more detailed information they were left uncorrected.

Monthly variation in overall abundance of woody plant leaves

Leaf density estimates were not made for all woody species and therefore the estimate of monthly variation in total leaf abundance was approximated as follows. All woody species that were not sampled regularly, except for the evergreen Euclea divinorum, were assumed to have a leaf density equal to the average of the four species selected for continuous monthly measurement. The average of the leaf density estimates for Euclea divinorum made in the dry seasons of 1976 and 1977 is assumed to represent the entire year. Since there was little leaf loss on Euclea shrubs in the dry season this assumption is reasonable. This mean leaf density was used to estimate the leaf abundance of Euclea. The leaf abundance of the four species Acacia nigrescens, Combretum apiculatum, C. hereroense and Securinega virosa were estimated as described in the preceding section. The sum of the leaf abundance of these four species, plus that of Euclea plus the approximated value for all other species gave the total woody plant leaf abundance. The monthly estimates of total leaf abundance of woody plants are shown in Fig. 18 together with the values for forb leaves (the average of the unburnt slopes and pediment from Fig. 6).

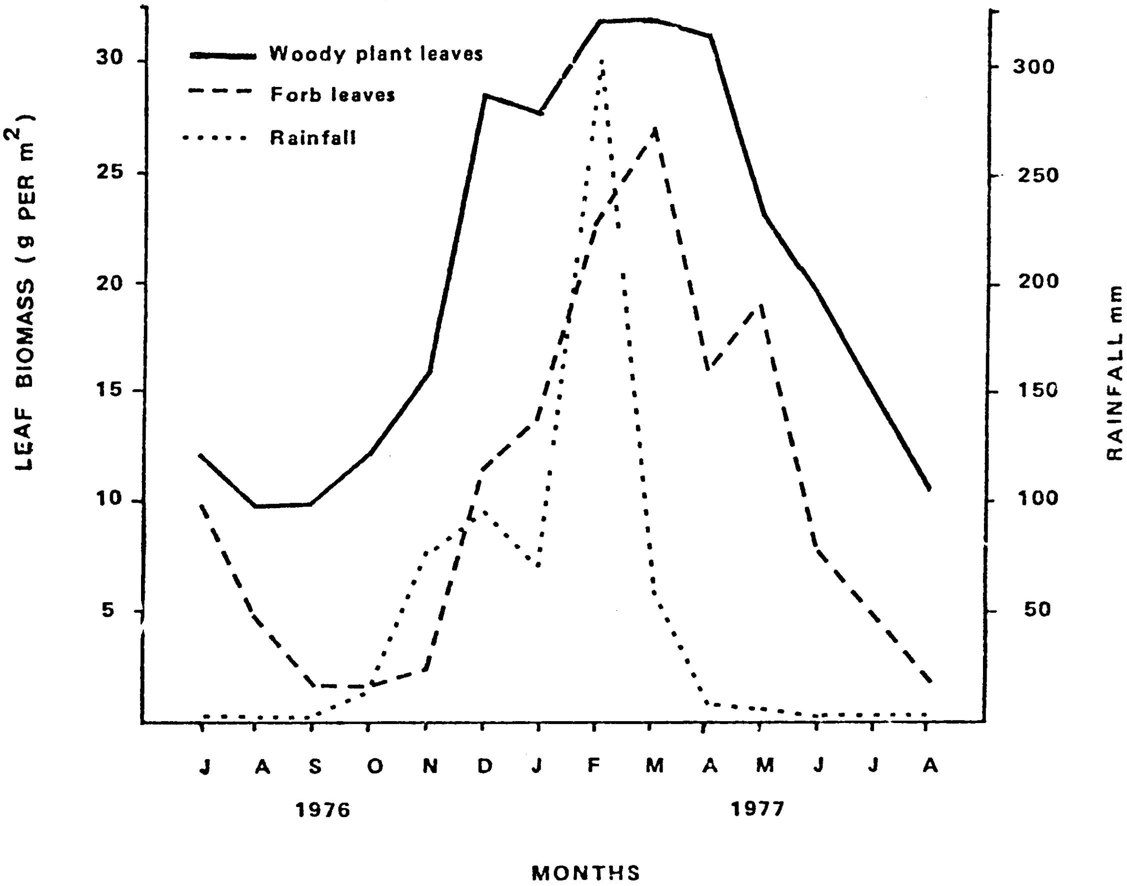

FIG. 18 MONTHLY VARIATION IN BIOMASS OF FORB AND WOODY PLANT LEAVES AVAILABLE TO KUDUS IN THE HILL BASE ECOTONE, SHOWING THE RELATIONSHIP WITH RAINFALL

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Seasonal variations in leaf abundance of individual woody species

For estimation of leaf abundance of individual woody species sample sizes (the number of frame samples clipped) were inadequate to permit subdivision into monthly intervals. Instead the study period was divided into the following seasons:

(i) The dry season of 1976 (May to mid-September).
(ii) The pre-rain flush (the period before the first good rain when many woody plants began leaf production - mid-September to November).
(iii) The wet season (December 1976 to April 1977)
(iv) The dry season of 1977 (May to August).

Seasonal variations in the vegetation were gradual, and therefore the greater the number of seasonal subdivisions the more accurately would these gradual changes in food abundance be reflected. However if the four seasons recognized above are further subdivided the sample sizes for some of the infrequently sampled species would be too small for reliable estimation of average canopy leaf density.

The seasonal estimates of mean canopy leaf densities were derived as follows: For the four species that were sampled monthly (*Acacia nigrescens*, *Combretum apiculatum*, *C. hereroense* and *Securinega virosa*) each season's estimate was the average of all monthly sample values within that season. However no samples were taken in May 1976 and so the values from May 1977 were used in calculating the average for the dry season of 1976. For the other species the seasonal estimates were also means of the monthly values within each season, but with the following exceptions: For *Euclea divinorum*, *Maytenus heterophylla*, *Ehretia amoena* and *Dichrostachys cinerea* sample sizes were inadequate in one or both of the dry seasons, so values from the two dry seasons were pooled to calculate an overall average for both. For *Dichrostachys cinerea* the leaf density estimate of May 1977 was the highest of the year. The plants from which this sample was collected had not begun shedding their leaves and so the May sample was included with the wet season rather than the dry. As

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discussed above the dry season leaf density of Euclea divinorum was assumed to hold for all seasons. Woody species that were not sampled to estimate leaf density were combined into a single category 'other woody species', and their leaf density was assumed to be equal to the average of the values for the four regularly sampled species.

The estimates of leaf biomass are shown in Tables 20 a and b for each the two most important subdivisions of the hill base ecotone, the hill slopes (the zone 80 m upslope and 20 m out from the knick at the hill base), and the pediment (the region extending 20 m to about 400 m from the knick).

DISCUSSION

Forb leaves contributed by far the greatest proportion of potential food in the herb layer. The leaves of woody plant seedlings made up no more than five per cent, while forb reproductive parts made a significant contribution only during the early dry season. At this time (April to July) the fruits of Solanum panduraeforme were ripening, and their abundance on the unburnt pediment was 1,7 g per m^2, estimated to be about 7,5 per cent of the total potential food in the herb layer. At other times of the year the contribu= tion of forb reproductive parts was negligible.

Forb leaves were significantly more abundant in the hill base eco= tone than the knobthorn savanna, and the two transect surveys suggested that forb abundance declined gradually with increasing distance from the hills. Within the hill base ecotone there was no significant difference between the slopes and pediment in forb leaf biomass.

As with the forbs the average density of woody plants was lower in the knobthorn savanna than the hill base ecotone. Within the hill base ecotone the density of woody plants was highest at the hill base, intermediate on the upper slopes and lowest on the pediment.

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TABLE 20a: THE BIOMASS OF LEAVES AVAILABLE BELOW 2,5 m IN g DRY WEIGHT PER m^2 OF SOME WOODY PLANT SPECIES ON THE SLOPES[x] OF THE NWAMURIWA HILLS

Species	Dry Season 1976 (May to Mid-Sept.)	Pre-rain flush (Mid-Sept. to November)	Wet Season (December to April)	Dry Season 1977 (May to August)
Acacia nigrescens	1,90	1,45	5,23	2,25
Combretum apiculatum	0,86	0,35	2,82	1,39
Combretum hereroense	0,37	0,36	0,72	0,38
Securinega virosa	0,21	0,11	0,60	0,24
Ziziphus mucronata	0,39	-	0,84	0,40
Dichrostachys cinerea	0,33	0,10	0,79	0,33
Maytenus heterophylla	0,27	0,10	0,64	0,27
Ehretia amoena	0,14	0,01	0,22	0,14
Euclea divinorum	2,95	2,95	2,95	2,95
Other woody species	10,04	7,28	25,81	12,15
Total woody plants	17,50	13,30	40,60	20,50
Forb leaves	8,30	1,60	17,60	6,10
Overall Total	25,80	14,90	58,20	26,60

[x] The 'slopes' are regarded to extend from 20 m out from the knick at the hill base to 80 m upslope from the knick.

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ABLE 20 b: THE BIOMASS OF LEAVES AVAILABLE BELOW 2,5 m in g DRY WEIGHT PER m^2 OF SOME WOODY PLANT SPECIES ON THE PEDIMENT^x OF THE NWAMURIWA HILLS

Species	Dry Seasons 1976 (May to Mid-Sept.)	Pre-rain flush (Mid-Sept. to November)	Wet Season (December to April)	Dry Sea= son 1977 (May to August)
cacia nigrescens	1,90	1,45	5,23	2,25
ombretum apiculatum	0,00	0,00	0,01	0,00
ombretum hereroense	0,28	0,27	0,54	0,29
ecurinega virosa	0,02	0,01	0,06	0,02
iziphus mucronata	0,15	-	0,33	0,16
ichrostachys cinerea	0,47	0,14	1,12	0,47
aytenus heterophylla	0,07	0,03	0,18	0,07
hretia amoena	0,12	0,01	0,20	0,12
uclea divinorum	6,75	6,75	6,75	6,75
ther woody species	3,29	2,31	8,47	3,99
otal woody plants	13,10	11,60	22,90	14,10
orb leaves	12,50	2,10	18,70	9,90
verall Total	25,60	13,70	41,60	24,00

x The pediment is regarded to extend from 20 m to 400 m away from the knick at the hill base.

The pattern of seasonal variation in the nutritional value of forb leaves differed between the hill slopes and the pediment. Forb leaves on the pediment were higher in both protein and moisture than those on the slopes during the dry seasons but in the wet season there was little difference between them. This may have been due to a difference between the two regions in soil moisture content. The contrast between the slopes and pediment in soil moisture was probably most pronounced in the dry season. So long as the rains lasted the slopes would remain fairly wet but, being sandier (Coetzee 1977) with greater run-off, would lose moisture more quickly and to a greater extent than the pediment in the dry season. A low soil water content may thus account for the lower dry season nutrient content of forb leaves on the hill slopes.

Summer fires are unusual in the study area; burning usually takes place in the late dry season. Because of the greater water content of the vegetation, the fire of January 1977 was probably cooler than a typical late dry season fire, and only the plants in the herb layer and some of the lower leaves of the woody plants were affected. Although the fire caused a marked decline in the abundance of forb leaves and terminal stems, recovery was rapid; within a few months the quantity of leaves and terminal stems on the burnt areas equalled that on the unburnt. In contrast main stems remained less abundant on the burns than the unburnt areas throughout the dry season following the fire.

During the dry season after the fire the protein and moisture content of forb leaves on the burnt areas was significantly lower than those on unburnt areas. As indicated by their lower main stem biomass the burnt forbs had not reached full growth by the time the dry season set in, and this may have accounted for their lower dry season protein and moisture content. However, the difference was not necessarily caused by the fire, it could reflect inherent differences (for example in soil type or species composition) between the two areas.

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The effects of the fire and other habitat factors on the foraging behaviour of kudus are discussed in Chapter 3.

The seasonal cycle in biomass of both forb and woody plant leaves was closely correlated with the seasonal cycle in rainfall (Fig. 18). Production of forbs was clearly directly related to water availability. In the early growing seasons of both 1975 and 1976 little new growth of forbs appeared before the first good rains (which arrived in November). The drought in January 1977 retarded forb growth as the immature plants wilted, and there were no signs of recovery until rain fell in February. In contrast the production of woody plant leaves was less closely associated with rainfall. Some woody species flushed in advance of the rain, the most common being Acacia nigrescens, Combretum hereroense, Lonchocarpus capassa, Acacia gerrardii and Sclerocarya caffra. Woody species which did not flush extensively before the start of the rains in November were Combretum apiculatum, Securinega virosa, Ziziphus mucronata, Dichrostachys cinerea and Ehretia amoena. These differences between the woody species were observed during the preliminary observations in the early growing season of 1975 as well as during 1976, so there are evidently consistent differences between species in the timing of spring leaf production.

For the early flushing species leaf production is probably triggered by photoperiodic or temperature cues, and would depend on stored reserves rather than the current season's rainfall. For the late flushing species it is open to question whether the start of leaf production actually depends on the arrival of the rains or whether they simply respond more tardily to temperature or photoperiod. The increase in the standing crop of woody plant leaves from December to February (Fig. 17) indicates that considerable growth occurred after the rain arrived, but it is uncertain to what extent this depended on stored reserves or the current season's rain.

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The timing of leaf fall and flush varied not only between species of woody plants but also between individuals within species. At least in Acacia nigrescens, within-species variation depended on tree size, the larger specimens lost their leaves earlier in the dry season than the smaller ones. Differences in phenology between adult and juvenile plants have been reported for Heteromeles arbutifolia, an evergreen shrub from southern California (Mooney, Parsons & Kummerow 1974). Stem growth ceases earlier in the season in the mature reproductive plants than in the non-reproductive juveniles, evidently because the mature plants divert resources from vegetative growth to reproductive parts. In Acacia nigrescens the mature trees flower in September even before the leaves appear, whereas saplings do not produce flowers. It is possible that here too the demands of reproduction account for the observed differences in phenology between the smaller and larger individuals. There was also some indication that the larger Acacia nigrescens trees flushed earlier than the small ones, although the evidence for this was not conclusive. The saplings would have shallower roots than the trees, and may therefore depend to some extent on the arrival of rain for leaf production rather than entirely on stored reserves. Combretum apiculatum also showed differences between mature and juvenile specimens in phenology, again the larger trees tended to lose their leaves earlier in the dry season. The timing of the spring flush varied between trees in different localities, and here microclimatic differences were probably responsible.

Similar patterns in phenology were observed in savanna trees in Malawi by Hall-Martin and Fuller (1975). They reported that nine out of 13 selected deciduous woody species produced new leaves before the rainy season commenced, whereas in the remaining four species leaf production began only after the first rains fell. In Acacia nigrescens Hall-Martin and Fuller also observed considerable between-individual variation in the timing of leaf fall. Goodman (1975) and Pellew (1980) both noted that some savanna woody plants commence leaf production before the first spring rains.

The seasonal cycle in abundance of forb leaves was more pronounced than that of woody plants. For forbs the greatest leaf abundance in March was 18 times that of September-October; whereas for woody plants the peak in February-March was only three times that of the lowest values in August-September. However if the evergreen Euclea divinorum is excluded the highest abundance of woody plant leaves (27 g per m^2) was 5,4 time the lowest (5 g per m^2). Although woody plant leaves were more abundant than forb leaves throughout the year the difference between them was relatively less pronounced in the wet season than at other times.

For both woody plants and forbs highest leaf protein contents (20 - 25 per cent) were found early in the growing season when the new leaves appeared (which varied from September to November depending on species). These initial high values declined when the leaves matured in summer (December to April) and thereafter declined further in April when leaf fall commenced. This would be expected from the known relationship between the protein content of plants and their phenology. In immature leaves the protein content is high but when they fully expand at maturity there is an increase in the content of structural carbohydrates and lignin and a decrease in protein content. A further decrease in protein content can occur before the leaves are shed if the plant translocates protein from the leaves to storage organs in preparation for dormancy (Beevers 1976).

Protein contents of over 20 per cent for newly emerging woody plant leaves have been reported in other studies (Sauer 1977, Pellew 1980) and are probably characteristic of a wide variety of African browse species. Pellew (1980) found that the high protein contents of new Acacia leaves in East Africa (23 per cent) lasted only a few days - the values declined to an average of about 16 per cent once the leaves expanded and hardened. These protein contents are very similar to those of new and mature Acacia nigrescens leaves (see Table 16). But whereas Pellew found that the East African Acacia species showed no further decline in protein content, the protein content of A. nigrescens declined from 16 per cent in the wet season to 13-14 per cent in the dry season. Similar declines in protein content from the wet season to the dry were found in other species analysed in this study (Table 16). Two factors may account for this decline. The analyses for leaf protein content were done on subsamples taken form the material clipped to estimate abundance, and thus represent the 'average' quality of available food. In the wet season samples of both woody and forb leaves contained mostly mature leaves and some new leaves, whereas in the dry season they included mature and falling leaves with very few new leaves. Thus the observed decline in protein content from the wet season to the dry may have been either because the samples included fewer new leaves in the dry season than in the wet or because of translocation of protein from the leaves before they were shed in the dry season.

The seasonal variations in phosphorus and moisture contents were similar to that of protein. However leaf calcium content was higher in the dry seasons than the pre-rain flush for both forb and woody plant leaves. Seasonal variations in calcium content are known to differ from those of other nutrients (Du Toit, Louw and Malan 1940). Garten (1978) noted that calcium has a structural role in the plant cell; it is found in cell walls, and the concentrations of both nitrogen and phosphorus tend to be negatively correlated with that of calcium. This would explain the tendency for calcium content to be higher in the dry seasons than the early growing season.

Although the seasonal cycle in protein content of woody plant and forb leaves was basically similar, the difference between them in phenology meant that the cycles were slightly out of phase, and as a result the relative difference in quality between forbs and woody plants changed over the year (Fig. 17). Because some woody plants flushed before the spring rain arrived the average protein content of woody plant leaves was higher than that of forbs during September and October. Later, from December to April, most woody plant leaves had matured while the forbs were still growing actively, and so the forb leaves averaged higher in protein content. During the dry season there was little difference between the average protein contents of woody plant and forb leaves. The effects of these seasonal differences on food selection in kudus are discussed in Chapter 2.

For kudus in the study area the time of greatest food abundance is from January to April. As would be expected the period of maximum abundance coincides with the calving season - which is at its peak from January to March (Owen-Smith unpublished). At this time the high nutrient requirements of the cows during late pregnancy and lactation could be most easily met. The time of greatest food scarcity and lowest nutrient content is from the end of July to mid-September, after which the early flushing woody plants commence production. The early flushing woody plants could be of critical importance to kudus, particularly in years when the rains are late, because they offer highly nutritious food at a time when little else is available.

Evaluation of the method of estimating potential food abundance: Comparison with related studies

The leaf density as estimated using the 0,1 m^3 frame provided an index of abundance to compare between species and between seasons. The method was successful in identifying the seasonal trends and also helped to assess differences between species in phenology. The seasonal changes in the frame sample estimates were consistent with results based on descriptive records of phenology. The frame method had the additional advantage of providing an objective method of collecting leaves for analysis of nutrient content. However in estimating leaf abundance per unit area the method was susceptible to bias; leaf weight per unit frame volume tended to overestimate leaf weight per unit canopy volume for some species. The degree of bias is likely to vary between species depending on typical growth form. Detection and correction of the bias proved laborious, and this must be considered an important difficulty with the method. However alternative methods of estimating seasonal variations in browse abundance are not without difficulties. The

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most common approach involves the use of regression techniques (Rutherford 1979). A regression equation is calculated relating some easily measured dimension of the plant, such as stem diameter or canopy volume (termed the predictor variable) to biomass. The predictor variable is then surveyed in plots of known size and biomass is estimated using the regression equation. This approach would be adequate for estimating the standing wet season crop as was done by Dayton (1978) in the Kruger Park. However if variations over the seasons are required a considerable amount of sampling would be necessary to derive the regression equations. In view of the relationship between leaf fall and tree size found in the present study separate prediction equations would have to be derived for different seasons for each category of plant size. In the spring, when a large number of woody plants are bare, the relationship between tree dimensions and leaf mass is variable, and it would be difficult to derive accurate prediction equations.

Pellew (1980) tried the regression technique as a means of estimating year-round availability of Acacia browse in East Africa but found it unsatisfactory because of excessive variance. He employed a direct estimation technique which proved accurate to within ten per cent. The Point-Centred Quarter method was used to obtain available canopy volume per unit ground area. Each tree contacted by this method was categorized by species and by foliage density class on a scale of 0-5. Every tenth tree of each category was photographed and harvested to determine browse biomass m^{-3} of canopy volume. Sample trees that were not harvested were awarded biomass m^{-3} values by comparison with the photographed trees. The technique has the disadvantage of not being suitable for treatment by normal statistical analysis (Pellew 1980).

In the Serengeti National Park, Tanzania, Pellew (1980) reported maximum available browse biomass (leaves as well as current season's shoots) of 71,2 g per m^2 at the end of the rains, which declined to a minimum of 16,7 g per m^2 in the late dry season. The extreme interseasonal range was thus a factor of 4,3 times. This is similar to the values found in this study for inter=seasonal variation in total woody plant leaf abundance (3,2 times if the evergreen *Euclea divinorum* is included, 5,4 times if it is excluded).

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CHAPTER TWO: FOOD SELECTION

The choices involved in food selection occur at different levels (Johnson 1980, Owen-Smith and Novellie 1982). Firstly the animal can select certain plant communities from among the range of com= munities encountered. Secondly it can select between different patch types or subcommunities of plants present within each main community. The third level of selection is that of the individual plant; the herbivore can select between species or between indi= viduals of a species. Next the herbivore can select certain parts of any individual plant, either leaves, stems or reproductive parts. Further selection can take place within this level, for example the animal can choose certain individual leaves or leaf groups of different growth stages.

The only selection level for which quantitative data could be obtained in this study was the plant species selected. In order to assess community selection it would have been necessary to record the relative amount of foraging time spent in the different subdivisions of the study area. Records of the time apportio= ment between habitat subdivisions were biased because, owing to differences in vegetation and topography, it was more difficult to find the kudus in some habitat subdivisions than others. An attempt was made to solve the problem using radio telemetry to locate the animals, but the transmitters did not function suffi= ciently long. From the usual observation distance (see Methods below) the plant parts eaten by kudus could sometimes be recognised, but it was not usually possible to determine the relative propor= tions of leaves, shoots and reproduction parts that were taken. Plant part selection could therefore be studied only qualitatively.

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METHODS

The choice of methods suitable for estimating the diet composition was limited by practicality as well as the objectives of the study. Since the major objective was to investigate the role of food as a factor affecting population success any method involving destructive sampling, such as the analysis of rumen contents, could not be considered. The most accurate method of measuring diet composition is by means of the oesophageal fistula, but although this may have some potential for use with tamed wild animals, it is not feasible in most field studies. Another method is to identify food plants from undigested fragments in the faeces (Stewart 1967). However although grasses can be readily identified in this way other plant types are more difficult. Also different food items are digested to different degrees, and therefore relative quantities of different species in the faeces may not reflect the proportions in the diet. Yet another possibility is the use of vegetation-based techniques (Barnes 1976). These can take the form of surveys of the vegetation to assess utilization or, alternatively, exclosures can be constructed to exclude herbivores, and utilization is then assessed by comparing the vegetation inside the exclosures with that outside. However for this study the vegetation-based approach had several disadvantages. Firstly the study area was utilized by a number of herbivores besides kudus so that there was a risk that food plants of these other species could wrongly be ascribed to kudus. Also kudus do not occur at such high densities as many grazers for example, and the impact of the population is spread over a wider area. Use of exclosures would therefore be impractical.

The most suitable method under the circumstances was direct observation of foraging kudus. Diet composition was estimated from the relative amount of feeding time spent on the different species, as described by Owen-Smith (1979). A foraging kudu was kept under continuous observation for a period which varied from one to thirty minutes. A complete record of the animal's foraging behaviour as well as the plants eaten was obtained by means of a portable tape recorder. The commentary was synchronised with the actions of the kudu so that the sequence was recorded as closely as possible. The tape was later transcribed and the duration of each activity was timed by means of a stopwatch. A number of such recording sessions were made in each month of the study period (Table 21, see below).

The procedure was designed to obtain a quantitative record of patterns of foraging behaviour as well as diet composition. Foraging behaviour is discussed in Chapter 3, and only those aspects of the method relevant to food selection are dealt with here.

Food plants eaten were classified into two basic groups:

(i) Woody plants which were visible above the herb layer (trees, saplings and shrubs more than about 0,5 m tall).

(ii) Plants in the herb layer including grass, forbs and seedlings of woody plants (woody plants under 0,5 m tall), which were usually invisible to the observer because of the dense ground cover.

Thus the woody plant species could be identified, but since the plants in the herb layer could not be seen the proportions of these species in the diet could not be established by direct observation. For each recording session the time spent feeding in the herb layer and on each woody species was calculated. Feeding time included reaching for food and gathering it as well as chewing.

In addition the numbers of individual woody plants of each species fed on were recorded. A kudu could sometimes interrupt feeding on one woody plant to feed on adjacent plants, then return to the first plant. This was counted as only one record of feeding on the first plant, not two.

It sometimes happened that I was uncertain of the identity of one or more woody plants fed on during a recording session. In these cases a description of the position of the doubtful plants was recorded on the tape after the session had ended. The sites were

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subsequently visited and the identity of the plants checked. It sometimes proved impossible to locate the plants, however, and they had to be recorded as 'unidentified'.

I attempted to identify plants eaten in the herb layer by inspecting sites where kudu had been feeding, but this proved time consuming in relation to the amount of information obtained. Results were probably biased towards the larger species, partly because they were easier to locate but also because the kudus sometimes left only unidentifiable fragments of the smaller species. Because of these limitations only a rough indication could be obtained of the plant species utilized in the herb layer.

The duration of recording sessions varied according to circumstances. If a kudu performed any activity other than feeding for longer than two minutes the session was regarded as terminated at the start of such activity. This was an arbitrary decision but the exact criterion has little influence on results; as shown by Owen-Smith (1979) very few intervals between feeding bouts last longer than 90 seconds.

It often happened that the kudu under observation became obscured behind the vegetation. The tape was turned off the moment the animal disappeared; if it reappeared within three minutes the recording session was continued as if no interruption had occurred, otherwise it was terminated.

Another factor which could restrict the duration of recording sessions was the need to locate the unidentified woody plants. This was difficult if the session continued too long or the kudu moved a long distance during the session. If the kudu foraged continuously and conditions were favourable the recording lasted a maximum of thirty minutes.

The kudus were accustomed to vehicles but not to observers on foot, and so most observations were made from a Land Rover. On the pediment the animals could be followed in the vehicle and recording distance could be as close as 5 - 10 m. For kudus foraging at the hill base or on the slopes the observation distance was usually much further. Recordings were sometimes made from the hill tops and under these conditions the observation distance could be about 800 m. Binoculars were used at distances of less than about 100 m and a telescope at greater distances. The activities of the foraging kudu could generally be seen at the longer observation distances but food plants could not be identified satisfactorily. The longer the distance the greater the risk of bias towards the larger more distinctive species. Food plants were therefore seldom identified at distances of over 400 m.

The data reported here were gathered over the period May 1976 to August 1977. A number of recordings were made between October 1975 and April 1976 but these were not accompanied by measurements of the quantity and quality of the vegetation so these data are not reported in detail. The number of sessions and total recor=ding time is shown for each month of the main study period in Table 21.

Although data were collected each month, sample sizes were insuf=ficient to examine selection amongst woody species on a monthly basis. The study period was therefore subdivided into the four seasons recognised in Chapter 1 (see Table 20). If these seasons are further subdivided the sample size in each season becomes too small to reliably assess selectivity for the less common woody species. For the dominant woody species, however, finer subdivi=sions are possible and feeding time spent on these species are examined on a monthly as well as a seasonal basis.

Estimating acceptance of woody plants

The diet composition of an animal will obviously be determined partly by the array of food types available to it. If the animal exercises no selectivity in feeding, but simply accepts food items

TABLE 21 : THE NUMBER OF RECORDING SESSIONS AND TOTAL RECORDING TIME PER MONTH GATHERED BETWEEN MAY 1976 AND AUGUST 1977

Month	Total		With food plants identified	
	Number of sessions	Recording time (hours)	Number of sessions	Recording time (hours)
May 1976	13	2,35	9	1,40
June	34	5,35	23	3,30
July	31	5,07	23	3,80
August	37	6,02	32	5,55
September Pre-flush	18	3,17	14	2,40
September Post-flush plus October	40	6,90	35	6,18
November	21	3,12	18	2,68
December	36	4,47	25	3,65
January 1977	32	4,30	23	3,08
February	27	4,22	27	4,22
March	8	1,20	8	1,20
April	29	3,20	17	1,57
May	29	3,60	24	3,12
June	37	4,30	31	3,53
July	41	5,20	41	5,20
August	34	4,42	31	3,98
Total	467	66,89	381	54,86

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as it encounters them, the proportions of the different food types in its diet will be the same as the relative proportions available in the environment. Feeding is said to be selective if the food types are eaten disproportionately to their relative availability (Chesson 1978). The degree of selectivity shown in feeding is therefore assessed by examining diet composition in relation to the availability of the various dietary components.

Several measures have been proposed which allow different food types to be ranked in terms of their relative acceptabilities (Chesson 1978, Johnson 1980). The approach used here has been employed in a number of studies (Petrides 1975, Chesson 1978); an indication of the acceptance of a food type is given by its "selectivity rating", calculated as the ratio of its proportion in the diet to the proportion available in the habitat. The proportion of a food type in the diet of kudus was estimated as the proportion of the total feeding time spent on it, and the relative availability of a food type was given by its proportion of total available leaf biomass.

Statistical analysis

Differences in the selectivity ratings of different food types may arise simply by chance (because of sampling variation) and therefore it is desirable to determine the statistical reliability of the ratings.

For the purpose of statistical analysis the proportion of feeding time spent on each woody species was separated into two components:

(i) the <u>relative frequency of utilization</u> of a species, equal to the number of individual plants of that species fed on, expressed as a percentage of the total number of woody plants fed on.

(ii) <u>the mean time spent feeding on an individual plant</u>, equal to the total time spent feeding on a species divided by the number of utilized plants of that species.

The methods of analysis are described for each of these components below.

The frequency of utilization of woody plants

To analyse selection amongst individual woody plants the relative frequency of utilization of each species was compared with the relative numbers of each available. The total number of woody plants of each species fed on by kudus in each season was counted over all recording sessions. The numbers of individual plants of the various woody species available (calculated as described below) were then used to derive the number of utilized plants of each species which would be expected if utilization were proportional to availability. Chi-square goodness-of-fit tests were used to determine the significance of deviations between observed and expected values. The null hypothesis tested was that the relative numbers of the different woody species fed on by kudus were directly proportional to the relative numbers available. The alternative hypothesis was that the kudus select certain species either more or less frequently than would be expected on the basis of their availability.

Only those woody species with an overall density of more than 15 per ha were considered in this analysis as the expected values for the remainder would be too small to apply the chi-square test. It is generally recommended that the chi-square test only be applied if there is an expected value of at least one in each cell and that no more than 20 per cent of all cells contain less than five expected observations. However Roscoe and Byars (1971) indicate that these conditions may be conservative and that the chi-square can be used as long as the average expected obser=vation is six or more for the 0,01 level of the test. The latter criterion was applied to the present analysis.

Although the chi-square tests show that the sets of observed values deviate from the expected they do not determine significant preference or avoidance of specific species. The Bonferroni z statistic was therefore used as described by Neu, Byers and Peek (1974) to estimate whether each species was fed on more or less frequently than expected.

This technique involves constructing 90 per cent confidence intervals for the observed percentage utilization of each species in order to determine whether the expected percentage lies within the interval. Since several parameters are estimated simultaneously the level of significance of the intervals requires adjustment (Neu <u>et al</u>. 1974). The appropriate statistic used in constructing each interval estimate is

$$z_{(1-\alpha/2k)}$$

where k is the number of simultaneous estimates being made and α is the level of significance (in this case $\alpha = 0{,}10$). The resulting confidence intervals are wider than for an estimate of only one parameter.

The mean time spent feeding on individual woody plants

For each woody species the recorded number of seconds spent by kudus feeding on individual plants was divided by the mean weight of leaves (in grams) available per plant. The resulting ratios of feeding time to weight of leaves available per plant were than compared among the different woody species. The values for feeding time spent on a plant showed evidence of heterogeneity of variance and lack of normality. The logarithmic transformation was applied, but this did not eliminate heterogeneity of variance. Thus data from each season were first tested using the F_{max} test (Sokal and Rohlf 1969) to determine whether homogeneity of variance could be assumed. If the assumption of homogeneity of variance was accepted comparisons among means were made using the Newman Keuls test. If not the approximate test of equality of means when the variances are heterogeneous (Sokal and Rohlf 1969) was used. The null hypothesis of these tests was that there

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are no differences among woody species in the ratio of feeding time to weight of leaves available per plant.

Estimating availability of woody plants

The estimates of the relative amounts of each food type available, used in calculating the selectivity ratings, should reflect con= ditions as experienced by the kudus in the areas where they chose to forage. This would depend on the amount of time the kudus apportioned to the various habitat subdivisions. Estimates of availability as experienced by the kudus were therefore approxi= mated as shown below. For each season the percentage of recor= ding time obtained from each of the nine subdivisions of the hill base ecotone was calculated (Table 22). These percentages were used to derive weighted abundance estimates for all woody plants combined and for each woody species with an overall density of more than 15 per ha. (For those species with densities less than this selectivity could not be assessed reliably.)

Weighted estimates of available canopy volumes were derived as:

$$\sum_{k=1}^{n} t_k c_k$$

where t_k is the fraction of recording time obtained in the k^{th} habitat subdivision, c is the canopy volume per unit area in the k^{th} habitat subdivision, and n is the number of habitat subdivi= sions (n=9). These estimates were converted to leaf weight by multiplying by the mean leaf weights per unit canopy volume given in Chapter 1. The values for available leaf weights represent the quantities of each woody species encountered by the kudus in the areas where the foraging data were gathered.

TABLE 22 : PER CENT OF RECORDING TIME OBTAINED IN EACH HABITAT SUBDIVISION. US = UPPER SLOPES, B = HILL BASE, P = PEDIMENT

Season		Habitat			
		West slopes Nwamuriwane	East slopes Nwamuriwane	West slopes Nwamuriwa	Total
Dry Season 1976	US	10%	2%	5%	17%
	B	3%	9%	16%	28%
	P	25%	13%	17%	55%
		38%	24%	38%	100%
Pre-rain flush	US	0%	4%	10%	14%
	B	0%	0%	28%	28%
	P	4%	14%	40%	58%
		4%	18%	78%	100%
Wet Season	US	34%	1%	13%	48%
	B	7%	2%	18%	27%
	P	8%	8%	9%	25%
		49%	11%	40%	100%
Dry Season 1977	US	5%	2%	13%	20%
	B	9%	5%	8%	22%
	P	33%	14%	11%	58%
		47%	21%	32%	100%

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Estimates of the relative numbers of the different woody species available, used to compare with the relative frequency of utili= zation, were derived in a similar way.

Acceptance of plants in the herb layer

The data on the proportion of time spent feeding in the herb layer were sufficient to test for differences between months as well as between the four seasons. The percentage of feeding time spent on plants in the herb layer as opposed to woody plants was calculated for each recording session of over 2 min duration. The significance of differences among monthly means were then tested using the Newman-Keuls test. The variates were percen= tages which varied between 0 and 100, and so the arcsin transfor= mation was applied (Sokal and Rohlf 1969).

In order to compare utilization of plants in the herb layer with their relative availability a monthly estimate was derived of the percentage of total leaf biomass (i.e. woody plants plus forbs) made up by forb leaves. The relative proportions of recording time obtained in each of the habitat subdivisions were used to derive these percentages in a similar way to that described above for woody plant species.

Limitations and possible sources of error in the method

Estimates of diet composition in terms of feeding time have one important limitation; feeding time is not necessarily an accurate representation of the quantity of material ingested. The relative proportion of feeding time spent on different species is an unbiased

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estimate of relative mass ingested only if the ingestion rate per unit feeding time does not differ between plant species. As will be discussed later this condition is unlikely to hold.

Some workers (see e.g. Wallmo *et al*. 1973, Stephens 1975) have recorded the number of bites taken from food plants as a measure of utilization. In this study observation distances were usually too long to record this. Also bite sizes were very variable, so it is doubtful whether bite counts would have provided superior estimates of quantity ingested.

Estimates of feeding time made from a distance may also be subject to bias. Wallmo *et al*. (1973) compared the results of distant observers using feeding time to estimate diet composition of a tame deer with those of observers stationed next to the deer. The distant observers tended to overestimate the use of shrubs and to underestimate the use of grasses and forbs. The use of the largest and most conspicuous shrubs was also overestimated. Furthermore results could vary between observers, some were more inclined to guess at uncertain food species than others. Wallmo *et al*. concluded that quantitive estimates based on feeding time could be seriously in error.

There was no opportunity to systematically check the accuracy of observations made during this study. However there is reason to think that the procedures followed in recording would give protection against the degree of bias found by Wallmo and co-workers. In the present study the vegetation divided easily into the visible woody component and the invisible herb layer, and no attempt was made to record plant species utilized in the herb layer. It is unlikely that there was a bias in favour of one or other of these two main categories. Secondly the identity of uncertain woody plants was checked whenever possible.

Nevertheless some degree of bias is possible. Unidentified woody plants which afterwards could not be located were often low-growing and not clearly visible above the herb layer. This means that species which typically had this growth form (e.g. *Combretum*

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mossambicense and Maerua parvifolia) could have been underrepresented in the samples.

Another possible source of error was that the kudus sometimes fed on plants growing within the crown of a larger species and from a distance it could appear that the larger species was the one being utilized. In the study area creeper species such as Cucumis metuliferus sometimes grew within the canopy of woody plants. The kudus were observed on a few occasions pulling these creepers out of the crown of a shrub and chewing on them. It is uncertain to what extent this factor could have biased results but it is unlikely to have been a major source of error. If a kudu under observation was suspected to be eating a plant within the canopy of another the site was later inspected and the plants examined for signs of utilization.

RESULTS

Diet composition in relation to availability: the selectivity ratings

The diet composition of kudus in the hill base ecotone showed marked seasonal variations (Table 23 a-d). Thus in the wet season and the 1976 and 1977 dry seasons 64-68 per cent of feeding time was spent on plants in the herb layer, but this declined to only 17 per cent in the pre-rain flush. There were also seasonal variations in the proportion of feeding time spent on the two dominant woody species, Acacia nigrescens and Combretum apiculatum. A comparatively greater proportion of feeding time was spent on C. apiculatum than A. nigrescens in the dry seasons, but a much lower proportion in the pre-rain flush (Table 23 a-d). Combretum hereroense was fed on mainly in the dry seasons and the pre-rain flush, but comprised only a small proportion of the diet in the wet season. Feeding time spent on Securinega virosa on the other hand was higher during the we season than at other times.

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TABLE 23 : SELECTIVITY RATINGS FOR THE COMMON WOODY SPECIES AND FOR PLANTS IN THE HERB LAYER

TABLE 23a - DRY SEASON 1976 : MAY TO MID-SEPTEMBER

Species	A Per cent of feeding time	B Per cent of dry mass of leaves available	Selectivity rating (A/B)	Rank of rating
Acacia nigrescens	2,8	7,4	0,38	8
Combretum apiculatum	4,6	1,7	2,71	4
Combretum hereroense	4,7	1,3	3,62	2
Securinega virosa	0,1	0,4	0,25	9
Ziziphus mucronata	1,8	0,7	2,57	5
Dichrostachys cinerea	1,6	1,9	0,84	7
Maytenus heterophylla	2,9	0,9	3,22	3
Ehretia amoena	2,0	0,4	5,00	1
Euclea divinorum	2,0	20,8	0,10	10
Other woody species	9,5	29,5	0,31	-
Herb layer	68,0	35,0	1,94	6
	100	100		

TABLE 23b - PRE-RAIN FLUSH : MID-SEPTEMBER TO NOVEMBER

	A Per cent of feeding time	B Per cent of dry mass of leaves available	Selectivity rating (A/B)	Rank of rating
Acacia nigrescens	42,5	11,2	3,79	5
Combretum apiculatum	3,4	0,5	6,80	2
Combretum hereroense	9,7	1,9	5,11	3
Securinega virosa	0	0,1	0	11
Dichrostachys cinerea	1,0	0,7	1,43	7
Maytenus heterophylla	1,7	0,2	8,5	1
Dalbergia melanoxylon	4,2	0,9	4,67	4
Ehretia amoena	0,2	0,1	2,00	6
Lonchocarpus capassa	3,4	3,2	1,06	9
Euclea divinorum	0,7	37,4	0,02	10
Other woody species	16,2	30,9	0,52	-
Herb layer	17,0	12,9	1,32	8
	100	100		

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TABLE 23c - WET SEASON : DECEMBER TO APRIL

	A Per cent of feeding time	B Per cent of dry mass of leaves available	Selectivity rating (A/B)	Rank of rating
Acacia nigrescens	7,0	14,1	0,50	8
Combretum apiculatum	6,1	8,7	0,70	6
Combretum hereroense	0,3	2,3	0,13	9
Sercurinega virosa	2,3	1,5	1,53	3
Ziziphus mucronata	3,3	1,1	3,00	1
Dichrostachys cinerea	1,9	1,6	1,19	4
Maytenus heterophylla	2,2	3,3	0,67	7
Ehretia amoena	0,3	0,3	1,00	5
Euclea divinorum	0	10,2	0	10
Other woody species	10,8	25,9	0,42	-
Herb layer	65,8	31,0	2,12	2
	100	100		

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TABLE 23d - DRY SEASON 1977 : MAY TO AUGUST

Species	A Per cent of feeding time	B Per cent of dry mass of leaves available	Selectivity rating (A/B)	Rank of rating
Acacia nigrescens	7,0	9,9	0,71	7
Combretum apiculatum	11,1	2,1	5,29	1
Combretum hereroense	3,1	1,2	2,58	2
Securinega virosa	0,1	0,8	0,13	9
Ziziphus mucronata	1,2	1,1	1,09	6
Dichrostachys cinerea	2,9	2,1	1,38	5
Maytenus heterophylla	0,5	0,8	0,63	8
Ehretia amoena	0,9	0,4	2,25	4
Euclea divinorum	0,2	18,9	0,01	10
Other woody species	9,5	34,7	0,27	-
Herb layer	63,5	28,0	2,27	3
	100	100		

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The seasonal variations in diet composition found in this study are very similar those reported by Owen-Smith (1979). Evidently the diet composition of kudus in the study area follows a definite seasonal pattern which remains consistent from one year to the next. Table 23 a-d does indicate some differences between years, however; both A. nigrescens and C. apiculatum comprised a relatively greater proportion of the diet in the dry season of 1977 than that of 1976.

The question arises of whether the seasonal variations in diet composition simply reflect corresponding seasonal variations in the relative availability of the different food types, or whether selection amongst food types actually varies between seasons. To some extent variations in diet composition are correlated with variations in relative availability. Thus the low proportion of feeding time spent on plants in the herb layer during the pre-rain flush corresponds with the low availability of forb leaves relative to woody plant leaves at this time (Table 23 b). C. apiculatum tended to produce leaves later than A. nigrescens, and so its availability compared to A. nigrescens was low during the pre-rain flush. This, in part, could account for the fact that C. apiculatum comprised a lower proportion of the kudus' diet compared to A. nigrescens in the pre-rain flush than at other times of the year.

However, the differences between food types in the selectivity ratings do not remain consistent between seasons. This indicates that seasonal variations in diet composition are not entirely attributable to variations in availability, but that selection amongst food types does vary between seasons - a species favoured in one season may be avoided in another. Thus, as noted, Combretum apiculatum comprised a greater proportion of the kudus' diet than Acacia nigrescens in the dry seasons, but a lower proportion at other times. This was despite the fact that the relative abundance of Acacia nigrescens was greater than that of C. apiculatum throughout the year (Table 23 a-d). This means that the kudus favoured C. apiculatum more strongly relative to

A. nigrescens in the dry seasons than in the other seasons. The selectivity ratings of C. apiculatum are actually higher than those of A. nigrescens in all seasons, but the difference between them is proportionately greatest in the dry seasons. Seasonal differences in acceptance of other woody species are discussed in the following sections.

The proportion of feeding time spent on plants in the herb layer

Variation between months in the proportion of time spent feeding on plants in the herb layer are shown in Fig 19. Comparison among the monthly means, using the Newman-Keuls test, showed the October value to be significantly lower than all other months ($P < 0,05$), but differences between remaining months were not significant. This confirms that plants in the herb layer com=prised a smaller proportion of the diet in the pre-rain flush than during the other seasons. The proportion of feeding time spent on plants in the herb layer did not differ much between the wet and dry seasons.

Fig. 19 shows that the proportion of time spent feeding on plants in the herb layer was higher than would be expected from the relative availability of forb leaves in all months except October. This shows that the kudus favoured forbs over woody plants at all times except possibly during the pre-rain flush.

Table 23 and Fig. 19 relate the time spent feeding in the herb layer to the relative availability of forb leaves. But since food from the herb layer includes forb reproductive parts, woody plant seedlings and a little grass as well as forbs, the selectivity rating for the herb layer will be biased on the high side. However little grass was eaten,(see below), and forb fruits and woody plant seedlings comprised only a small proportion of herb layer biomass, so the bias would be slight.

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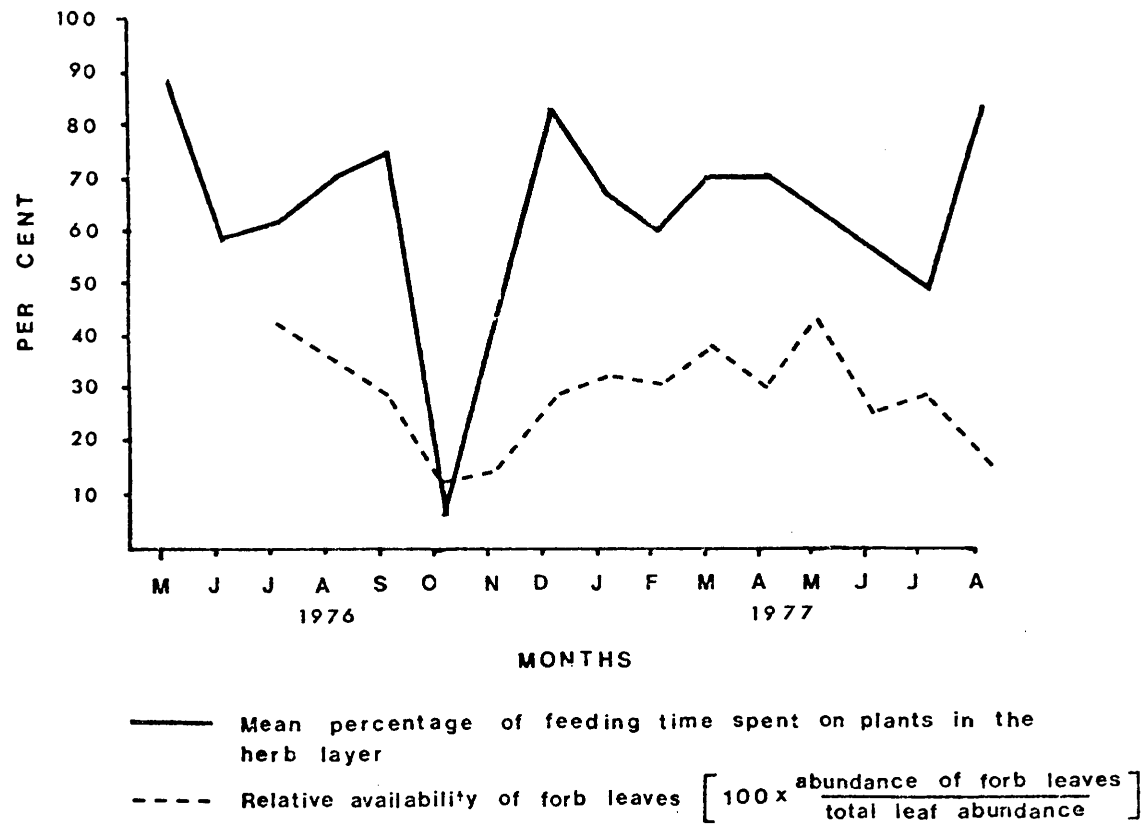

FIG. 19 MONTHLY MEAN PERCENTAGE OF FEEDING TIME SPENT ON PLANTS IN THE HERB LAYER COM= PARED WITH THE RELATIVE AVAILABILITY OF FORBS

Plant species eaten in the herb layer

As discussed under Methods, detailed quantitative information on the forb species utilized could not be obtained. A rough indication of the frequency of utilization of the various forb species is given in Appendix I. Observation of foraging kudus and inspection of areas where they had been foraging indicated that very little grass was eaten except in spring when the new growth began. The knobthorn savanna west of Little Nwamuriwa (Fig. 1) was burnt in September 1976. In November the grass on the burns flushed and at this stage the kudus were frequently observed eating large quantities of the new grass. The protein content of the new grass leaves in November was 15,3% but by December this had declined to 13%. In December the kudus were no longer eating the grass but were feeding extensively on forbs, which had increased markedly in abundance from November to December (see Fig. 16). The fact that they did accept grass in November may have been due to the relatively high nutritional value of the new grass leaves at that time.

The frequency of utilization of individual woody plants

Table 24 a-d shows the observed numbers of each of the common woody species fed on by kudus during the four seasons of the study period. The observed numbers are compared with the numbers that would be expected if utilization were directly proportional to availability. The chi-square goodness-of-fit tests, used to test the significance of deviations between observed and expected values, gave highly significant chi-square values for all four seasons. This shows that kudus do not feed on individual plants in proportion to their availability but tend to select certain species and avoid others.

The 90 per cent confidence intervals for the observed percentage utilization of each woody species, calculated using the Bonferroni

TABLE 24 : FREQUENCY OF UTLIZATION OF THE COMMON WOODY SPECIES COMPARED WITH THE EXPECTED FREQUENCY BASED ON AVAILABILITY. DIFFERENCES BETWEEN OBSERVED AND EXPECTED VALUES TESTED USING THE CHI-SQUARE GOODNESS-OF-FIT TEST. THE 90% CONFIDENCE LIMITS WERE CALCULATED USING THE BONFERRONI Z STATISTIC (SEE TEXT)

TABLE 24a : THE DRY SEASON OF 1976 : MAY TO MID-SEPTEMBER

Species	Recording sessions No = %	Observed number utilized (0)	Expected number utilized (E)	$\frac{(O-E)^2}{E}$	Observed percentage utilized with 90% confidence limits	Expected percentage utilized
Acacia nigrescens	14	17	54,4	25,7	3,5← 9,7→15,9 (rej)	31,1
Combretum apiculatum	12	19	14,2	1,6	4,4←10,9→17,4 (ns)	8,1
Combretum hereroense	19	27	5,3	88,9	7,8←15,4→23,0 (acc)	3,0
Securinega virosa	3	3	4,4	0,5	1,7*	2,5
Ziziphus mucronata	4	4	4,0	0	2,3*	2,3
Dichrostachys cinerea	12	13	7,2	4,7	1,9← 7,4→12,9 (ns)	4,1
Maytenus heterophylla	12	14	3,7	28,7	2,3← 8,0→13,7 (acc)	2,1
Dalbergia melanoxylon	5	6	13,3	4,0	0 ← 3,4→ 7,2 (rej)	7,6
Acacia gerrardii	2	2	8,2	4,7	1,1*	4,7
Ehretia amoena	14	15	2,8	53,2	2,7← 8,5→14,3 (acc)	1,6
Acacia tortilis	0	0	5,8	5,8	0*	3,3
Cissus lonicerifolia	0	0	3,9	3,9	0*	2,2
Dombeya rotundifolia	3	3	4,7	0,6	1,7*	2,7
Pterocarpus rotundifolius	2	2	5,6	2,3	1,1*	3,2
Euclea divinorum	6	7	6,5	0,1	0 ← 4,0 → 8,0 (ns)	3,7
Grewia monticola	0	0	6,7	6,7	0*	3,8
Lonchocarpus capassa	2	2	3,3	0,5	1,1*	1,9
Other species	-	41	21,2	18,5	14,6←23,4→32,2 (acc)	12,1
Totals	101 (sessions)	175	175	250,2	100	100

Chi-square = 250,2 df = 17 $P < 0,001$

*Sample size too small to calculate confidence intervals

(acc) Significant acceptance

(rej) Significant rejection

(ns) Not significant

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TABLE 24b : THE PRE-RAIN FLUSH : MID SEPTEMBER TO NOVEMBER

Species	Recording sessions No	Recording sessions %	Observed number utilized (O)	Expected number utilized (E)	$\frac{(O-E)^2}{E}$	Observed percentage utilized with 90% confidence limits	Expected percentage utilized
Acacia nigrescens	30	57	63	54,1	1,5	29,7 ← 40,6 → 51,5 (ns)	34,9
Combretum apiculatum	7	13	9	7,1	0,5	0,6 ← 5,8 → 11,0 (ns)	4,6
Combretum hereroense	10	19	21	4,7	56,5	5,9 ← 13,5 → 21,1 (acc)	3,0
Securinega virosa	0	0	0	3,3	3,3	0*	2,1
Ziziphus mucronata	3	6	3	3,3	0	1,9*	2,1
Dichrostachys cinerea	2	4	4	5,3	0,3	2,6*	3,4
Maytenus heterophylla	2	4	2	2,9	0,3	1,3*	1,9
Dalbergia melanoxylon	4	8	4	9,8	3,4	2,6*	6,3
Acacia gerrardii	4	8	6	7,3	0,2	3,9*	4,7
Ehretia amoena	2	4	3	2,9	0	1,9*	1,9
Acacia tortilis	1	2	1	5,0	3,2	0,6*	3,2
Cissus lonicerifolia	1	2	1	2,9	1,2	0,6*	1,9
Dombeya rotundifolia	2	4	3	2,0	0,5	1,9*	1,3
Pterocarpus rotundifolius	0	0	0	4,7	4,7	0*	3,0
Euclea divinorum	3	6	3	9,3	4,3	1,9*	6,0
Grewia monticola	1	2	1	9,6	7,7	0,6*	6,2
Lonchocarpus capassa	8	15	10	3,4	12,8	1,0 ← 6,5 → 12,0 (ns)	2,2
Other species			21	17,4	0,7	6,1 ← 13,8 → 21,5 (ns)	11,3
Totals	53 (sessions)		155	155	101	100	100

Chi-square = 101 df = 17 $P < 0,001$

*Sample size too small to calculate confidence limits

(acc) Significant acceptance

(ns) Not significant

TABLE 24c : THE WET SEASON : DECEMBER TO APRIL

Species	Recording sessions No = %	Observed number utilized (O)	Expected number utilized (E)	(O-E)²/E	Observed percentage utilized with 90% confidence limits	Expected percentage utilized
Acacia nigrescens	16	33	44,1	2,8	14,7←25,2→35,7 (ns)	33,7
Combretum apiculatum	17	19	20,7	0,1	6,0←14,5→30,0 (ns)	15,8
Combretum hereroense	3	4	2,6	0,8	3,1*	2,0
Securinega virosa	7	7	4,6	1,3	0 ← 5,3→10,7 (ns)	3,5
Ziziphus mucronata	7	8	2,4	13,1	0,3← 6,1→11,9 (ns)	1,8
Dichrostachys cinerea	7	9	4,6	4,2	0,8← 6,9→13,0 (ns)	3,5
Maytenus heterophylla	7	7	4,7	1,1	0 ← 5,3→10,7 (ns)	3,6
Dalbergia melanoxylon	3	3	7,7	2,9	2,3*	5,9
Acacia gerrardii	2	3	3,4	0,1	2,3*	2,6
Ehretia amoena	5	5	1,4	9,3	3,8*	1,1
Acacia tortilis	0	0	3,0	3,0	0*	2,3
Cissus lonicerifolia	3	3	5,4	1,1	2,3*	4,1
Dombeya rotundifolia	1	1	1,0	0	0,8*	0,8
Pterocarpus rotundifolius	1	1	1,0	0	0,8*	0,8
Euclea divinorum	0	0	3,3	3,3	0*	2,5
Grewia monticola	2	2	4,6	1,5	1,5*	3,5
Lonchocarpus capassa	2	2	1,2	0,5	1,5*	0,9
Other species	-	24	15,2	5,1	8,9←18,3→27,7 (ns)	11,6
Totals	100 (sessions)	131	131	50,2	100	100

Chi-square = 50,2 df = 17 P< 0,001
* Sample size too small to calculate confidence limits
(ns) Not significant

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TABLE 24d : THE DRY SEASON OF 1977 : MAY TO AUGUST

Species	Recording sessions		Observed number utilized	Expected number utilized	$\frac{(O-E)^2}{E}$	Observed percentage utilized with 90% confidence limits	Expected percentage utilized
	No	%	(O)	(E)			
Acacia nigrescens	31	24	51	58,2	0,9	18,1←27,0→35,9 (ns)	30,8
Combretum apiculatum	27	21	43	17,0	39,8	14,3←22,8→31,3 (acc)	9,0
Combretum hereroense	11	9	15	5,1	19,2	2,5← 7,9→13,3 (ns)	2,7
Securinega virosa	2	2	2	4,5	1,4	1,1*	2,4
Ziziphus mucronata	7	6	7	4,7	1,1	0 ← 3,7→ 7,4 (ns)	2,5
Dichrostachys cinerea	14	11	14	9,1	2,6	2,1← 7,4→12,7 (ns)	4,8
Maytenus heterophylla	2	2	2	3,8	0,9	1,1*	2,0
Dalbergia melanoxylon	1	1	1	12,1	10,2	0,5*	6,4
Acacia gerrardii	7	6	8	7,4	0	0,2← 4,2→ 8,2 (ns)	3,9
Ehretia amoena	6	5	7	3,2	4,5	0 ←3,7→ 7,4 (ns)	1,7
Acacia tortilis	7	6	8	8,1	0	0,2←4,2→ 8,2 (ns)	4,3
Cissus lonicerifolia	0	0	0	4,3	4,3	0*	2,3
Dombeya rotundifolia	1	1	1	4,0	2,3	0,5*	2,1
Pterocarpus rotundifolius	2	2	2	5,1	1,9	1,1*	2,7
Euclea divinorum	3	2	4	6,0	0,7	2,1*	3,2
Grewia monticola	0	0	0	6,4	6,4	0*	3,4
Lonchocarpus capassa	1	1	1	3,6	1,9	0,5*	1,9
Other species	-		23	26,3	0,4	5,6←12,2→18,8 (ns)	13,9
Totals	127		189	189	98,4		100

Chi-quare = 98,4 df = 17 $P < 0,001$

*Sample size too small to calculate confidence intervals

(acc) Significant acceptance

(ns) Not significant

z statistic, are shown in Table 24 a-d. Observed percentages differ significantly ($P < 0,10$) from the expected percentages if the latter lie outside the confidence limits.

Some difficulties arise in applying these tests to the data given in Table 24 a-d which must be discussed before the results are presented. Firstly the test statistic is a normal approximation of a variable which follows the binomial distribution. There= fore if the percentage utilization of a species is close to zero or one the sample size should be larger to maintain a good approxi= mation. For many of the less frequently utilized species the sample size is inadequate so no interval estimates could be made for them. Another limitation is that the tests assume that each utilized plant is independent of every other. In fact many spe= cies tend to grow in groups so that the plants utilized within recording sessions would not be independent. This could affect results, for example it could happen that the set of recordings from one season included one session in which kudus fed on a large number of individuals of a certain species growing in a clump. The sample from another season may not have included any of this species simply because the sampled animals did not happen to encounter such a clump. Considering only the number of utilized plants could give a false impression. To guard against this the numbers of sessions in which each species was utilized are included in Table 24, and these have to be considered in addition to the test results in interpreting the data. Further= more the tests are also strictly appropriate only when k (the number of estimates) is small (Neu _et al._ 1974), whereas in this case it is large (18). The tests are nevertheless presented because they provide some guidelines to interpreting the data.

In the dry season of 1976 _Combretum hereroense_, _Maytenus hetero= phylla_ and _Ehretia amoena_ were accepted significantly more fre= quently than would be expected from their abundance. (For these species the expected percentages utilized are lower than the 90 per cent confident intervals for the observed percentages utilized, see Table 24a). The category 'other species' was also accepted more frequently than expected. Acacia nigrescens and Dalbergia melanoxylon were fed on significantly less frequently than would be expected from their availability (their expected percentages are greater than the 90 per cent confidence limits, Table 24a). For the remaining species the observed percentages either do not differ significantly from the expected or the sample sizes are too small to decide.

In the pre-rain flush Combretum hereroense was accepted significantly more frequently than expected. No species were significantly rejected, although in most cases the sample sizes were inadequate.

In the wet season the chi-square value is significant (Table 22c), showing that observed and expected numbers differ significantly over the whole set of species. However differences cannot be declared significant for any specific species. For the species Ziziphus mucronata, Dichrostachys cinerea and Ehretia amoena, and for the 'other species' category, deviations of observed from expected values are fairly high. A larger sample size may have revealed significant acceptance of these species.

The frequency of utilization of the different woody species in the dry season of 1977 differed from that of 1976. In 1977 only Combretum apiculatum was significantly accepted and no species were significantly rejected. Differences between the two dry seasons are discussed below.

Seasonal differences in the frequency of utilization of individual woody plants

Seasonal changes in selection for individual woody species were assessed by comparing the observed number of a species fed on in each season with an expected number calculated assuming utilization to be proportional to availability. The availability of any particular species as experienced by the kudus varied between seasons because of seasonal differences in the proportion of recording time spent in the various habitat subdivisions (Table 22). Also, the sample sizes (number and durations of recording sessions; Table 21) differed between seasons, and this could account for differences in the number of plants recorded as utilized. Therefore both sample size and avail= ability were considered in calculating the expected numbers of individual plants fed on in each season.

Again the chi-square test was used to determine whether observed values differ significantly from the expected, and the Bonferroni z statistic to establish specifically for which seasons the dif= ferences are significant. The null hypothesis is that observed differences between seasons in the numbers of a woody species fed on is due only to seasonal differences in sample size and availability. The alternative hypothesis is that the degree of selection for any specific woody species varies between seasons.

The results are summarized in Fig. 20. Only for seven species could seasonal differences in selection be analysed, for the remainder the expected values were too small to permit the chi-square test.

Acacia nigrescens was selected significantly less frequently than expected in the 1976 dry season, and more than expected in the pre-rain flush. The confidence limits also allow comparison between seasons. The frequency of utilization of Acacia nigrescens was significantly lower in the dry season of 1976 than in that of 1977 (the confidence interval for 1976 does not over= lap with that of 1977, Fig. 20).

Combretum apiculatum was fed on less frequently than expected in the wet season and more than expected in the 1977 dry season. Here too the differences between the two dry seasons was signifi= cant, with 1976 lower than 1977.

For Combretum hereoense overall differences between seasons are significant. The frequency of utilization appears lower than expected in the wet season but a confidence interval could not

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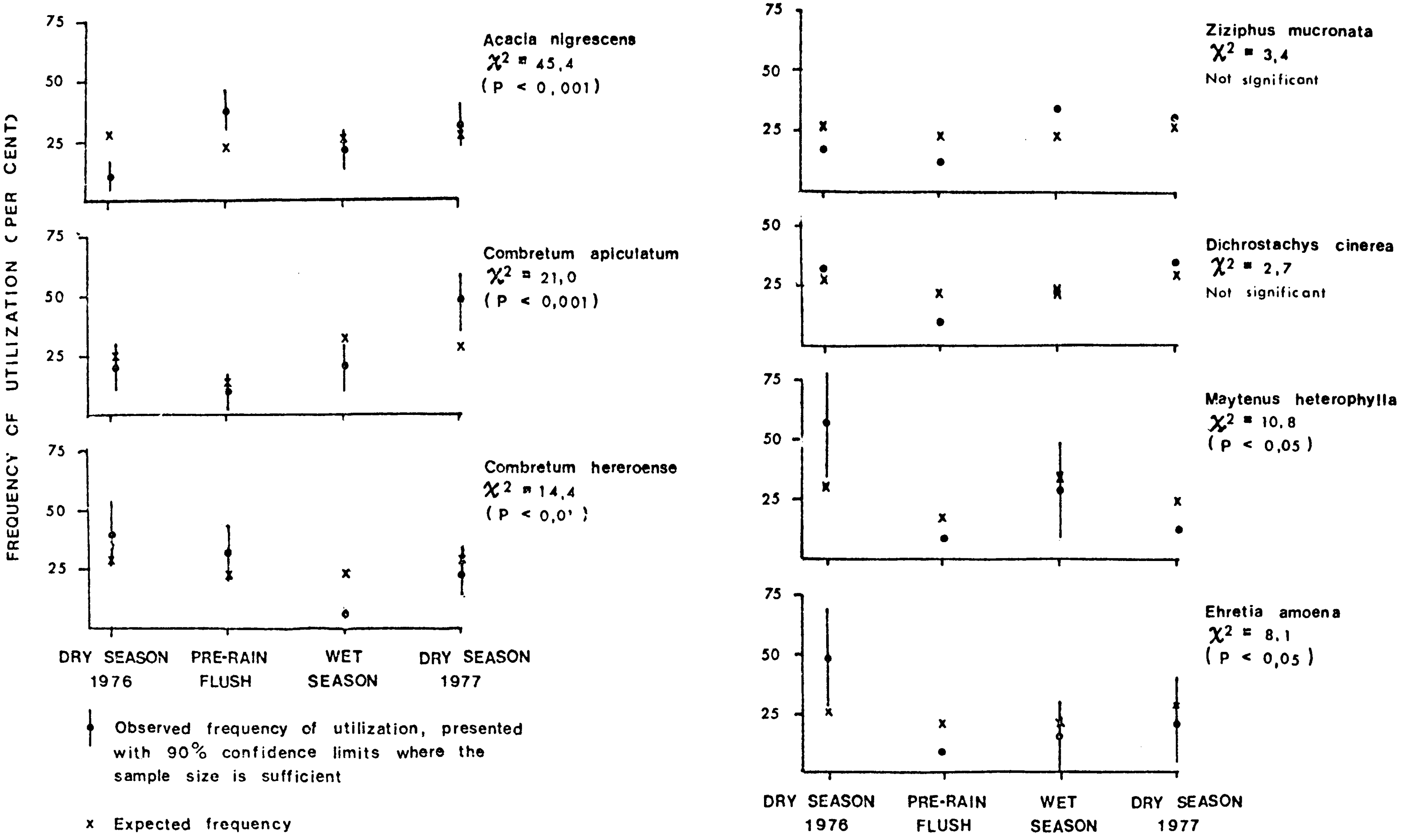

FIG 20: SEASONAL CHANGES IN OBSERVED FREQUENCY OF UTILIZATION BY KUDUS OF SOME COMMON WOODY PLANTS COMPARED WITH EXPECTED VALUES BASED ON AVAILABILITY AND SAMPLE SIZE. THE SIGNIFICANCE OF DIFFERENCES BETWEEN OBSERVED AND EXPECTED VALUES TESTED USING CHI-SQUARE GOODNESS-OF-FIT TESTS

be calculated because the sample size was insufficient for the normal approximation of the binomial distribution. The frequency of utilization was higher in the 1976 dry season than in 1977 but the difference is not significant.

For Maytenus heterophylla there is a marked difference between the two dry seasons in frequency of utilization. In the dry season of 1977 the sample size was too small to construct a confidence interval but a chi-square contingency test shows the difference between the two dry seasons to be significant ($P < 0{,}01$).

The frequency of utilization of Ehretia amoena was significantly higher than expected in the 1976 dry season. It appears lower than expected in the pre-rain flush but the sample size was inadequate to calculate a confidence interval. The difference between the two dry seasons is not significant.

For Ziziphus mucronata and Dichrostachys cinerea observed percentages do not differ significantly from the expected, so apparently selectivity for these two species does not vary over the seasons, at least in terms of frequency of utilization.

As noted, it is desirable to examine the percentage of recording sessions in which a species was utilized,in addition to the number of individual plants fed on. However percentages of sessions (Table 24 a-d) shows essentially the same features discussed above.

Mean duration of feeding on individual plants in relation to the weight of leaves available

The ratio of feeding time to mean weight of leaves available on an individual plant (expressed as seconds spent feeding per plant per gram of leaves available) is compared between woody species in Table 25. Sample sizes (the number of plants fed on) were sufficient to consider only the most frequently utilized species.

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TABLE 25 : MEAN TIME (SECONDS) SPENT FEEDING ON INDIVIDUAL PLANTS PER GRAM OF LEAVES AVAILABLE. SAMPLE SIZES (NUMBER OF PLANTS) ARE GIVEN IN PARENTHESES

Species	Dry Season 1976	Pre-rain Flush	Wet Season	Dry Season 1977	Row Means
Acacia nigrescens	0,69 (n=17)	2,12 (n=63)	0,46 (n=33)	0,62 (n=50)	0,88
Combretum apiculatum	1,58 (n=17)	3,64 (n=9)	0,61 (n=19)	1,13 (n=43)	1,53
Combretum hereroense	0,46 (n=26)	0,73 (n=21)	0,42 (n=4)	0,48 (n=15)	0,52
Securinega virosa	0,34 (n=3)	-	0,66 (n=6)	0,18 (n=2)	0,38
Ziziphus mucronata	0,96 (n=4)	-	0,55 (n=8)	0,56 (n=7)	0,68
Dichrostachys cinerea	0,47 (n=13)	1,64 (n=4)	0,32 (n=9)	0,68 (n=14)	0,71
Maytenus heterophylla	0,84 (n=14)	6,52 (n=2)	0,47 (n=7)	1,38 (n=2)	1,62
Ehretia amoena	0,58 (n=15)	2,23 (n=3)	0,22 (n=5)	0,58 (n=7)	0,77
Euclea divinorum	0,07 (n=7)	0,04 (n=3)	-	0,01 (n=4)	0,04
Column Means	0,62	1,98	0,46	0,57	

Note: The means presented are antilogs of means of log transformed data (see text)

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Since the ratios were transformed to logarithms (see Methods) the means given in Table 25 are antilogs of means calculated in the logarithmic scale (geometric means, Sokal and Rohlf 1969) and are slightly lower than means in the normal scale.

The mean ratios of feeding time to weight of leaves available varied between seasons. For most species values were highest in the pre-rain flush, intermediate in the dry seasons and lowest in the wet season (see column means Table 25). Despite the fact that leaf abundance was lowest during the pre-rain flush the mean feeding time spent on individual woody plants was the highest of the year.

Differences between woody species in duration of feeding on individual plants

Differences between woody species in seconds spent feeding on individual plants per gram of leaves available are discussed below for each of the four seasons. Only those species in Table 25 with a sample size of five or more were included in these analyses.

The dry season of 1976

For the seven species considered in the 1976 dry season (Table 26a) variances remained significantly heterogeneous in spite of the transformation to logarithms. Both the variance and the mean of Euclea divinorum are much lower than those of the other species, and if Euclea is excluded the remaining variances are not significantly heterogeneous. Since conclusions about Euclea are obvious the Newman-Keuls test was carried out on the remaining species. This showed the mean for Combretum apiculatum to be significantly higher than those of the other species. Remaining differences were not significant.

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TABLE 26 : DIFFERENCES BETWEEN SPECIES IN FEEDING TIME (SECONDS) PER PLANT PER GRAM OF LEAVES AVAILABLE TESTED WITHIN EACH SEASON. MEANS FOLLOWED BY THE SAME SUPERSCRIPT ARE NOT SIGNIFICANTLY DIFFERENT. FOR DETAILS OF STATISTICAL TESTS SEE TEXT.

Note: The means are antilogs of means of log transformed data (geometric means)

TABLE 26a : DRY SEASON 1976 : MAY TO MID-SEPTEMBER

Species	Combretum apiculatum	Maytenus heterophylla	Acacia nigrescens	Ehretia amoena	Dichrostachys cinerea	Combretum hereroense	Euclea divinorum
Variance	0,081	0,025	0,047	0,025	0,018	0,026	0,003
Mean	$1,58^a$	$0,84^b$	$0,69^b$	$0,58^b$	$0,47^b$	$0,46^b$	0,07

Comparisons among means using the Student-Newman-Keuls test $\alpha = 0,05$. *Euclea divinorum* excluded because of obviously lower variance.

TABLE 26b : PRE-RAIN FLUSH : MID-SEPTEMBER TO NOVEMBER

Species	Combretum apiculatum	Acacia nigrescens	Combretum hereroense	Lonchocarpus capassa
Variance	0,101	0,121	0,038	0,015
Mean	$3,64^a$	$2,12^a$	$0,73^b$	$0,36^b$

Variances significantly heterogeneous. Paired comparisons between means made using the t test for samples with unequal variance ($\alpha = 0,005$)

TABLE 26c : WET SEASON : DECEMBER TO APRIL

Species	Securinega virosa	Combretum apiculatum	Ziziphus mucronata	Maytenus heterophylla	Acacia nigrescens	Dichrostachys cinerea	Ehretia amoena
Variance	0,047	0,034	0,029	0,035	0,018	0,012	0,004
Mean	$0{,}66^a$	$0{,}61^a$	$0{,}55^a$	$0{,}47^a$	$0{,}46^a$	$0{,}32^a$	$0{,}22^a$

Analysis of variance shows no significant differences between species.

TABLE 26d : DRY SEASON 1977 : MAY TO AUGUST

Species	Combretum apiculatum	Dichrostachys cinerea	Acacia nigrescens	Ehretia amoena	Ziziphus mucronata	Combretum hereroense	Acacia gerrardii
Variance	0,040	0,029	0,023	0,049	0,019	0,018	0,013
Mean	$1{,}13^a$	$0{,}68^{ab}$	$0{,}62^{ab}$	$0{,}58^{ab}$	$0{,}56^{ab}$	$0{,}48^b$	$0{,}32^b$

Comparisons among means using Student-Newman-Keuls test $\alpha = 0{,}05$.

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The pre-rain flush

Here sample sizes from only four species were sufficient (Table 26b). The variances of these four species were significantly heterogeneous, *Combretum hereroense* and *Lonchocarpus capassa* having a lower variance than *Acacia nigrescens* and *Combretum apiculatum*. This probably reflects the marked differences between them in phenology during the flush period. *Combretum hereroense* did not lose its leaves to the same extent as *Acacia nigrescens* or *C. apiculatum* and there was considerably less variation between individuals in phenology (see Fig. 14). This could account for the lower variability between individuals in feeding time per gram on *Combretum hereroense*.

Because of this, alternative tests were used to compare the four means. The approximate test of equality of means when the variances are heterogeneous (Sokal and Rohlf 1969) was used to test whether the four means are from the same population. The null hypothesis of equality of means was rejected at $P < 0{,}005$ ($F_s = 16{,}6$ df = 3, 26). Paired comparisons were made using the t test for two samples whose variances are assumed to be unequal (Sokal and Rohlf 1969). This showed that both *Acacia nigrescens* and *Combretum apiculatum* were significantly higher in mean feeding time per gram of leaves available than both *Combretum hereroense* and *Lonchocarpus capassa* (Table 26b). These paired comparisons involved six separate tests, so that there was a higher risk of wrongly rejecting the null hypotheses. However the differences noted above are all highly significant ($P < 0{,}005$).

The wet season

For the seven species analysed in the wet season (Table 26c) the overall F test showed no significant differences between the means ($F = 0{,}70$ df = 6, 80).

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The dry season of 1977

Variances were not significantly heterogeneous and so the Newman-Keuls test was applied. Mean feeding time per gram of leaves available on Combretum apiculatum is significantly higher than on Combretum hereroense and Acacia gerrardii. Remaining differences between species are not significant (Table 26d).

For two of the species considered in these analyses, Lonchocarpus capassa in the pre-rain flush and Acacia gerrardii in the 1977 dry season, the estimates of leaf densities were based on only one month's frame samples (see Chapter 1). Estimated leaf weight per plant could therefore be inaccurate, so the above conclusions for these two species are tentative.

Utilization of the less common woody species

Table 27 shows the relative frequency of utilization and mean time spent feeding per individual plant for the woody species that occurred at densities of less than 15 per ha. An indication of the availability of each species is given by its relative density. Because of the smaller numbers of the less common species contacted in the belt transects estimates of canopy volume per plant are unreliable, and so these are not presented. Two of the rare species that were highly favoured were Grewia flavescens and Spirostachys africana.

DISCUSSION

Some of the assumptions made in applying the statistical tests above were unrealistic. As discussed under Methods the chi-square test requires that observations be independent; and the confidence limits calculated using the Bonferroni z statistic

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TABLE 27 : FREQUENCY OF UTILIZATION (PER CENT) AND MEAN TIME (SECONDS) SPENT FEEDING PER PLANT FOR THE LESS COMMON WOODY SPECIES, COMPARED WITH RELATIVE DENSITY (PER CENT OF INDIVIDUAL PLANTS AVAILABLE)

A : FREQUENCY OF UTILIZATION
B : FEEDING SECONDS PER PLANT

Species	Dry Season 1976		Pre-rain Flush		Wet Season		Dry Season 1977		Per cent of individuals available
	A	B	A	B	A	B	A	B	
Commiphora mollis	0	-	0	-	0	-	0	-	0,92
Maerua parvifolia	0,6	8	0	-	0	-	0,5	287	1,68
Cassia abbreviata	0	-	0	-	0,8	48	0	-	0,23
Diospyros mespiliformes	1,1	31	0	-	0	-	0	-	0,46
Grewia flavescens	0,6	192	0,6	432	1,5	342	1,6	59	0,15
Grewia hexamita	0	-	1,9	41	0	-	0	-	0,76
Grewia bicolor	0,6	9	0	-	0	-	0	-	0,08
Lannea stuhlmannii	0	-	0,6	30	1,5	23	0,5	358	0,61
Acacia nilotica	3,4	27	0	-	0	-	0,5	4	0,38
Combretum mossambicense	0	-	0	-	3,8	58	1,1	95	2,29
Spirostachys africana	1,7	240	0	-	0	-	1,6	147	0,38
Commiphora africana	0	-	0	-	1,5	175	0	-	0,38
Mundulea sericea	0,6	69	0	-	0	-	2,1	30	0,38
Peltophorum africanum	0	-	1,3	139	2,3	35	0	-	1,22
Sclerocarya caffra	0,6	325	2,6	131	0	-	0	-	1,37
Bridelia micrantha	0	-	0	-	0,8	156	0	-	0,08
Phyllanthus reticulatus	0	-	0	-	0,8	44	0	-	0,99
Acacia senegal	1,1	74	3,2	71	0	-	0	-	0,08
Albizia harveyi	0	-	0	-	0,8	16	0	-	0,46
Ficus ingens	0	-	0	-	0	-	0	-	0,08
Schotia brachypetala	1,7	30	0,6	112	0	-	0	-	0,15
Strychnos madagascariensis	0	-	0	-	0	-	0,5	380	0,46
Ehretia rigida	0	-	0	-	0	-	0	-	0,69
Acacia caffra	0,6	31	0,6	24	0,8	40	0,5	112	0,23
Acacia exuvialis	0	-	0	-	0	-	0	-	0,46
Acacia erubescens	0	-	0	-	0,8	170	0	-	0,15
Combretum imberbe	2,3	44	0	-	0	-	0,5	20	0,53
Ximenia caffra	0,6	12	0	-	0	-	0	-	0,15
Balanites maughami	0,6	91	0	-	0	-	0,5	151	0,23
Terminalia phanerophlebia	0	-	0	-	0	-	0,5	46	0,15
Ormocarpum trichocarpum	0,6	27	0	-	0	-	0	-	0,08
Ximenia americana	0	-	0	-	0	-	0,5	12	0,31
Berchemia zeyheri	2,3	39	0,6	33	0	-	0,5	17	*
Galpinia transvaalica	0,6	31	0	-	0	-	0	-	*
Manilkara mochisia	0,6	15	0	-	0	-	0	-	*
Gardenia spatulifolia	0,6	11	0	-	0	-	0,5	8	*
Acacia spp.	1,7	6	0	-	0	-	0,5	45	*
Ozoroa engleri	0	-	0,6	79	0	-	0	-	*
Pappea capensis	0	-	0	-	1,5	48	0	-	*
Elephantorrhiza burkei	0	-	0	-	0,8	17	0	-	*

*Density unknown (species not contacted in the belt transects).

requires that the number of food types be small (Neu et al 1974). Neither of these requirements were met, and the consequences of these shortcomings are difficult to assess. The tests also did not consider sampling errors made in estimating the availability of different food types. Another possibly weak assumption, frequently made in interpreting selectivity ratings, is that the ratings indicate preference or avoidance; a value of more than one showing preference, less than one showing avoidance (see Petrides 1975). The method of Neu et al. (1974) applied to the data of Table 24 and Fig. 20, makes the assumption that food types can be regarded as favoured or avoided depending on whether the observed frequency of utilization differs significantly from the expected. This approach has been criticized by Johnson (1980) on the grounds that conclusions about whether a food type is used above, in proportion to, or below its availability depends on the array of food types which the investigator, often arbitrarily, deems available to the animal. He stresses that selectivity measures can be used to develop rankings in order of relative acceptability, but should not be used to make absolute statements about preference and avoidance.

However alternative methods of testing the significance of differences among food types in acceptability could not be used in the present study. Johnson's (1980) approach employs measures of food acceptance and availability for individual animals as the unit of observation, which is not feasible for the kudu foraging data. Hobbs and Bowden's (1982) method of calculating confidence limits on selectivity ratings requires replicated estimates of diet composition which is also not possible for the kudu data.

Thus for the kudus the reliability of the measures of selectivity depend on the estimates of food availability. The latter in turn, depend on the assumptions made in Chapter 1 as to what constitutes potential food, and are also subject to sampling error. Errors in the estimates of the relative numbers of woody plants available are likely to be greater for species with a clumped distribution like Euclea divinorum and Combretum hereroense.

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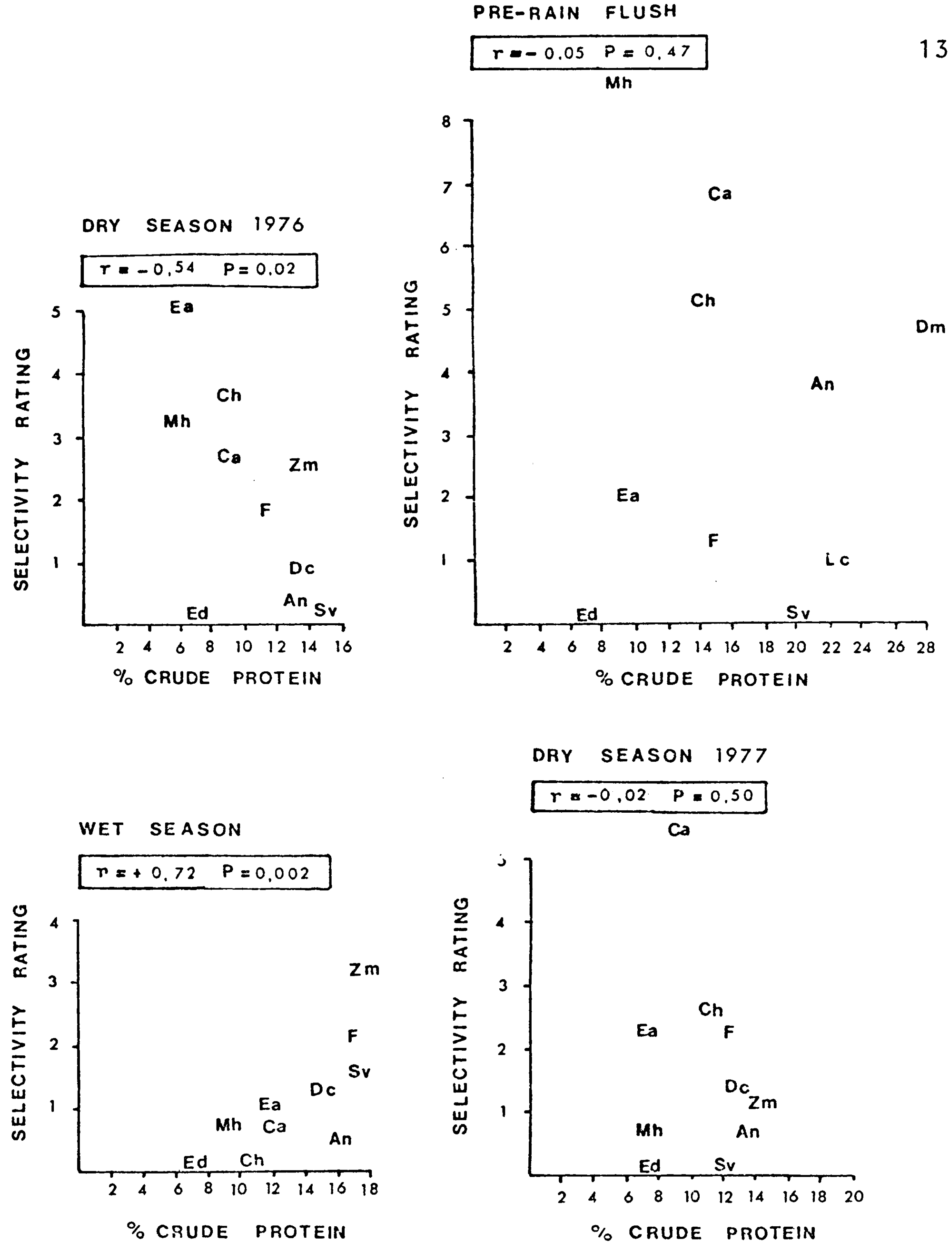
Nevertheless there can be no doubt that the kudus discriminated between woody species, both in choosing individual plants on which to feed and in the amount of feeding time spent on individual plants. The above analyses support the idea that seasonal changes in diet composition cannot be explained only in terms of changing food availabilities, and that preference among species varies with season. There was also evidence of considerable between year differences, Acacia nigrescens and Combretum apiculatum were both selected more frequently in the dry season of 1977 than that of 1976.

FACTORS AFFECTING FOOD SELECTION

The remainder of this chapter examines some hypotheses that may account for the observed seasonal and between plant species variations in the selectivity ratings. The first of these is that the kudus tend to favour food types with a high nutritional value. This hypothesis would predict a positive correlation between the selectivity ratings of the various food types and their leaf nutrient contents.

Relationships between the selectivity ratings and leaf nutrient contents are examined in Fig. 21 a-c. The values for protein, phosphorus and water contents given in Fig. 21 are the means of the monthly values within each season. The values for protein and phosphorus cover all four seasons, but no analyses for water contents were done in the dry season of 1976 and the pre-rain flush. Kendall rank correlation coefficients were calculated relating the selectivity ratings to the content of each nutrient. The correlation coefficients and the probabilities associated with each value of the coefficients are shown in Fig. 21 a-c.

For the wet season the results are as predicted; protein, phosphorus and water contents all show significant positive correlations with the selectivity ratings ($P < 0{,}01$ for protein and phosphorus, $P < 0{,}05$ for water). However for the remaining seasons



F	Forbs	Dc	Dichrostachys cinerea
An	Acacia nigrescens	Mh	Maytenus heterophylla
Ca	Combretum apiculatum	Dm	Dalbergia melanoxylon
Ch	Combretum hereroense	Ea	Ehretia amoena
Sv	Securinega virosa	Lc	Lonchocarpus capassa
Zm	Ziziphus mucronata	Ed	Euclea divinorum

FIG 21a RELATIONSHIPS BETWEEN THE SELECTIVITY RATINGS AND LEAF CRUDE PROTEIN CONTENT FOR THE COMMON WOODY SPECIES AND FOR FORBS. KENDALL'S RANK CORRELATION COEFFICIENT τ AND ASSOCIATED PROBABILITY IS SHOWN FOR EACH SEASON

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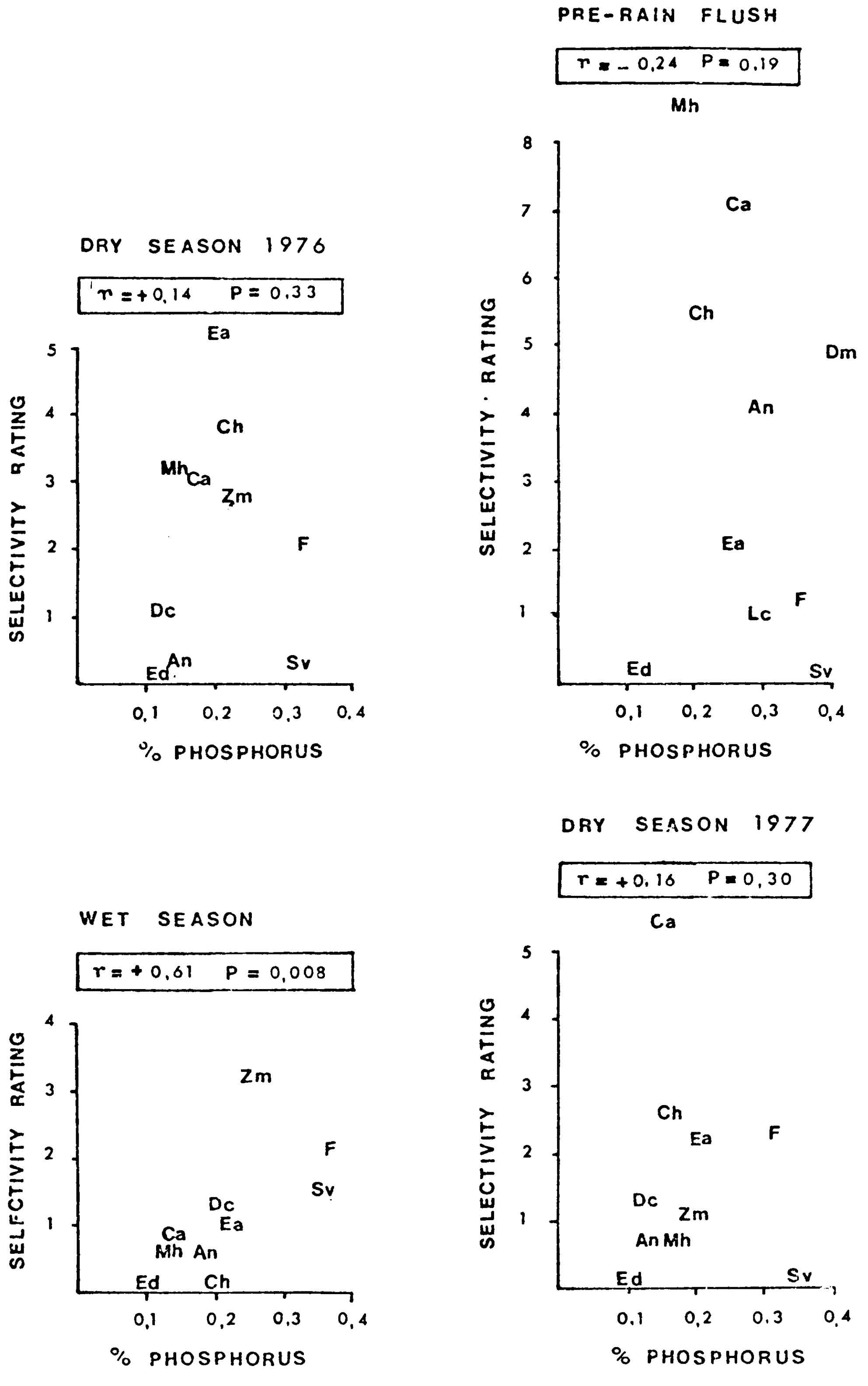

FIG. 21b RELATIONSHIPS BETWEEN THE SELECTIVITY RATINGS AND LEAF PHOSPHORUS CONTENT FOR THE COMMON WOODY SPECIES AND FOR FORBS. SYMBOLS AS FOR FIG. 21a

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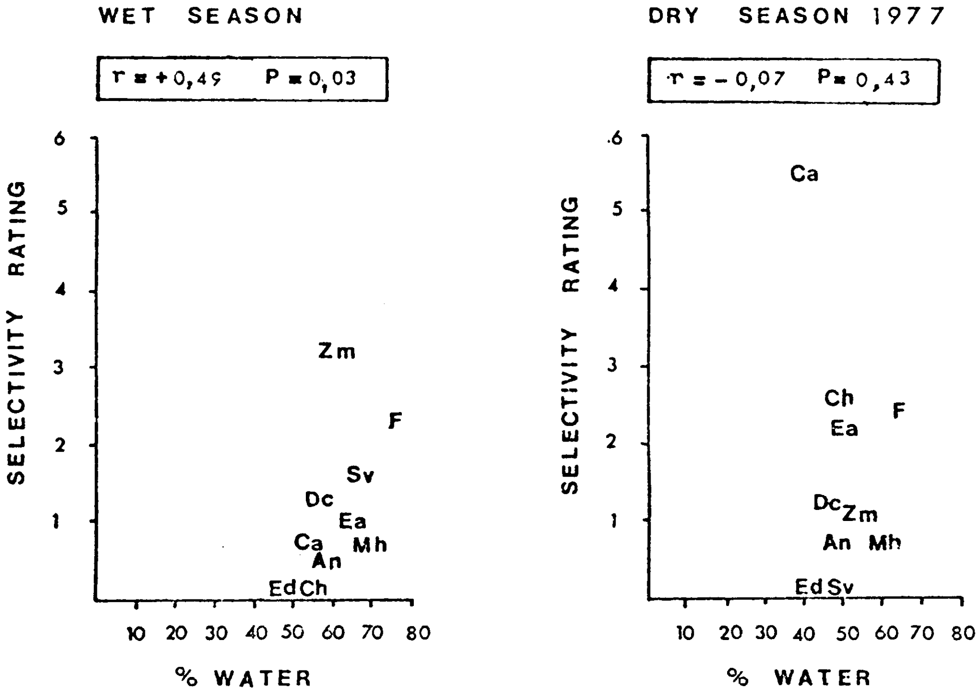

FIG. 21c RELATIONSHIPS BETWEEN THE SELECTIVITY RATINGS AND LEAF WATER CONTENT FOR THE COMMON WOODY SPECIES AND FOR FORBS. SYMBOLS AS FOR FIG. 21a

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there are no significant positive correlations between the selec=tivity ratings and protein, phosphorus or water contents.

Few plant species were analysed for calcium content and so cor=relation coefficients relating calcium content to the selecti=vity ratings were not calculated. However comparison of Tables 19 and 23 shows no relationship between leaf calcium contents and the selectivity ratings.

The significant relationships between the protein, phosphorus and water contents and the selectivity ratings in the wet season is consistent with the idea that the kudus tend to select plants with a high nutritional value. But the absence of the expected correlations at other times of the year shows that differences among food types in nutrient content are inadequate to explain the observed differences in acceptance. Clearly selection is also influenced by other factors.

An important consideration is the defences evolved by plants to deter herbivory. Two types of defences can be recognized: structural or morphological defences, for example thorns and spines, and chemical deterrents (Rosenthal and Janzen 1979).

Chemical defences can be divided into two categories (Cates and Rhoades 1977):

(i) digestibility reducing compounds which act to inhibit digestion, so reducing the value of the forage to the herbivore
(ii) toxic substances which directly affect the herbivore or its symbiotic micro-organisms.

Chemical deterrents are potentially important in determining food selection by kudus, but lack of information on either the concen=trations of chemical deterrents in food plants, or the effect these have on the animals prevents the question from being considered further. Possible effects of structural defences are evaluated below, but before considering these the known effects of plant structure on food intake rate by herbivores are discussed.

Thorns or spines do not prevent feeding by large herbivores but reduce the rate at which leaves and shoot ends can be eaten. The food value of a plant is thus better represented by the rate at which the herbivore can ingest nutrients rather than the actual concentration of nutrients in the foliage (Owen-Smith and Novellie 1982). The rate of nutrient intake is a function of the nutrient concentration in the food and the eating rate (the weight of food eaten per unit of feeding time). Eating rate in turn depends on the average bite size and the rate of bites.

Studies which have measured eating rates for large herbivores indicate that this can be influenced by a number of plant characteristics, e.g. thorns, abundance and density of foliage, leaf size, and toughness of leaves and shoots (Theron and Booysen 1966, Chacon, Stobbs and Dale 1978, Dunham 1980, Trudell and White 1981). Dunham (1980) measured the bite rates, bite sizes and food intake rates of a tame impala feeding on 10 African browse species, and showed quantitatively that the thorns of an Acacia species reduced eating rate. Eating rates varied between plant species from 7,48 g dry weight per minute for the most rapidly ingestable foliage to 0,91 g per minute for the slowest. Mean bite size was positively correlated with mean leaf weight. Trudell and White (1981) examined relationships between forage structure and food intake rate of reindeer. They also found that plant species differed in the rate at which their foliage could be ingested. Food intake rate increased with standing crop for all plants except forbs, which could be eaten rapidly even when scarce. Chacon, Stobbs and Dale (1978) measured the effect of pasture characteristics on the bite sizes of cattle. They concluded that cattle grazing low-yielding short swards were forced to take small bites and this depressed dry matter intake. Theron and Booysen (1966) found that the force required to remove mouthfuls from grass plants was the most important factor influencing food selection by sheep. This may be because intake rate was lower for the tougher plants.

It thus seems likely that the rate at which kudus could harvest leaves would vary between species depending on thorns, leaf density, leaf size and toughness. Intake rate can also be expected to vary between seasons for a number of reasons. The density of leaves within woody plant canopies decline with advancing leaf fall and this would cause an increase in the average interval between bites in the dry season. New shoots present in spring may allow larger average bite sizes because a larger proportion of shoot could be included with each bite of leaves. Thorns present on new growth are soft and likely to be less effective than mature thorns. Tough-leaved species tend to have soft new leaves in spring. Eating rates are therefore likely to be higher when new growth is abundant than during the dry season.

Eating rates could not be measured in this study but the foraging behaviour and food selection of kudus can be compared between the armed and unarmed woody species to assess possible effects of structural defences. Leaf, twig and thorn structures of some commonly utilized woody species are shown in Fig. 22.

Differences between food plants in the proportion of feeding time spent chewing

It was possible to record differences between food types in the proportion of feeding time spent by the kudus standing with their heads raised chewing. This refers specifically to the time spent standing and chewing, not to total chewing time because the kudus sometimes chewed between bites without raising their heads from the vegetation. This could not be recorded because the kudu's mouth was usually obscured. There is reason to expect that the proportion of feeding time spent standing and chewing would reflect structural differences between food species. A kudu feeding on a species which offered small average bite sizes and a low rate of bites would not spend as long standing and chewing as one feeding on a species which allowed a faster gathering rate. Time spent chewing would also depend on leaf texture, as hard leaves would require more chewing.

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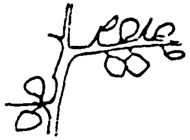
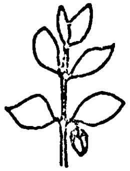
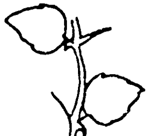
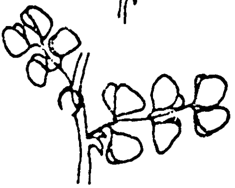
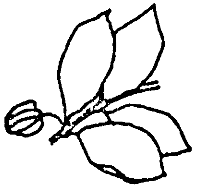
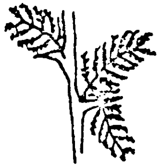
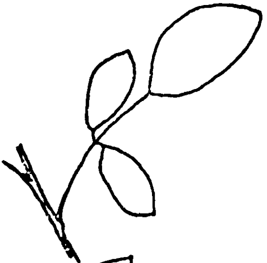
ARMED SPECIES			UNARMED SPECIES	
	*Securinega virosa*	SPINIFORM TWIGS		*Combretum hereroense*
	*Ziziphus mucronata*	CURVED & STRAIGHT THORNS		*Euclea divinorum*
	*Acacia nigrescens*	CURVED THORNS		*Combretum apiculatum*
	*Maytenus heterophylla*	STRAIGHT THORNS		
	*Dichrostachys cinerea*	SPINIFORM TWIGS		*Lonchocarpus capassa*
	*Acacia gerrardii*	STRAIGHT THORNS		*Ehretia amoena*

FIG. 22 FOLIAGE STRUCTURE AND MORPHOLOGICAL DEFENCES OF SOME WOODY PLANTS FED ON BY KUDUS

TABLE 28 : THE PERCENTAGE OF FEEDING TIME SPENT STANDING AND CHEWING COMPARED BETWEEN THE COMMON WOODY SPECIES AND PLANTS IN THE HERB LAYER

Species	Dry Season 1976	Pre-rain Flush	Wet Season	Dry Season 1977	Species Means
Acacia nigrescens	6	6	13	7	8
Combretum apiculatum	18	9	29	21	19
Combretum hereroense	8	11	25	22	17
*Securinega virosa	4	-	19	4	9
Ziziphus mucronata	6	5	6	6	6
Dichrostachys cinerea	6	2	12	8	7
Maytenus heterophylla	12	12	13	8	11
*Dalbergia melanoxylon	6	1	10	6	6
*Acacia gerrardii	3	3	17	3	7
Ehretia amoena	24	7	33	12	19
Lonchocarpus capassa	-	15	-	-	15
Euclea divinorum	12	15	-	26	18
Herb.layer	21	23	27	17	22
Seasonal means	10,5	9,1	18,5	11,7	

*Sample sizes insufficient in one or both dry seasons so data from both dry seasons are pooled.

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Table 28 shows that the mean chewing time is highest for plants in the herb layer, followed by Combretum apiculatum, Ehretia amoena, Euclea divinorum, Combretum hereroense and Lonchocarpus capassa in that order. These species are all unarmed and all have simple leaves. The other woody plants shown in Table 28 are all armed, and for them the means are considerably lower.

Chewing time is thus higher for those species which one would expect could be more rapidly harvested. The large simple leaves of some of the unarmed species (Combretum apiculatum, Ehretia amoena, Lonchocarpus capassa) would probably require more time to chew than the smaller compound leaves of some of the armed species. It seems likely, however, that the gains in terms of higher gathering rate offered by the unarmed species would outweigh the cost in terms of extra time required to chew them. The amount of food swallowed per unit feeding time would then be higher for the unarmed species.

Differences between seasons in the overall average per cent of feeding time spent standing and chewing are also shown in Table 28. Chewing time is considerably higher in the wet season than at other times. The wet season is the time of maximum leaf biomass, so that bite size and rate of bites would be highest and this could account for the high chewing time. However, there are other factors which could influence chewing time besides the structure of food plants. Time spent standing and chewing could reflect the need to maintain vigilance against predators, or to take brief pauses to rest during foraging. The kudus maintained foraging efficiency in the dry season partly by reducing the proportion of foraging time spent standing alert and on other miscellaneous activities (see Chapter 3). This could be another factor accounting for the difference between seasons in chewing time.

Average protein content compared between armed and unarmed woody species

Because of the effect of the thorns one would expect the kudus to favour unarmed species over armed ones, given no difference in nutrient content. However of the plant species analysed in this study most of those with thorns or spines had higher protein contents than the unarmed species. This suggests that the species which are most likely to suffer herbivory have envolved morphological defences. The number of woody species considered in this study is too small to draw general conclusions but Sauer (1977) analysed the crude protein content of the leaves of a large number of Transvaal trees. If the results of Sauer's study are combined with this one, then the mean crude protein content of 16 armed species is 16,5 per cent, compared with the mean of 11,3 per cent for 26 unarmed species. (The values for each species were averaged over the whole seasonal cycle.) Thus (apart from some exceptions discussed below) the armed species offer high quality foliage, but probably allow only a slow eating rate. Unarmed species on the other hand generally have poorer quality foliage but this can be harvested more rapidly.

Seasonal differences in acceptance of armed and unarmed woody species

If the thorns on newly produced shoots are in fact less effective than mature, hardened thorns then the relative difference between armed and unarmed species in the rate of which kudus could harvest food would vary between seasons. The difference would be least in the growing season and greatest in the dry season. Owen-Smith (1979) suggested this effect as a possible reason accounting for the fact that the unarmed Combretum apiculatum comprised a higher proportion of the kudus' diet than the armed Acacia nigrescens in the dry season but a lower proportion at other times of the year.

The following hypothesis can thus be advanced: In the growing season structural defences have a lesser effect, and kudus tend to select the higher quality armed species in preference to the unarmed species. In the dry season the rate at which food can be harvested from the armed species declines more markedly than for unarmed species. The unarmed species, despite their lower nutritional value, thus allow a higher nutrient intake rate per feeding time than the armed species. The kudus then select these in preference to the armed species.

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The diet composition and selectivity ratings are now examined to evaluate this. Fig. 23 shows the monthly proportions of feeding time spent by the kudus on armed and unarmed woody species. The proportions of feeding time spent on the most important species, Acacia nigrescens, Combretum apiculatum, and C. hereroense are also shown. The relative contribution of armed and unarmed species to the diet clearly varied seasonally, with the former more prominent in the growing seasons (October 1976 to May 1977) and the latter increasing in importance in the dry seasons.

This seasonal pattern is due in part to the seasonal change in the relative contribution of the two dominant woody species, A. nigrescens and Combretum apiculatum, to the kudus' diet. However even if these two species and C. hereroense are excluded from the data the seasonal pattern remains; Fig. 23 shows that the ratio of "other armed species" (i.e. excluding A. nigrescens) to "other unarmed species" (i.e. excluding C. apiculatum and C. hereroense) is consistently high over the wet period from November to March, but is generally lower over the remainder of the year.

It remains to compare these variations in diet with variations in availability. Fig. 24 compares seasonal changes in the relative contributions of armed and unarmed species to the kudus' diet with seasonal changes in the relative availability of leaves of armed and unarmed species. The relative availability of armed species changed over the seasons, from highest in the wet season to lowest in the pre-rain flush. This was largely because the common unarmed Euclea divinorum is evergreen,and therefore made up a relatively greater proportion of available leaves in the pre-rain flush when many deciduous plants were bare (see Chapter 1). Fig.24 shows that seasonal changes in the proportion of feeding time spent on armed as opposed to unarmed species do not correspond to seasonal changes in relative availability. Selectivity ratings for armed species (calculated as the ratio of per cent in the diet to per cent available, from the values in Fig. 24) are highest in the pre-rain flush (2,4), intermediate in the wet season (1,3) and lowest in the dry seasons (1,1). These changes in the selectivity ratings cannot be ascribed to variation in relative nutritional

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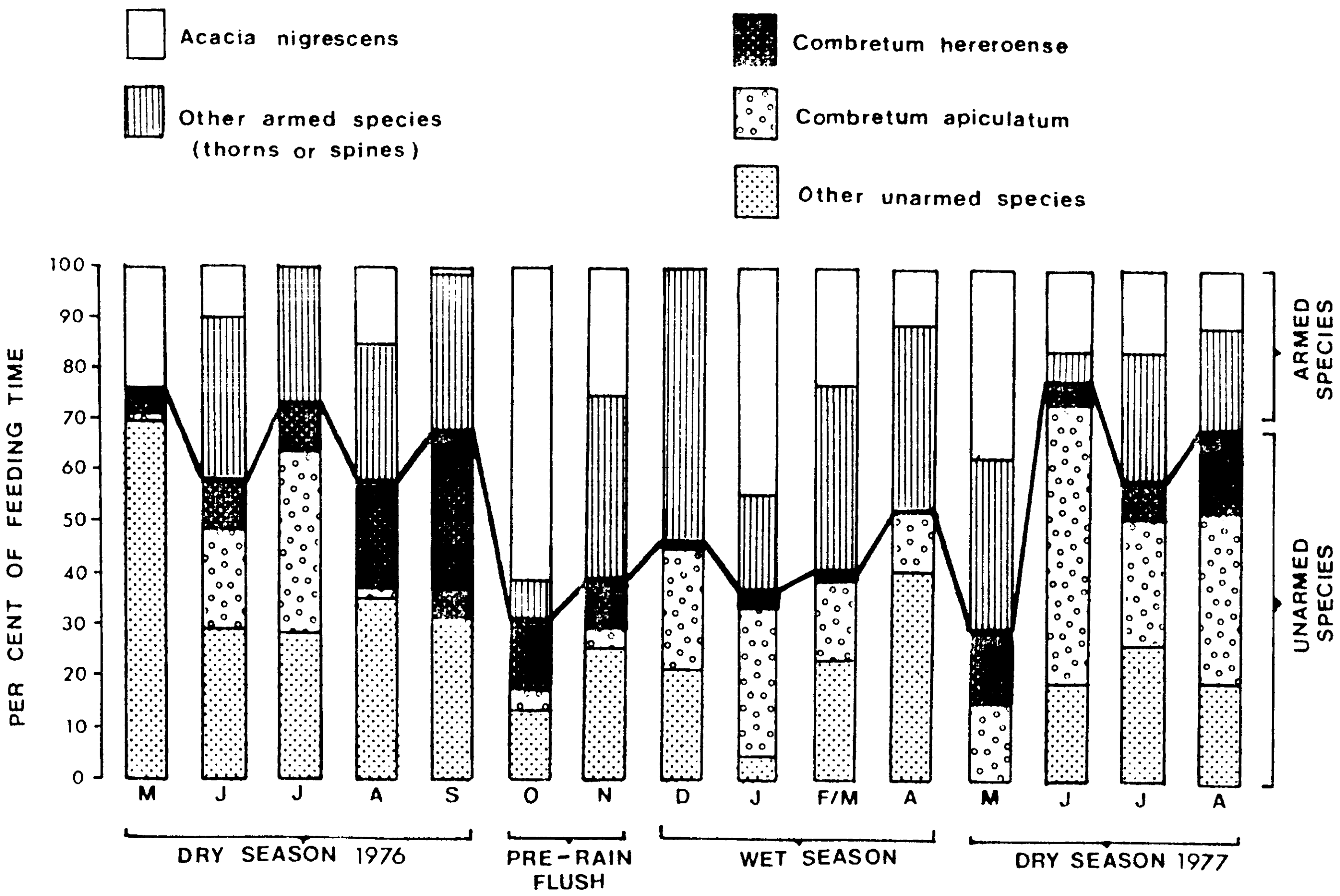

FIG. 23 MONTHLY VARIATION IN THE RELATIVE PROPORTION OF FEEDING TIME SPENT BY THE KUDUS ON ARMED AND UNARMED WOODY SPECIES

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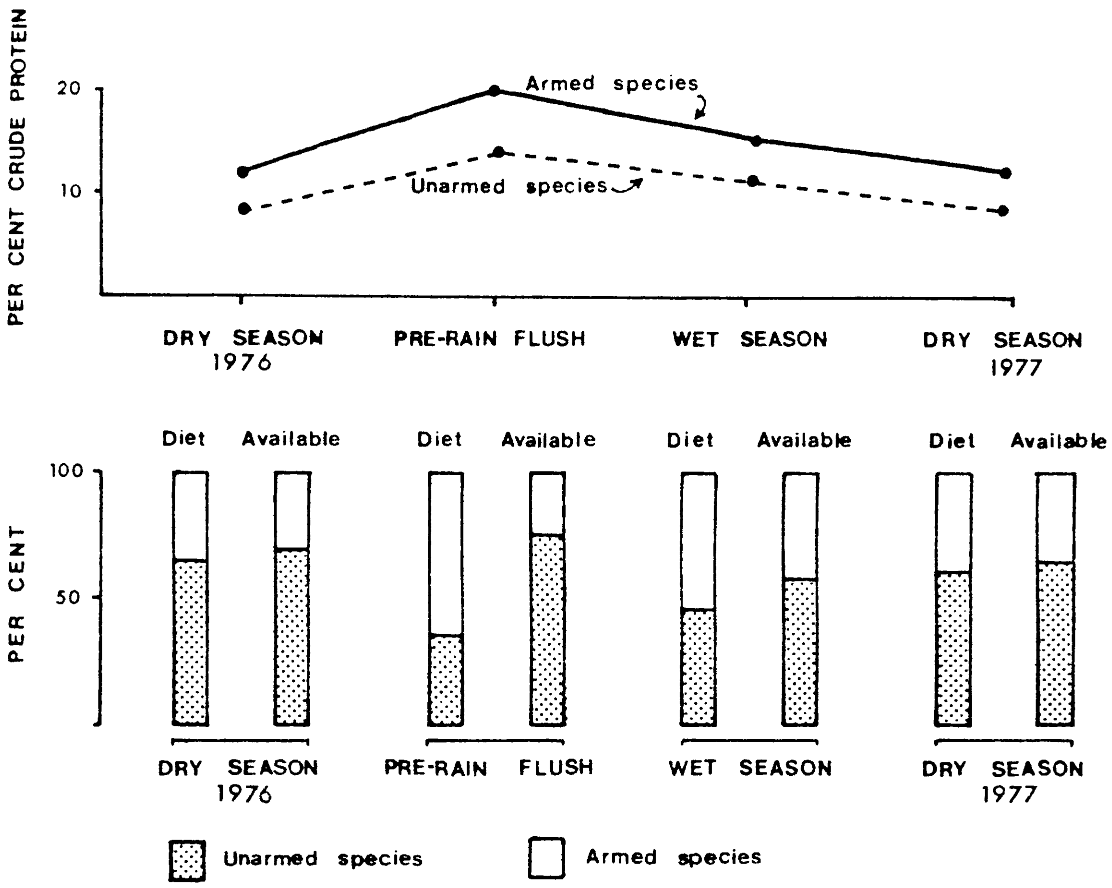

FIG. 24 THE RELATIVE CONTRIBUTION OF ARMED AND UNARMED WOODY SPECIES TO THE DIET OF KUDUS COMPARED WITH THE RELATIVE AVAIL= ABILITY OF LEAVES OF EACH. AVERAGE LEAF PROTEIN CONTENTS ARE ALSO COMPARED BETWEEN ARMED AND UNARMED WOODY SPECIES

value, the leaf protein contents of armed species remained about 1,4 times that of unarmed species in all seasons (Fig. 24). The fact that armed species are most favoured in relation to their availability in the pre-rain flush when most new growth appears, and least favoured in the dry seasons, supports the above hypothesis.

Seasonal variations in acceptance of individual woody species

In Table 29 the common woody food plants of each season are listed according to their selectivity ratings, from highest to lowest. The unarmed species would be expected to appear relatively higher on the lists in the dry seasons than in the wet season or the pre-rain flush, whereas the reverse would be true of the armed species.

The selectivity ratings of the armed species Acacia nigrescens, Securinega virosa, Dichrostachys cinerea and Ziziphus mucronata all ranked relatively low in the dry seasons thus conforming to the expected pattern. However the season of highest rank varied between these armed species. S. virosa and D. cinerea ranked lower in the pre-rain flush than they did in the wet season, whereas the reverse was true of A. nigrescens. Z. mucronata was ranked highest of all species in the wet season. The leaf density of this species was not estimated in the pre-rain flush so no selectivity rating could be calculated, but Z. mucronata did not feature prominently in the kudus' diet in the pre-rain flush so it was probably also selected for more strongly in the wet season than the pre-rain flush. This difference between A. nigrescens and the other armed species is probably related to the difference between them in the timing of leaf production (Chapter 1). A. nigrescens flushed early so the most favourable period for browsing by kudus would have been the pre-rain flush. The other three species flushed late, few new leaves were available

TABLE 29 : THE COMMONLY UTILIZED WOODY PLANT SPECIES LISTED IN EACH SEASON IN ORDER OF SELECTIVITY RATING FROM HIGHEST TO LOWEST

Rank according to selectivity rating	Dry Season 1976	Pre-rain Flush	Wet Season	Dry Season 1977
1	E. amoena	*M. heterophylla	*Z. mucronata	C. apiculatum
2	C. hereroense	C. apiculatum	*S. virosa	C. hereroense
3	*M. heterophylla	C. hereroense	*D. cinerea	E. amoena
4	C. apiculatum	*A. nigrescens	E. amoena	*D. cinerea
5	*Z. mucronata	*D. melanoxylon	C. apiculatum	*Z. mucronata
6	*D. cinerea	E. amoena	*M. heterophylla	*A. nigrescens
7	*A. nigrescens	*D. cinerea	*A. nigrescens	*M. heterophylla
8	*S. virosa	L. capassa	C. hereroense	*S. virosa
9	E. divinorum	E. divinorum	E. divinorum	E. divinorum
10		*S. virosa		

* Armed species

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before November (Chapter 1), so the time when the leaves could be gathered most rapidly was probably the wet season.

Feeding on S. virosa was frequent in the wet season, but the selectivity ratings for this species were low in other seasons. Unlike any other woody species examined, the ratio of feeding time spent to weight of leaves available per individual plant for S. virosa was higher in the wet season than at other times of the year (Table 25). By comparison Z. mucronata and D. cinerea were fed on fairly frequently in the dry seasons. A possible explanation of this is that both the latter species retained leaves to a greater extent than S. virosa over the dry season (Fig. 14). The seasonal trend in browsing on S. virosa seems very consistent from year to year. During the preliminary observations in the spring and wet season of 1975-76 feeding on S. virosa was seen only in mid-summer. Owen-Smith (1979) reported that it comprised a high proportion of the kudus' diet in the wet season of 1975.

One armed species which did not follow the expected pattern was Maytenus heterophylla, which had a high selectivity rating in the dry season of 1976 (Table 29). Unlike most other armed species M. heterophylla did not have a high protein content, but its water content was the highest of all woody plants analysed. This may have accounted for its selection in the dry season.

The unarmed species Combretum apiculatum, C. hereroensc, and Ehretia amoena all appear high on the lists in the dry seasons, again as would be expected (Table 29). The two Combretum species were also listed high in the pre-rain flush. For C. hereroense this would be expected, as it did not lose leaves to the same extent as other species in the dry season and tended to flush early. In the pre-rain flush it offered fair quality (14% protein) food when little else was available, and it was prominent in the diet at this time, not only in this study but also in that of Owen-Smith (1979).

In contrast C. apiculatum made up only a small proportion of the pre-rain flush diet. Its high selectivity rating at this time was

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due mainly to its low estimated availability. In spring the kudus appeared to spend most of their foraging time on the pediment where the abundance of the early flushing *A. nigrescens* trees was highest. Consequently the proportion of recording time obtained on the hill slopes was low, and hence the estimated availability of *C. apiculatum* was low. However since utilization was high relative to availability the selectivity rating was high. As discussed in Chapter 1 the timing of the flush on *C. apiculatum* varied between areas, some groups of trees flushed as early as August, but in general most new growth appeared in November. This meant that high quality browse was available on *C. apiculatum* very early in the season but only in certain localities.

A conspicuous difference between the two *Combretum* species is that *C. apiculatum* comprised a much greater proportion of the diet than *C. hereroense* in the early dry season, whereas the reverse was true in the late dry season (see Fig. 23). This is probably a reflection of their different phenology, *C. apiculatum* lost leaves to a much greater extent over the late dry season

(Fig. 14).

Euclea divinorum was utilized only in the late dry seasons and to a small extent also in the pre-rain flush. At all times its overall rating was low compared to other species. This seasonal trend in utilization appears consistent from year to year as Owen-Smith (1979) noted that it was fed on only in the late dry season. *Euclea* is evergreen and unarmed and so probably offers a high ingestion rate, but its protein content is low. Its rejection in the wet season and weak acceptance in the dry season is thus consistent with the above hypothesis.

An unarmed species which did not follow the predicted pattern was *Lonchocarpus capassa*. The leaf weight per unit canopy volume of this species was estimated only in the pre-rain flush so selectivity ratings could not be calculated for the other seasons. However Table 24 suggests that *L. capassa* was fed on more frequently than expected in the pre-rain flush and less than expected in the dry seasons. For Lonchocarpus the sample sizes were too small to statistically test these results but the same seasonal pattern was observed during the preliminary observations in 1975 and was reported also by Owen-Smith (1979) for 1974-75. The mature leaves of this species are very hard, and the difficulty of chewing these probably restricts utilization in all seasons except spring when the soft new leaves appear. One would expect that hard-leaved species would have a high content of structural carbohydrates, and because of the general negative relationship between protein and structural carbohydrate, protein content should be low. However the protein content of a sample of mature Lonchocarpus leaves collected in the wet season (Table 16) was higher than that of many soft-leaved species.

Less commonly browsed woody plants

The following fairly common species all tended to be utilized less frequently than their availability would indicate.

Acacia tortilis was fed on less frequently than expected in all seasons except the dry season of 1977 when its utilization was roughly proportional to availability. Time spent feeding per tree was low. The phenology of this species seemed to be erratic and out of phase with the other species and this probably explains its very high protein content in May 1976 (21%) and July 1977 (20%). It has minute compound leaves and is armed with both straight and hooked thorns, so its structure is probably the main factor accounting for its rejection (see Dunham 1980).

Cissus lonicerifolia and Grewia monticola are both unarmed with large leaves which should allow easy harvesting. Protein content of Cissus was not analysed but that of Grewia is comparable to the Combretum species (Table 16). The reason for its rejection throughout the year is obscure, but may be related to the presence of chemical deterrents. Pterocarpus rotundifolius is similar to Lonchocarpus capassa in that it has large but tough

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leaves and these are likely to be the reason for its lack of favour. Like Lonchocarpus its protein content is higher than many soft leaved-species (Table 16).

There were two rare species which were fairly consistently favoured. Grewia flavescens was eaten in all seasons and time spent feeding per plant was almost always very high. It was utilized more frequently than the much more common G. monticola. The two species have roughly the same protein content (Table 16), and their structure and leaf density are very similar. The leaves of G. flavescens are softer than those of G. monticola, but this does not seem sufficient to account for the great difference in selectivity between the two.

Another highly favoured rare species was Spirostachys africana which accounted for high proportions of feeding times in the mid-dry seasons of both 1976 and 1977. The distribution of this species was very clumped, and further data would be needed to confirm whether it does tend to be eaten particularly in the dry seasons. It has a relatively high protein content (Table 16).

Some moderately widespread species which were not frequently recorded as being eaten are Commiphora mollis, Maerua parvifolia and Combretum mossambicense but these species are not easily visible above the herb layer and may be under-represented in the samples.

Differences between years in diet composition

Diet composition differed significantly between the dry season of 1976 and that of 1977. Acacia nigrescens and Combretum apiculatum were both fed on significantly more frequently in 1977 than in 1976, while Maytenus heterophylla was browsed more frequently in 1976. The leaf densities of A. nigrescens and particularly C. apiculatum were on average higher in 1977 than 1976, and this

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may account for the difference in diet composition. However no measures of variation were made for the leaf density estimates of 1976 so the difference between years cannot be tested statistically. The leaf density of M. heterophylla was sampled too infrequently to draw conclusions about differences between the two dry seasons.

Leaf abundance in the dry season probably depends on climatic conditions during the preceding wet season. In terms of total precipitation there was little difference between the wet season of 1975-76 and that of 1976-77, but the distribution of the rain over time was different. In 1976-77 there was a drought in mid-summer during which growth was retarded (Chapter 1). In February 1977 most of the season's rain fell over a period of 10 days (Fig. 2). In the wet season of 1976 precipitation was much more evenly distributed between months. However it is not clear how this difference in precipitation pattern could have accounted for the observed difference in diet composition.

Comparison with related studies

Most studies on kudu diet composition have shown that grass is normally eaten only at the beginning of the rainy season when it is immature (Wilson 1965, Conybeare 1975). This would be expected since the digestive system of kudus is not adapted to a diet of mature grass (Hofmann and Stewart 1972). In the present study kudus accepted new grass leaves growing after a fire when they had an everage protein content of 15 per cent but rejected them when the protein content declined to 13 per cent.

Seasonal variations in the proportion of time spent by kudus feeding on plants in the herb layer differed between this study and that of Owen-Smith (1979). Means for the wet season were similar (65 per cent reported by Owen-Smith, 66 per cent in this study) but in the dry season the kudus spent 64 to 68 per cent of feeding time on plants in the herb layer in this study compared with 55 per cent in 1974-75 (Owen-Smith 1979). The rainfall during Owen-Smith's study period (542 mm in 1974-75) was lower than during this study (651 mm in 1975-76, and 668 mm in 1976-77). Possibly this caused the difference in dry season diet composition; forb abundance in the dry season may depend on precipitation in the previous wet season, in which case forbs would have been relatively scarcer in 1974-75.

Conybeare (1975), Owen-Smith (1979) and this study all noted that the ratio of woody plants to other food types in the diet of kudus was highest in the early growing season. This would be expected because woody plants tend to start leaf production earlier than plants in the herb layer, and in the early growing season would offer browse which is both more abundant and of higher quality.

The tendency to favour armed woody species in the growing season and unarmed ones in the dry season has also been observed in giraffe. Stephens (1975) reports that spine-bearing plants represented 90 per cent of bites taken by giraffe in the mid-wet season, but only 33 per cent in the late dry season.

CONCLUSIONS : ALTERNATIVE HYPOTHESES EXPLAINING THE SEASONAL VARIATIONS IN FOOD SELECTION

The observations discussed above support the hypothesis that immature thorns on newly emerging shoots are less effective in deterring kudus than mature thorns. This effect provides an explanation for the observed seasonal relationships between leaf protein content and the selectivity ratings. Since most armed species had higher leaf protein contents than unarmed species through all seasons one expects a positive correlation between the selectivity ratings and protein content in the growing seasons, when armed species were favoured, but not in the dry seasons, when the unarmed species were favoured. The selectivity ratings were in fact correlated with leaf nutrient contents in the wet seasons but not during the pre-rain flush. The most important factor determining acceptance during the pre-rain flush was apparently the timing and extent of leaf production; the early flushing woody species were favoured by the kudus. Some of the armed species with high protein contents (Securinega virosa, Dichrostachys cinerea and Ziziphus mucronata) produced only few, sparsely distributed new leaves during the pre-rain flush, and this may have been the reason why they were not favoured. However the sample sizes for the pre-rain flush were smaller than for the other seasons and further observations would be required to determine the factors underlying acceptance at this time.

Thus far the selectivity ratings have been interpreted entirely in terms of nutritional value (indicated by protein content) and eating rate as influenced by thorns. This ignores several important factors. Firstly protein content is not an absolutely reliable guide to nutritional value. As discussed previously (Methods, Chapter 1) the justification for assuming that protein content reflects nutritional value is that it is negatively correlated with the proportion of cell wall in the forage. The proportion of cell wall relative to cell sap is an important determinant of the digestion rate. However this represents a general tendency only and one cannot infer with certainty that because one species contains more crude protein than another it is necessarily lower in the relative proportion of cell wall (see for example Oldemeyer et al. 1977). The relative proportions of the different nutrients in the cell sap varies between species, and so a species high in protein may be low in some other nutrient. Protein content is not always closely correlated with energy availability (Barnes 1973, Bransby 1981).

An important point is that large herbivores probably cannot select specifically for protein content. Characteristics such as 'crude protein', 'fibre' or 'energy' are not recognizable as such to a herbivore because they are not present in this form at the molecular level in the plant (Arnold 1981). Herbivores can select only for what they can sense. Owen-Smith and Novellie (1982) suggested that there may be no more than four characteristics indicating food value: toughness indicating fibre content, succulence indicating moisture content, bitterness indicating toxin content and finally the rate at which the animal can harvest the food. The justification for assuming protein content to be the major selection criterion is that it is negatively correlated with fibre content, which is presumably detected as toughness. But again protein content is probably not an absolutely reliable indicator of the criteria whereby the animals select.

Thus an alternative explanation of the lack of correlation between the selectivity ratings and leaf protein content in the dry seasons is that the kudus were selecting for some plant characteristic not associated with protein. For example both *Combretum apiculatum* and *C. hereroense* had relatively high dry season phosphorus contents. *C. apiculatum* leaves were lower in phosphorus than those of *A. nigrescens* in the wet season but higher in the dry seasons. The phosphorus content of *C. hereroense* leaves was higher than those of *A. nigrescens* in all seasons except the pre-rain flush. It is thus possible that the relatively high selectivity ratings of the two *Combretum* species in the dry seasons was due to their phosphorus content rather than the fact that they are unarmed. There is reason to doubt whether herbivores can detect phosphorus concentrations; domestic cattle offered dicalcium phosphate show little evidence of a specific appetite for phosphorus (Coppock, Everett and Belyea 1976), but on the other hand bone chewing is frequently observed in phosphorus-deficient livestock, which suggests that they may be capable of an appropriate response.

A further possibility is that the kudus occasionally select a plant for its moisture content. Leaf water content was not correlated with protein content in the dry season; two species with low protein contents, *Maytenus heterophylla* and *C. hereroense*, had relatively high dry season water contents. However neither water nor phosphorus are likely to be of overriding importance;

the selectivity ratings were not significantly correlated with either in the dry seasons.

It therefore seems unlikely that food selection could be explained without considering the effects of plant structural defences on eating rate. Further understanding of the factors underlying diet selection would require measurements of the rates at which kudus can harvest foliage from the various food species. As noted, plant secondary compounds were not considered in this study, and it is also important to investigate the role of these in determining selection.

CHAPTER SUMMARY : STAPLE, FAVOURED AND AVOIDED PLANT SPECIES

The food types available to an animal can usually be divided into (i) those that make up a large proportion of the diet (the dietary staples or principle foods), (ii) those that are not common enough in the habitat to contribute significantly to the diet, but are nevertheless favoured by the animals (favoured or preferred foods) and (iii) those that are normally avoided (see Petrides 1975). For kudus the distinction is important because population performance is likely to be more closely associated with the abundance and quality of the favoured and staple food types rather than the total potential food abundance.

It cannot be stated with certainty that any woody plant species present in the study area was totally rejected by kudus. Over the study period they were observed feeding on 54 of the 60 odd species present in the hill base ecotone, but those few for which there were no feeding records were all rare or isolated (e.g. *Sterculia rogersii*, *Ficus ingens*, and *Ficus soldenella*) so further observation may reveal that they are in fact accepted occasionally.

Nevertheless there were relatively few woody species that comprised a significant proportion of the kudus' diet. The dietary staples among the woody plants were *Acacia nigrescens*, *Combretum apiculatum* and *C. hereroense*. These three together comprised 10 to 20 per cent of recorded feeding time in the wet and dry seasons, increasing to 55 per cent in the pre-rain flush. All other woody species combined made up no more than 25 per cent of the diet in any season. Scarce species that were highly favoured were *Spirostachys africana* and *Grewia flavescens*. Other woody species that were important in some seasons were: *Ziziphus mucronata* (wet season), *Securinega virosa* (wet season), *Dalbergia melanoxylon* (pre-rain flush), *Lonchocarpus capassa* (pre-rain flush), *Ehretia amoena* (dry season) *Maytenus heterophylla* (dry season), *Dichrostachys cinerea* (wet and dry seasons).

The rarely accepted species were *Acacia tortilis*, *Cissus lonicerifolia*, *Dombeya rotundifolia*, *Pterocarpus rotundifolius*, *Grewia monticola*, *Peltophorum africanum* and *Euclea divinorum*. Together these species made up 50 per cent or more of the total available woody plant leaves, but contributed to no more than 3 per cent of the diet at any time of the year.

Plants in the herb layer were strongly favoured during most of the year. Despite their lower abundance than woody browse they made up 65 to 70 per cent of recorded feeding time in both the wet and dry seasons, declining to below 20 per cent only in the pre-rain flush. Of the 78 species of forbs identified in the hill base ecotone 47 appeared in the feeding records during the study period. Of these 14 were recorded as being utilized more than five times (see Appendix I), the most common ones being *Barleria lancifolia*, *Justicia flava*, *Commelina* species, *Aspilia mossambicensis*, *Ipomoea* species, *Cucumis* species, *Rhynchosia totta*, *Hibiscus micranthus*, *Solanum panduraeforme* and *Tragia rupestris*. However both the list of forb species occuring in the hill base ecotone and the list of utilized species are probably incomplete. Further work is therefore required to establish which forb species comprise the greatest proportion of the kudus' diet.

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CHAPTER THREE : FORAGING BEHAVIOUR

This chapter evaluates Owen-Smith's (1979) indices of accepted food abundance (feeding time per unit distance moved during foraging) and food intake rate (the proportion of foraging time spent feeding). As discussed in the Introduction the indices are intended to assess long-term relationships between habitat conditions and population dynamics of kudus. The sensitivity of the indices to changing habitat conditions was evaluated by examining their relationship with seasonal and between-habitat variations in potential food abundance. A positive correlation between the indices and potential food abundance would be predicted. If this proved true it would support the validity of the indices.

In addition diurnal variations in the indices were analysed by comparing the early morning and late afternoon foraging periodes with foraging at midday. Seasonal variations in the activity budget of kudus (the proportion of daylight hours devoted to foraging, moving and being inactive) are also discussed.

METHODS

Data on foraging behaviour were collected using the methods of Novellie (1978) and Owen-Smith (1979). The procedures followed to obtain tape-recorded sequences of the activities of foraging kudus were described in Chapter 2. These recording sessions provided a record of the sequence of activities of a foraging kudu, as well as the duration of each bout of activity.

Foraging was regarded as comprising two main activities, feeding and walking between food items. During foraging periods the kudus often performed short bouts of other activities, mostly standing and looking around but also grooming, defecation, urination or brief social interactions with other group members. Provided a bout of such miscellaneous activities did not last longer than two minutes it was included in the foraging period. As discussed in Chapter 2, if the kudu engaged in any miscellaneous activity for longer than two minutes the foraging period was considered to have ended and recording was stopped. The monthly sample sizes of recording sessions are shown in Table 21.

Feeding and walking take place in alternating bouts; the animal stands and feeds at a certain place and after a time moves on. It may adjust its position by taking one or two steps without interrupting feeding, or it may stop feeding, walk a sequence of steps and commence feeding at another place. Goddard (1968) defined a 'feeding station' as the area accessible to a foraging animal without it moving its fore feet. The time spent feeding at a feeding station is termed the feeding station duration. The sequence of paces taken in moving between feeding stations is termed the step set. Foraging may thus be analysed in terms of an alternating series of feeding stations and step sets (Novellie 1978). The minimum duration of a feeding station was one second, and the minimum number of steps in a set was one. A bout of miscellaneous activity lasting less than two minutes was not considered to terminate a feeding station or step set. For example if a kudu fed at a station for 10 seconds then stood alert for a period, then fed once again for 4 seconds before moving on, the feeding station duration was scored as 14 seconds.

The foraging parameters can then be defined as follows: Consider a recording session of duration T. Let the total time spent feeding, walking and on miscellaneous activities be F, W and M respectively, and let the number of paces moved be S. Let there be n feeding stations in the recording session each of duration $f_1 \ldots f_i \ldots f_n$. If the recording starts with a feeding station and ends with a step set then there will also be n step sets, each comprising $s_1 \ldots s_i \ldots s_n$ paces.

Then $$\sum_{i=1}^{n} f_i = F$$ and

$$\sum_{i=1}^{n} s_i = S$$

The mean feeding station duration F/n is a measure of the time remained at the average feeding station. The mean number of steps per set S/n is a measure of the average distance moved between feeding stations. One would expect a positive relation=ship between the amount of food available at the average feeding station and the mean feeding station duration. It could also be predicted that the mean number of steps per set would tend to increase as food became scarcer.

The indices proposed by Owen-Smith (1979) can be expressed as follows: The proportion of foraging time spent feeding (F/T) is the index of the food intake rate while foraging. The feeding time achieved in relation to the number of steps moved (F/S) is the index of accepted food abundance per unit area. The propor=tion of recording time T is devoted to each of the activities F, W and M is termed foraging time apportionment.

Statistical analysis

Decision statistics are required to evaluate the significance of observed differences in the foraging parameters, and the question arises of how to sample them and of what constitutes a suitable unit of sampling. The foraging parameters are interrelated, and it is possible to express some in terms of others. Thus the index of accepted food abundance F/S is equal to the quotient of mean feeding station duration and mean steps per set (F/n / S/n = F/S). The sum of the values F/T, W/T and M/T is one, so that any one of the three can be expressed in terms of the other two.

It would therefore be unnecessary to sample and statistically test all the parameters as conclusions about some could be derived from the analyses of others. The parameters selected for sampling and analysis were: mean feeding station duration, mean steps per set, the proportion of recording time spent feeding and the proportion of recording time spent on miscellaneous activities. The value for feeding time per pace was derived from mean feeding station duration and mean steps per set.

Since the effects of a number of factors on the foraging para=meters (e.g. seasons, time of the day) have to be tested, multi-way analysis of variance is appropriate. This requires that the variates analysed be independent and normally distributed with homogeneity of variance. The feeding station durations and step sets defined above are not normally distributed but tend to follow the exponential or gamma distributions (see Baker 1973). Also the successive feeding stations or step sets within a recording session may not be independent of one another. Because of these problems the analyses were not carried out using the individual feeding station durations or step sets as the variates. Instead, for each recording session, the mean feeding station duration and mean number of steps per set were calculated, and these means were then regarded as the units of sampling. Sample sizes were insufficient to statistically test whether the means were in fact normally distributed. However their distributions were obviously skew (more values below than above the mean). Also, as is often the case with non-normal distributions, the variance was correlated with the mean, indicating the likelihood of heterogeneity of variance. To correct for this the logarith=mic transformation was applied (Sokal and Rohlf 1969).

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For the proportions of recording time spent on feeding and on miscellaneous activities the unit of observation was again the recording session. The proportions of time spent feeding and on miscellaneous activities were calculated for all sessions over 5 minutes in duration. The distributions of these propor= tions were also obviously skew so the arcsine transformation for proportions was applied (Snedecor and Cochrane 1967).

The analyses were performed by computer using the program Rummage (Scott et al. 1977). As noted in Chapter 1 the program output indicates whether the variates are normally distributed and whether the variance is homogeneous. The results showed that the above transformations were reasonably successful in meeting the requirements for the analysis. The consequences of moderate non-normality and heterogeneity of variance are in any case not serious for the overall test of significance. The means and confidence limits presented in this chapter are retrans= formed from means and confidence limits calculated from the transformed data (Sokal and Rohlf 1969).

RESULTS

Mean durations of feeding stations

Differences between the four seasons and between the time of the day (midday compared with early morning-late afternoon) in mean feeding station duration are shown in Table 30. The analysis of variance (Table 30b) shows no significant diurnal differences but the differences between seasons are highly significant. Mean feeding station durations were highest in the pre-rain flush and lowest in the two dry seasons. These differences do not corres= pond with the variations between seasons in the abundance of available leaves. Leaf biomass in the pre-rain flush was the lowest of the four seasons so the long mean feeding station dura= tion at this time is unexpected.

TABLE 30a : SEASONAL AND DIURNAL VARIATION IN MEAN FEEDING STATION DURATION (SECONDS PER STATION)

Time of day	Dry Season 1976	Pre-rain flush	Wet Season	Dry Season 1977	Overall Row Means
*Early morning-Late afternoon	15	24	19	13	17
Midday	17	21	20	16	18
Overall Column Means	16	22	19	15	

*Early-morning-Late afternoon : October to March, before 08h00 and after 16h00 : April to September, before 09h00 and after 15h00

Note: The means above are transformed back from means calculated in the logarithmic scale. They are lower than the means of untransformed data.

TABLE 30b : ANALYSIS OF VARIANCE OF SEASONAL AND DIURNAL VARIATION IN FEEDING STATION DURATION

Source of variation	df	Mean Square	F ratio	Signifi= cance
Seasons	3	0,433	9,20	P< 0,001
Time of day	1	0,042	0,88	n.s.
Seasons x Time interaction	3	0,065	1,37	n.s.
Error	372	0,047		
Total	379			

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Grouping of the data into the four seasons was necessary to provide a sufficiently large sample size for statistical analysis, but as discussed in the previous chapter the seasonal groupings represent an approximation. Monthly mean feeding station durations are therefore shown in Fig. 25 together with monthly variation in biomass of accessible leaves. These two parameters are related in that the highest mean feeding station durations in February-March coincide with the period of maximum leaf biomass, while the lowest durations in August-September coincide with lowest leaf abundance. However an obvious discrepancy is that feeding station durations in the pre-rain flush months, October and November, are as high or higher than those of the wet season months December, January and April whereas on the basis of differences in leaf abundance they would be expected to be much lower (Fig. 25). It is because of this discrepancy that the overall mean feeding station duration for the wet season (December to April) is lower than that of the pre-rain flush.

One possible factor accounting for the discrepancy is that the overall mean feeding station duration is influenced by the relative contribution of forbs and woody plants to the diet. As shown below the mean duration of feeding stations on woody plants is much longer than that on plants in the herb layer. Thus the overall mean feeding station duration tended to be relatively high in the pre-rain flush, when a high proportion of the diet came from woody plants, and lower in December, January and April when the diet comprised mostly forbs. The seasonal trends in feeding station durations on woody plants and in the herb layer are therefore examined separately below.

Feeding station durations in the herb layer (Fig. 26) show a clear seasonal trend which is significantly correlated with seasonal changes in the biomass of forb leaves ($r = 0{,}82$, $P < 0{,}01$). As expected mean durations were highest in the mid-wet season when leaf biomass was highest and were lowest in the late dry seasons at the time of lowest leaf abundance. In contrast the monthly variation in mean feeding station duration on

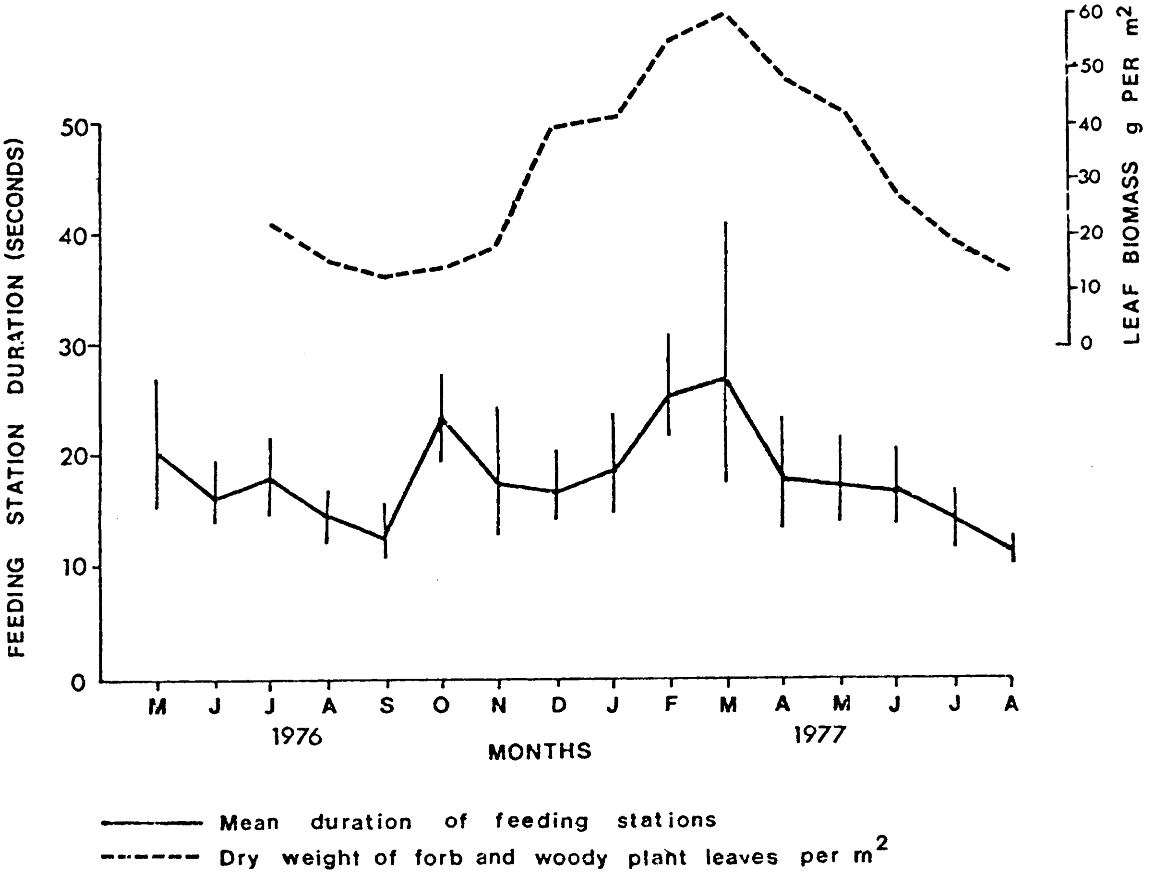

FIG. 25 MONTHLY MEAN FEEDING STATION DURATIONS COMPARED WITH TOTAL LEAF ABUNDANCE. FEEDING STATION DURATIONS ARE SHOWN WITH 95% CONFIDENCE LIMITS (TRANSFORMED BACK FROM VALUES CALCULATED IN THE LOGARITHMIC SCALE, SEE TEXT)

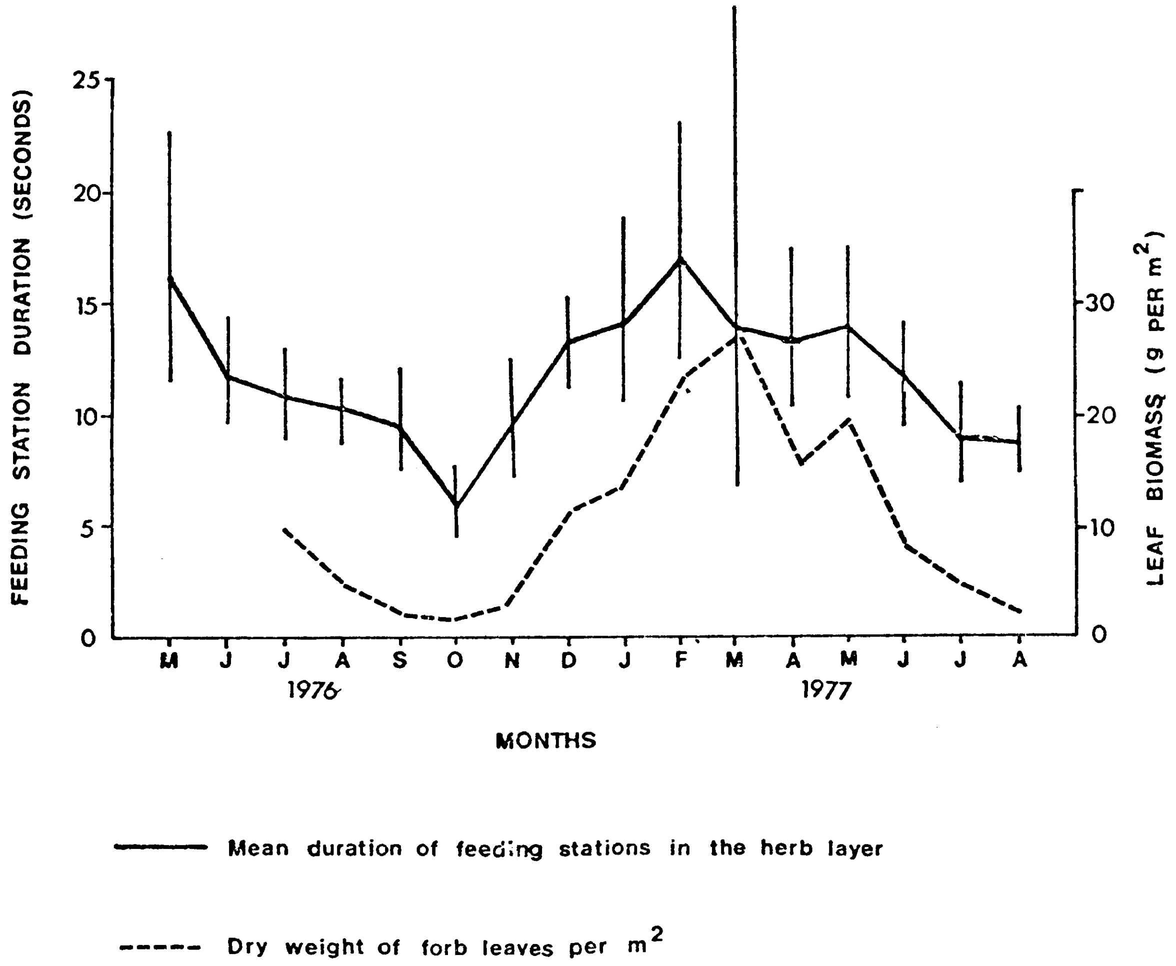

FIG. 26 MONTHLY MEAN DURATIONS OF FEEDING STATIONS IN THE HERB LAYER COMPARED WITH FORB LEAF ABUNDANCE. FEEDING STATION DURATIONS ARE SHOWN WITH 95% CONFIDENCE LIMITS (TRANS= FORMED BACK FROM VALUES CALCULATED IN THE LOGARITHMIC SCALE, SEE TEXT)

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woody plants (Fig. 27) was not related to seasonal variation in woody plant leaf biomass. A comparison of Figs. 26 and 27 shows that mean feeding station duration in the herb layer was lower than that of woody plants in almost all months of the study period.

Mean steps per set

A negative relationship between mean steps per set and the abundance of potential food would be expected because when food is scarce the kudus would on average move greater distances between feeding stations. The difference between the four seasons in mean steps per set (Table 31) follows the expected pattern in that the values are highest in the pre-rain flush, the season of lowest abundance, and lowest in the wet season, at the time of greatest abundance. However the seasonal differences are not marked and the analysis of variance (Table 31b) shows no significant seasonal or diurnal differences.

Feeding time per pace

As discussed above the feeding time achieved per pace walked was calculated by dividing the mean feeding station duration by the mean steps per set. Monthly variation in feeding time per pace is significantly correlated with total leaf biomass ($r = 0,77$ $P < 0,01$) (Fig. 28). Neither the overall mean feeding station duration nor the mean number of steps per set showed significant diurnal variation (Tables 30 and 31) and therefore there is no reason to suspect that feeding time per pace varied over the day.

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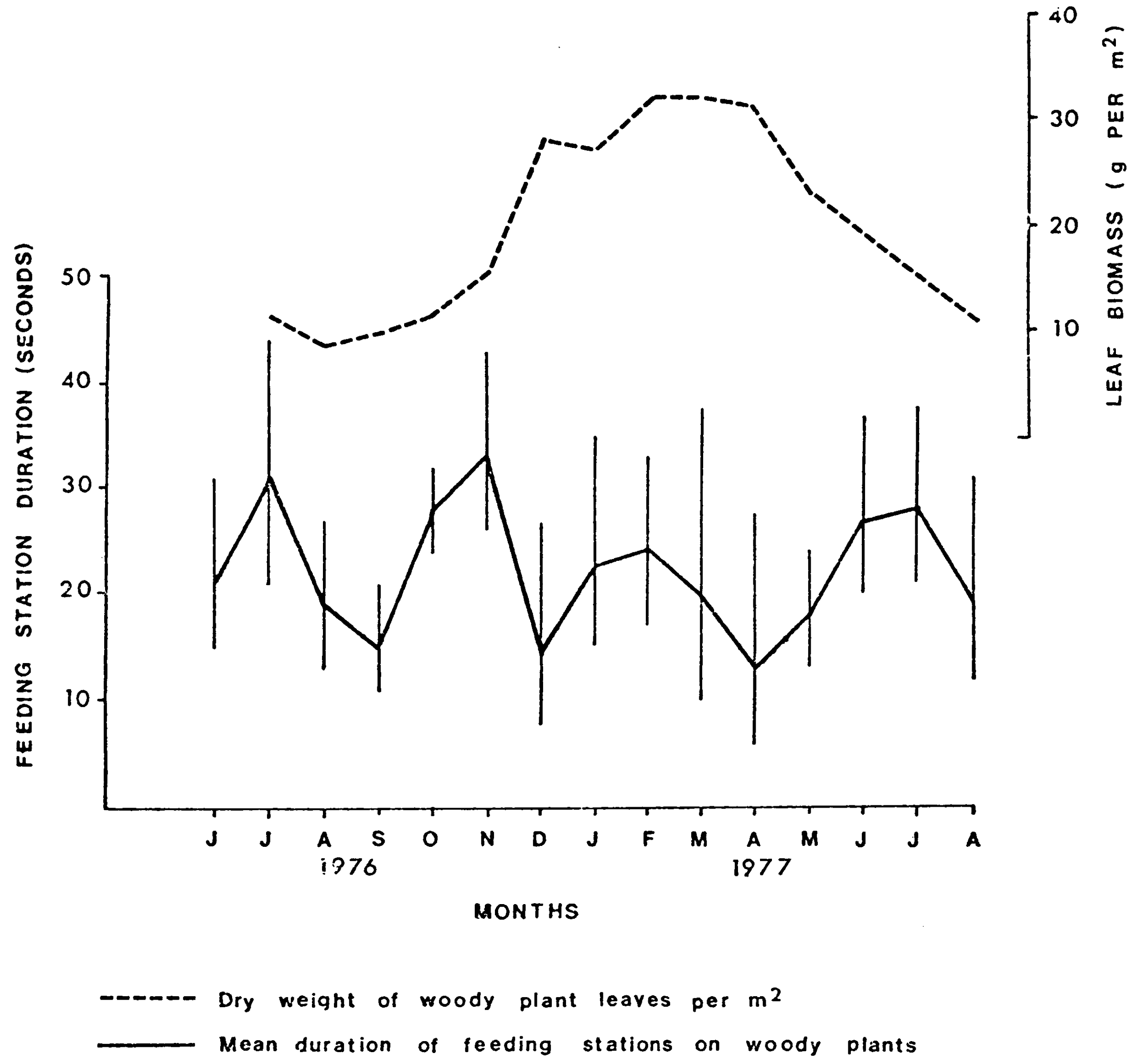

FIG. 27 MONTHLY MEAN DURATIONS OF FEEDING STATIONS ON WOODY PLANTS COMPARED WITH WOODY PLANT LEAF ABUNDANCE. FEEDING STATION DURATIONS ARE SHOWN WITH 95% CONFIDENCE LIMITS (TRANSFORMED BACK FROM VALUES CALCULATED IN THE LOGARITHMIC SCALE)

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TABLE 31a : SEASONAL AND DIURNAL VARIATION IN MEAN NUMBER OF STEPS PER SET

Time of day	Dry Season 1976	Pre-rain flush	Wet Season	Dry Season 1977	Overall Row Mean
*Early morning-Late afternoon	3,47	3,81	3,24	3,93	3,60
Midday	3,96	4,11	3,26	3,44	3,67
Overall Column Means	3,71	3,96	3,25	3,68	

*Early morning-Late afternoon : October to March, before 08h00 and 16h00 : April to September, before 09h00 and after 15h00

Note: The means above are transformed back from means calculated in the logarithmic scale. They are lower than the means of untransformed data.

TABLE 31b : ANALYSIS OF VARIANCE OF SEASONAL AND DIURNAL VARIATION IN MEAN STEPS PER SET

Source of variation	df	Mean Square	F ratio	Signifi=cance
Seasons	3	0,0825	1,420	n.s.
Time of day	1	0,0054	0,094	n.s.
Seasons x Time interaction	3	0,0627	1,079	n.s.
Error	372	0,0581		
Total	379			

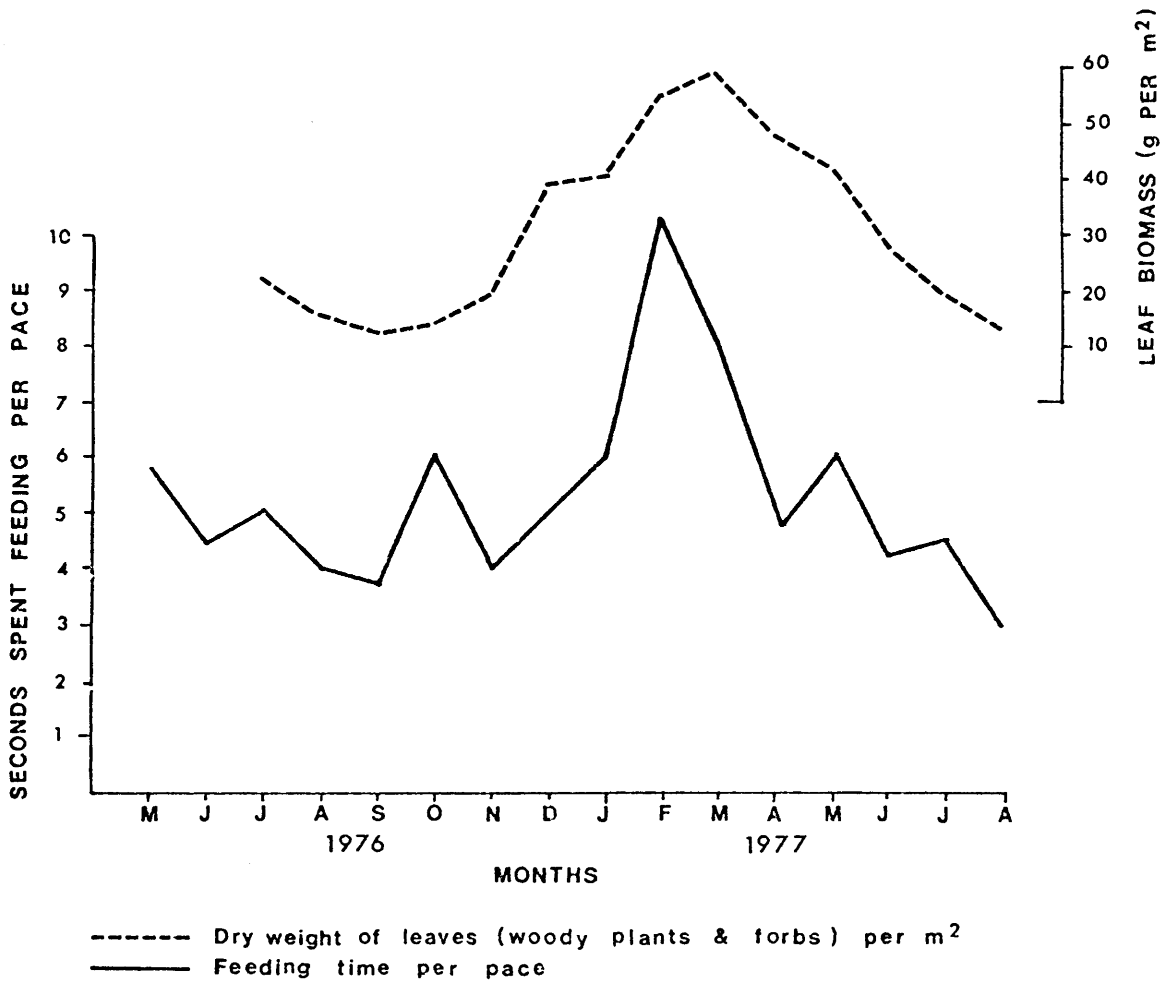

FIG. 28 MONTHLY VARIATION IN FEEDING TIME PER PACE COMPARED WITH TOTAL LEAF ABUNDANCE

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Seasonal differences in the foraging parameters; comparing woody plants and forbs

Plotted at monthly intervals the mean duration of feeding stations on woody plants show no clear seasonal trend. However the sample sizes in some months were small, and if the data are grouped into the four seasons there is evidence of a seasonal pattern (Fig. 29). The means were highest in the pre-rain flush and lowest in the wet season, with the two dry seasons intermediate. This seasonal difference in duration of feeding stations on woody plants is in fact negatively related to the seasonal variations in woody plant leaf abundance, not positively as would be expected. There is also a negative correlation between the feeding station durations in the herb layer and those on woody plants (Fig. 29), and it seems possible that the two are interrelated; the time spent at the average woody plant feeding station may increase when the availability of alternative food in the herb layer is low. In the pre-rain flush forbs were scarce, and moreover this was the only time of the year when the protein content of forb leaves was lower than the average of the woody plant leaves (Fig. 17). This may account for the fact that woody plant feeding station durations averaged longest in the pre-rain flush. In the wet season the abundance and nutritional value of forbs was highest relative to the woody plants (Figs 17 and 18) and this, in turn, may account for the low feeding station duration on woody plants at this time.

This interpretation is in accord with the evidence (Chapter 2) that forbs are the favoured food resource, with woody plants increasing in importance only when forbs are scarce. However despite the fact that the time spent at feeding stations on woody plants increased from the wet season to the dry, while that of forbs decreased, there was apparently little change in the relative proportions of forbs and woody plants in the diet from the wet season to the dry (Table 23). This was because the number of woody plant feeding stations located per pace walked during foraging (Fig. 30) was higher in the wet season than the dry. In other words, although the duration of woody plant feeding stations increased from the wet season to the dry this was balanced by a

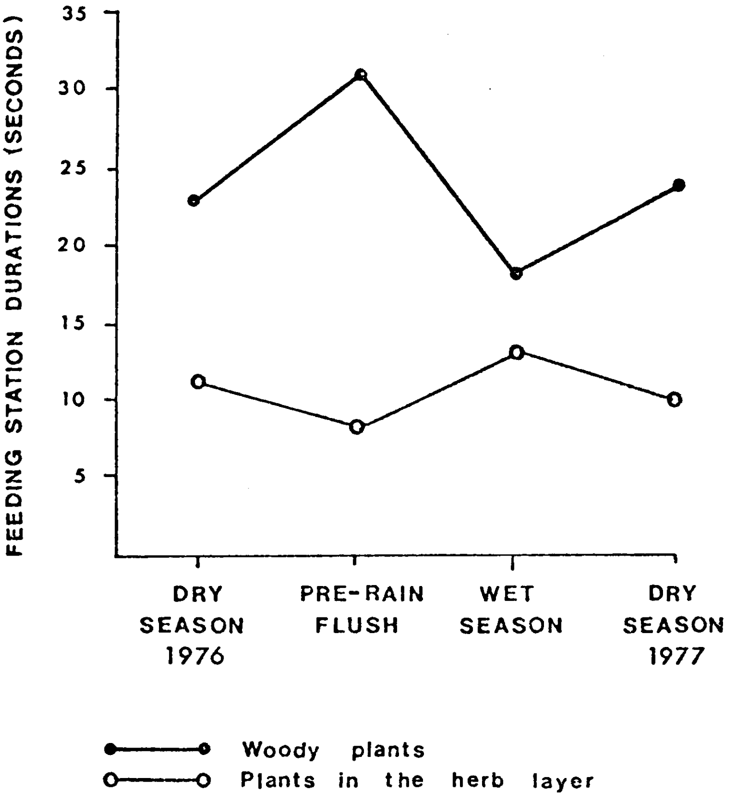

FIG. 29 SEASONAL VARIATION IN MEAN TIME SPENT AT FEEDING STATIONS ON WOODY PLANTS AND PLANTS IN THE HERB LAYER

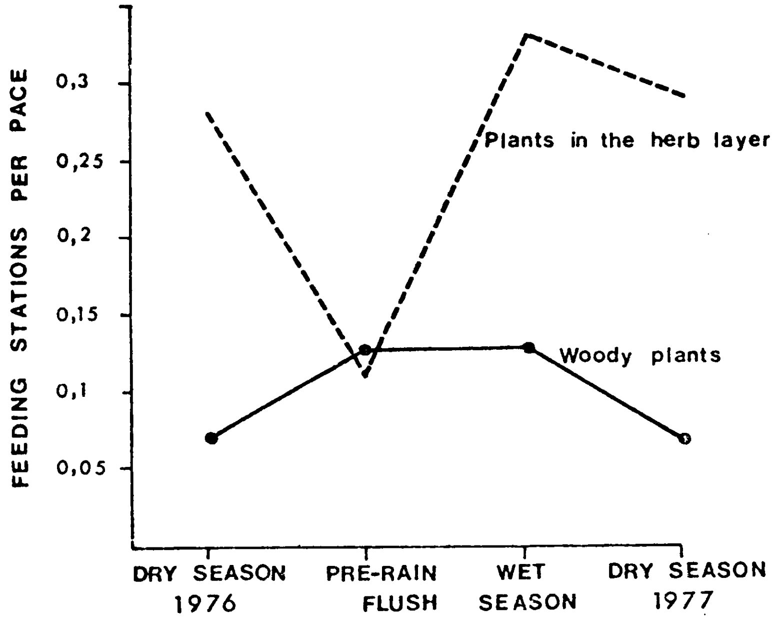

FIG. 30 SEASONAL VARIATION IN THE NUMBER OF FEEDING STATIONS LOCATED PER PACE WALKED DURING FORAGING, FOR WOODY PLANTS AND PLANTS IN THE HERB LAYER

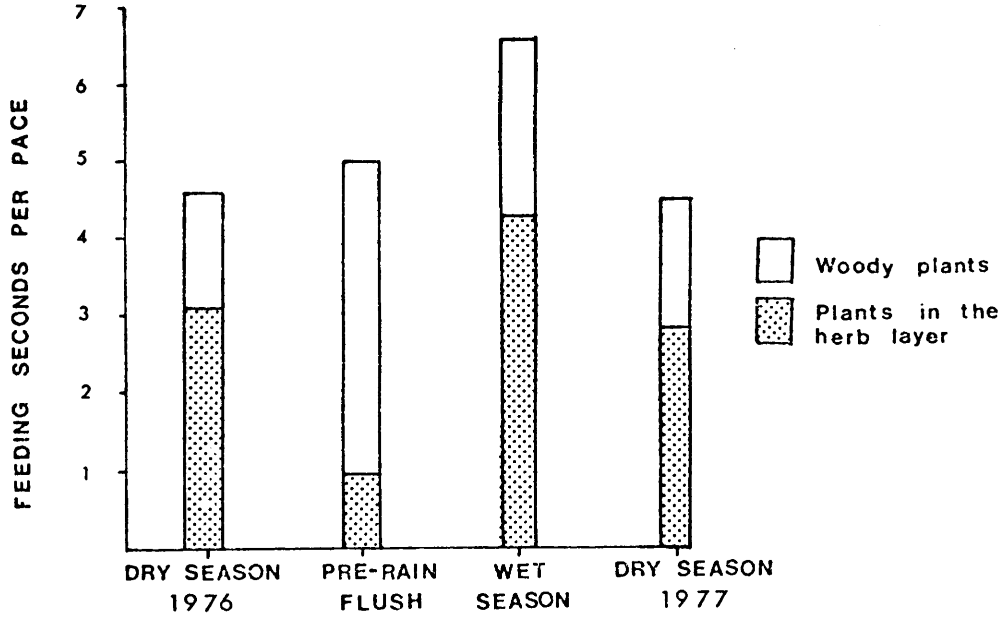

FIG. 31 SEASONAL VARIATION IN FEEDING TIME PER PACE, COMPARING WOODY PLANTS AND PLANTS IN THE HERB LAYER

decrease in the relative number of woody feeding stations located, and so the overall proportion of woody plants in the diet did not change appreciably.

Seasonal differences in feeding time per pace on woody plants and plants in the herb layer are summarized in Fig. 31. For plants in the herb layer feeding time per pace is highest in the wet season and lowest in the pre-rain flush, thus corresponding with seasonal variations in abundance of forb leaves. For woody plants, however, feeding time per pace is highest in the pre-rain flush, which is the time of lowest woody plant leaf abundance. Again this is probably due to the low availability of forbs during the pre-rain flush. This suggests that the seasonal variations in feeding time per pace on woody plants depends not so much on the abundance and quality of woody plant leaves as such, but rather on the abundance and quality of alternative food available in the herb layer.

Foraging time apportionment

The proportion of foraging time spent feeding showed little seasonal or diurnal variation, and the analysis of variance revealed no significant differences (Table 32). In contrast the proportion of time spent on miscellaneous activities was highest in the wet season, lower in the dry seasons and lowest in the pre-rain flush, although the difference is significant only at the ten per cent level (Table 33). Diurnal differences in time spent on miscellaneous activities are not significant.

As discussed above the amount of foraging time spent walking was not analysed statistically because conclusions about this component of foraging time apportionment can be derived from the analyses of the other two. Since the proportion of foraging time spent feeding did not vary greatly between seasons it follows that the seasonal variation in the proportion of time

TABLE 32a : SEASONAL AND DIURNAL VARIATION IN THE PERCENTAGE OF FORAGING TIME SPENT FEEDING

Time of Day	Dry Season 1976	Pre-rain flush	Wet Season	Dry Season 1977	Overall Row Mean
*Early morning-Late afternoon	75,9	77,2	74,5	69,9	74,4
Midday	70,4	78,4	74,9	74,6	74,6
Overall Column Means	73,2	77,8	74,7	72,3	

*Early morning-Late afternoon : October to March, before 08h00 and after 16h00 : April to September before 09h00 and after 15h00

TABLE 32b : ANALYSIS OF VARIANCE OF FORAGING TIME SPENT FEEDING

Source of variation	df	Mean Square	F ratio	Signifi=cance
Seasons	3	0,0377	1,19	n.s.
Time of day	1	0,0004	0,01	n.s.
Seasons x Time interaction	3	0,0571	1,80	n.s.
Error	339	0,0318		
Total	346			

TABLE 33a : SEASONAL AND DIURNAL VARIATION IN THE PERCENTAGE OF FORAGING TIME SPENT ON MISCELLANEOUS ACTIVITIES

Time of Day	Dry Season 1976	Pre-rain flush	Wet Season	Dry Season 1977	Overall Row Mean
*Early morning-Late afternoon	8,6	8,1	11,5	7,5	8,9
Midday	11,1	6,4	12,3	10,0	9,8
Overall Column Means	9,8	7,2	11,9	8,7	

*October to March, before 08h00 and after 16h00 : April to September before 09h00 and after 15h00

TABLE 33b : ANALYSIS OF VARIANCE OF FORAGING TIME SPENT ON MISCELLANEOUS ACTIVITIES

Source of variation	df	Mean Square	F ratio	Signifi= cance
Seasons	3	0,0631	2,14	P< 0,10
Time of day	1	0,0162	0,55	n.s.
Seasons x Time interaction	3	0,0160	0,54	n.s.
Error	339	0,0295		
Total	346			

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spent walking is negatively correlated with the proportion spent on miscellaneous activities, in other words high in the pre-rain flush and low in the wet season. This seasonal trend in the proportion of foraging time spent walking is negatively related to the abundance of potential food, which is to be expected because when food is scarce the kudus would have to spend more time walking between food items. Monthly variation in walking time (Fig. 32) is significantly negatively correlated with total leaf abundance ($r = -0,67$, $P < 0,01$).

If the proportion of time spent on miscellaneous activities had in fact remained constant over the seasons then the time spent on feeding would have been negatively related to walking time and thus positively correlated with food abundance. The fact that there is little seasonal variation in feeding time is due to the seasonal variation in time spent on miscellaneous acti=vities. This pattern of seasonal variation in foraging time apportionment is the same as that found by Owen-Smith (1979). He pointed out that the decrease in time spent on miscellaneous activities as the dry season advanced enabled the kudus to maintain a high feeding time per foraging time in the dry season despite the necessary increase in walking time. The present results confirm this conclusion.

The index of accepted food abundance compared between habitat subdivisions: Relationships with potential food abundance

Given that the proportion of potential food that is accepted by kudus remains constant, differences between habitats in the index of accepted food abundance will correspond with differences in potential food abundance. Discrepancies between potential and accepted food abundance should thus indicate differences between habitats in the proportion of potentially available food that is accepted. Such differences in acceptance could arise, for example, because of differences between habitats in the relative density of

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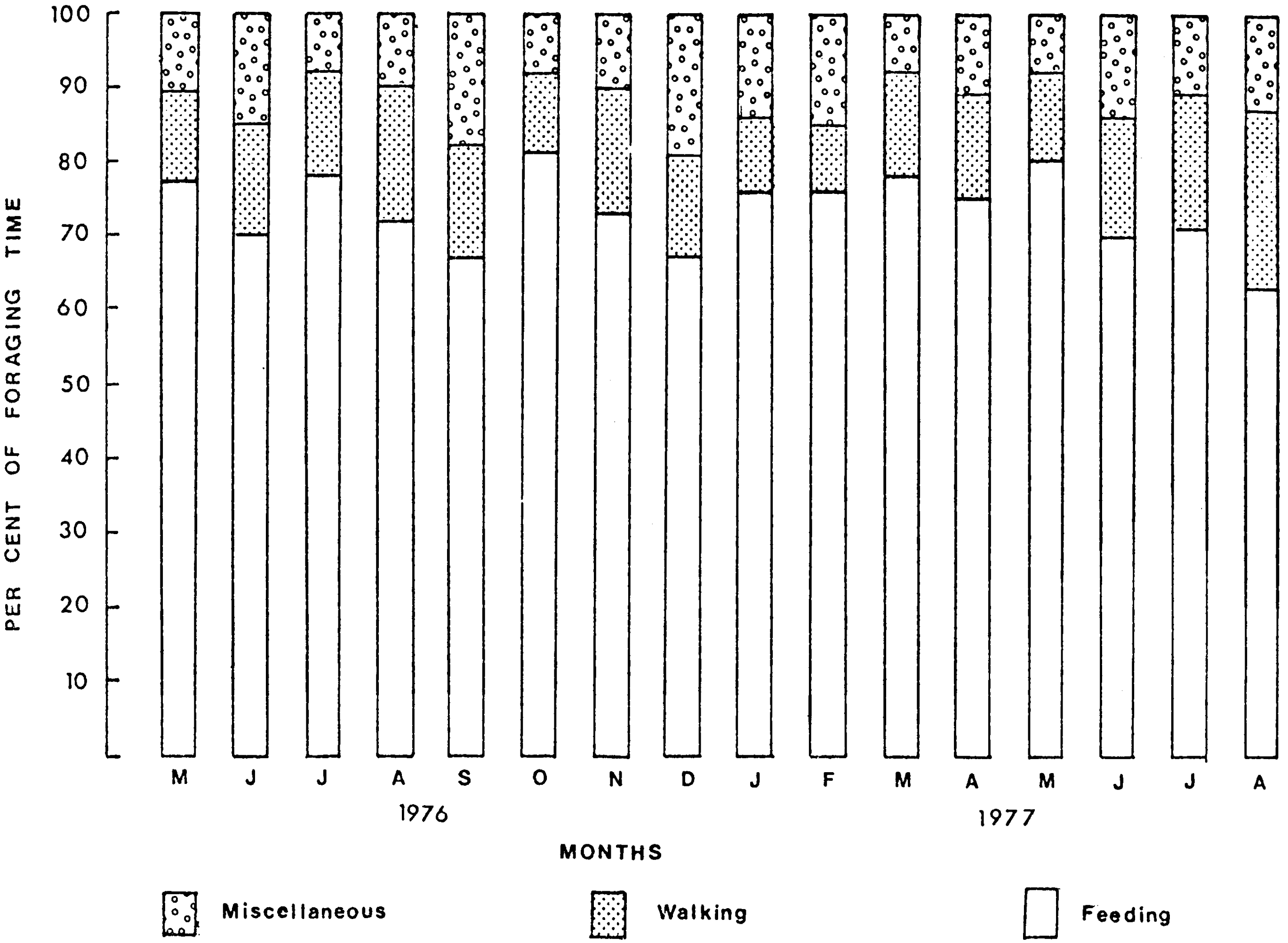

FIG. 32 MONTHLY VARIATION IN PROPORTION OF FORAGING TIME SPENT FEEDING, WALKING AND ON MISCELLANEOUS ACTIVITIES

favoured as opposed to avoided plant species or because of differences in the average nutrient content of food plants.

In this section the index of accepted food abundance, and potential food abundance are compared between the habitat subdivisions of the study area to assess possible differences between habitats in the proportion of available food accepted by the kudus. A possible confounding factor in these comparisons is that the average eating rate (weight of food eaten per feeding time) may vary between habitats, and because of this the index may not give a reliable reflection of differences in accepted food abundance. The likely effects of differences in eating rate are discussed further below.

In Chapter 1 forb abundance was compared between the hill slopes and the pediment, and also between regions burnt during the fire of January 1977 and unburnt regions. The slopes were regarded to be the zone extending 80 m up the hill slopes to 20 m out from the hill base thus including the upper slopes and the hill base, see Chapter 1. The pediment extended from 20 m to 400 m out from the hill base. The woody plant canopy volumes per unit area in each of these regions was also estimated, but differences between habitat subdivisions in woody plant leaf weight per unit canopy volume were not investigated. Thus in calculating leaf abundance of woody plants in each habitat subdivision it is assumed that leaf weight per unit canopy volume remain the same over all regions.

Seasonal variations in the index of accepted food abundance and potential food abundance on the slopes and pediment are shown in Fig. 33. The values for the 1977 dry season are for burnt and unburnt regions combined (differences due to the fire are considered separately below). The relative contributions of plants in the herb layer and woody plants to accepted food abundance are indicated in Fig. 33. These are compared with the quantities of woody plant and forb leaves available. The ratios of accepted food abundance to potential food abundance (seconds spent feeding per pace divided by g dry weight of leaves per m^2) are shown in

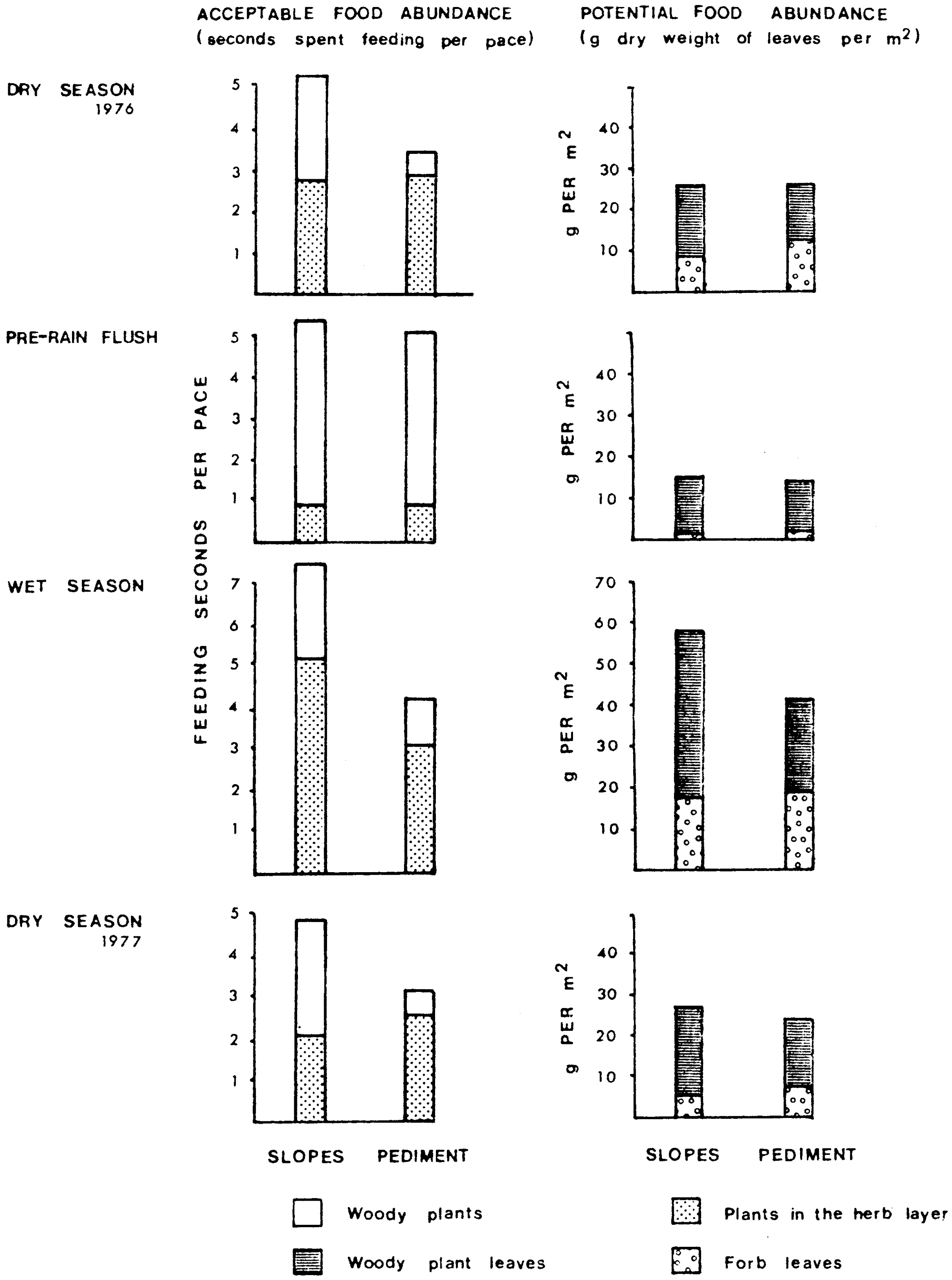

FIG. 33 DIFFERENCES BETWEEN THE HILL SLOPES AND THE PEDIMENT IN THE INDEX OF ACCEPTABLE FOOD ABUNDANCE AND POTENTIAL FOOD ABUNDANCE

Table 34 for plants in the herb layer and woody plants separately. High values for the ratios indicate that a high proportion of potentially available food was accepted.

Fig. 33 shows that total potential food abundance was higher on the slopes than on the pediment in the wet season, but in the pre-rain flush and the dry seasons there was little difference between the two regions in potential food abundance. In the wet season and the pre-rain flush differences between the pediment and the slopes in the index of accepted food abundance corres= pond with the differences in potential food abundance. This indicates that there were no major differences between the two regions in the proportion of potential food that was accepted during the wet season and the pre-rain flush. In both the 1976 and the 1977 dry seasons, however, feeding time per pace aver= aged higher on the slopes than the pediment, despite the rela= tive lack of difference between the two regions in potential food abundance. From Fig. 33 and Table 34 it is evident that the difference was largely due to the much higher feeding time per pace spent on woody plants on the slopes (feeding time per pace spent on plants in the herb layer differed little between the slopes and pediment). This means that in the dry seasons woody plants leaves on the slopes were on average more acceptable to kudus than those on the pediment. This would be expected from the seasonal variations in the composition of the kudu's diet discussed in Chapter 2. The dominant woody species on the slopes, Combretum apiculatum, was favoured by the kudus in the dry seasons, whereas the common species on the pediment were not favoured at this time.

On both slopes and pediment the ratios of accepted to potential food abundance for plants in the herb layer are consistently higher than for woody plants (Table 34). This shows that the kudus favoured forbs over woody plants on both the slopes and the pediment (see also Chapter 2).

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TABLE 34 : RATIOS OF ACCEPTED FOOD ABUNDANCE (SECONDS SPENT FEEDING PER PACE WALKED WHILE FORAGING) TO POTENTIAL FOOD ABUNDANCE (g DRY WEIGHT OF LEAVES PER m^2) COMPARED BETWEEN SLOPES AND PEDIMENT

(A) WOODY PLANTS

	Dry season 1976	Pre-rain flush	Wet Season	Dry season 1977
Slopes	0,13	0,32	0,06	0,13
Pediment	0,05	0,35	0,05	0,04

(B) PLANTS IN THE HERB LAYER

	Dry season 1976	Pre-rain flush	Wet Season	Dry season 1977
Slopes	0,35	0,60	0,29	0,35
Pediment	0,22	0,45	0,16	0,33

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Table 34 shows that the ratios of accepted to potential food abundance for plants in the herb layer on the slopes is higher than for those on the pediment in all seasons. This suggests that the forbs on the pediment were on average less palatable than those on the slopes throughout the year. This is unexpected, since the average protein content of the forb leaves on the pediment was equal to those on the slopes in the wet season and higher in the dry seasons (Chapter 1). As noted in Chapter 1 the species composition of forbs differed greatly between slopes and pediment, but further observation would be required to determine the factors underlying the apparant difference between the two zones in acceptability of forbs.

Comparison between burnt and unburnt regions

In Chapter 1 it was established that the fire in January 1977 caused a temporary reduction in forb abundance, but after good rain in February the biomass of forb leaves and terminal stems did not differ much between burnt and unburnt areas. However the protein content of forb leaves on the burnt areas was lower than those on unburnt areas in the dry season after the fire. No comparisons were made between the burnt and unburnt areas of the weight of woody plant leaves per unit canopy volume. Therefore in estimating woody plant leaf abundance it is assumed that the leaf density per unit canopy volume did not differ between burnt and unburnt areas. This assumption seems reasonable because, although the fire affected plants in the herb layer, it was not hot enough to seriously affect the woody plants.

The kudus left the burnt areas in January and did not return until April, so it is not possible to compare foraging behaviour on burnt and unburnt areas in the wet season. The data for the dry season of 1977 can however be compared to check for differences in accepted food abundance which might have been caused by the fire.

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Differences between burnt and unburnt areas in potential food abundance and in the index of accepted food abundance are shown in Fig. 34. Table 35 gives the ratios of accepted to potential food abundance for woody plants and plants in the herb layer.

On the pediment potential food abundance did not differ markedly between burnt and unburnt regions. In contrast, potential food abundance was higher on the unburnt than the burnt slopes. This was because woody plant canopy volume per unit area was higher on Nwamuriwane (the unburnt hill) than Nwamuriwa (the burnt hill), which probably reflect an inherent difference between the two regions and was not due to the fire. The variations in the index of accepted food abundance correspond approximately with these differences in potential food abundance; values for the burnt and unburnt pediments are similar, whereas the value for the unburnt slopes is higher than for the burnt slopes (Fig. 34).

Since the protein content of forb leaves on the unburnt regions was higher than on the burnt one would expect a relatively higher acceptance of the unburnt forbs. From Table 35 this seems to have been the case, the ratios of accepted to potential food abundance for plants in the herb layer were higher on unburnt than burnt areas for both the slopes and the pediment. Further observations would be required to clarify whether the difference in nutrient content and relative acceptability of forbs between the two regions is likely to have been due to the fire or to some other factor such as a difference in forb species composition.

Apart from the slight difference in acceptance of plants in the herb layer there is no evidence that the fire had any affect on accepted food abundance during the dry season of 1977.

Differences between the slopes and pediment, and between burnt and unburnt regions in the index of food intake rate (the proportion of foraging time spent feeding) were the same as described above for the index of accepted food abundance, and therefore the results are not presented.

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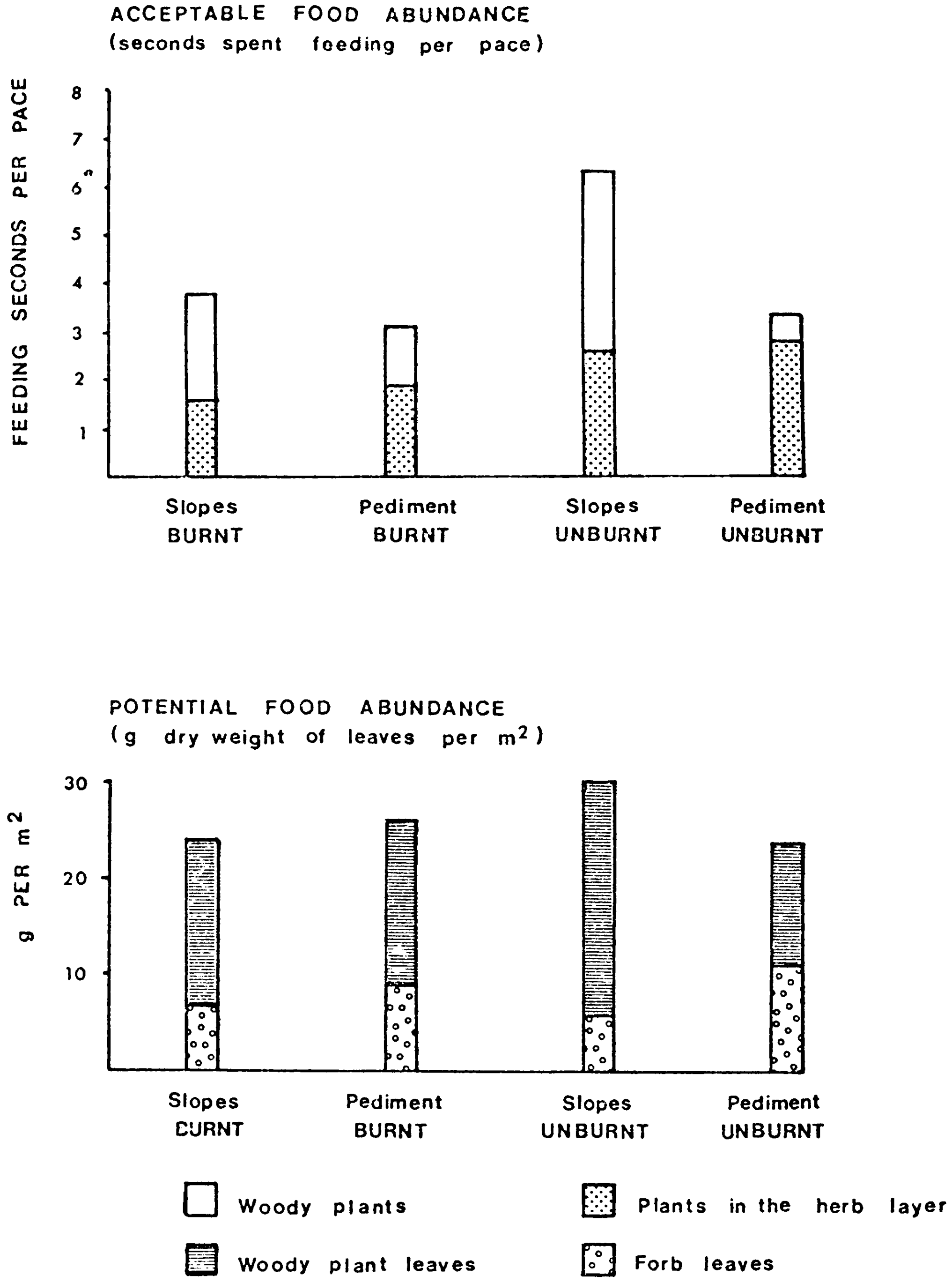

FIG. 34 DIFFERENCES BETWEEN UNBURNT REGIONS AND REGIONS BURNT IN JANUARY 1977 IN THE INDEX OF ACCEPTABLE FOOD ABUNDANCE AND POTENTIAL FOOD ABUNDANCE DURING THE DRY SEASON OF 1977

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TABLE 35 : RATIOS OF ACCEPTED FOOD ABUNDANCE (SECONDS SPENT FEEDING PER PACE WALKED WHILE FORAGING) TO POTENTIAL FOOD ABUNDANCE (g DRY WEIGHT OF LEAVES PER m^2) COMPARED BETWEEN BURNT AND UNBURNT REGIONS DURING THE DRY SEASON OF 1977

	Burnt Slopes	Burnt Pediment	Unburnt Slopes	Unburnt Pediment
Woody Plants	0,13	0,07	0,15	0,04
Plants in the Herb layer	0,23	0,21	0,43	0,25

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Comparison between the hill base ecotone and the knobthorn savanna

Owen-Smith (1979) found that feeding time per unit distance moved by kudus foraging in the knobthorn savanna was signifi= cantly lower than in the hill base ecotone. In Chapter 1 it was shown that the abundance of forbs and the density of woody plants was lower in the knobthorn savanna than the hill base ecotone. It is evident then, that the difference between the knobthorn savanna and the hill base ecotone in accepted food abundance corresponds with the difference between them in potential food abundance.

The magnitude of seasonal variation in accepted and potential food abundance

The magnitude of seasonal variation in the index of accepted food abundance was less than that of potential food abundance. Thus the peak wet season mean for feeding time per pace was 3,6 times the lowest dry season value (see Fig. 28), whereas the total potential food abundance (biomass of woody plant and forb leaves varied seasonally by a factor of 5 times. The seasonal variations in the ratios of accepted to potential food abundance (Table 34) indicate that the fraction of potential food abundance actually accepted was greatest in the pre-rain flush and lowest in the wet season, with the dry seasons intermediate. This sug= gests that the kudus expand their diets to include a greater porportion of potential food in seasons of food scarcity. There are some indications that this was the case, for example Euclea divinorum, a woody species with a relatively low protein content, was consistently accepted by kudus in the dry season but rejected in the wet season. However, as discussed further below, the eating rate is likely to be lower when food is scarce than when it is abundant, and therefore the true magnitude of seasonal variation in accepted food abundance would not be as great as suggested by variations in feeding time per pace.

Activity budgets

Data on the activity budget (the proportion of daylight hours allocated by the kudus to their various activities) were gathered by watching individual cow groups from as early as it was possible to contact them in the morning until nightfall (see also Owen-Smith 1979). Every 15 min the prevailing activity over a period of one minute of each of the adult members of the group was recorded according to the following categories:

(i) foraging (which included feeding as well as moving between feeding stations)
(ii) inactive (including standing or lying)
(iii) miscellaneous activities (including mostly moving, with some social interactions and drinking).

An important restriction was that one or more of the group members, especially those resting, were frequently obscured from the observer, sometimes for long periods. Thus if recording was confined to visible animals results would be biased in favour of foraging and moving. To avoid this bias the activity of each group member had to be accounted for at each 15 min sampling point, even though this meant inferring the activity of invisible animals. Inferences were made on the basis of what the individual had been doing when it was last seen, how long it had remained obscured and what the other group members were doing. Changes in activity of visible animals were recorded when observed within the 15 min interval, and these records also helped to assess the activity of animals which were invisible at the main sampling point. Although subjective judgement sometimes had to be used results were sufficiently accurate to reflect the main seasonal and diurnal trends.

The 15 min sampling interval would probably yield less accurate results than the standard 4 min interval used in other studies (e.g. Spinage 1969). However the longer interval was necessary because under unfavourable conditions it was difficult to record each group member's activity at shorter intervals.

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To assess diurnal variation in activity patterns the daylight period was divided into 1 h intervals. The relative proportions of each hour interval spent on each of the three activity categories was estimated from the four 15 min sampling points within the hour. Thus for example if three sampling points were scored as foraging and one as inactive the animal was assumed to have spent 75 per cent of the hour foraging and 25 per cent inactive. Mean proportions were then calculated for each hour interval within each of the four seasons. The proportions of the total daylight period spent on the three activity categories were derived from the hourly proportions.

Diurnal variation in time allocated to foraging

The pattern of diurnal variation in foraging is shown in Fig. 35 for the wet season and the combined 1976 and 1977 dry seasons. (The sample size in the pre-rain flush was too small to examine diurnal variation.)

In the wet season foraging tended to occur mostly in the cooler early morning and late afternoon periods. The frequency of foraging was lowest from 12h00 to 15h00. The pattern in the dry season was more variable but the period of least frequent foraging was again the early afternoon - 13h00 to 15h00.

Figure 35 suggests that during the dry season most foraging occurred in the late afternoon, whereas during the wet season the period of most frequent foraging was the early morning. However this impression is probably misleading because no data were obtained for the earliest part of the day during the dry season (07h00 to 08h00) and the dusk period in the wet season (18h00 - 19h00).

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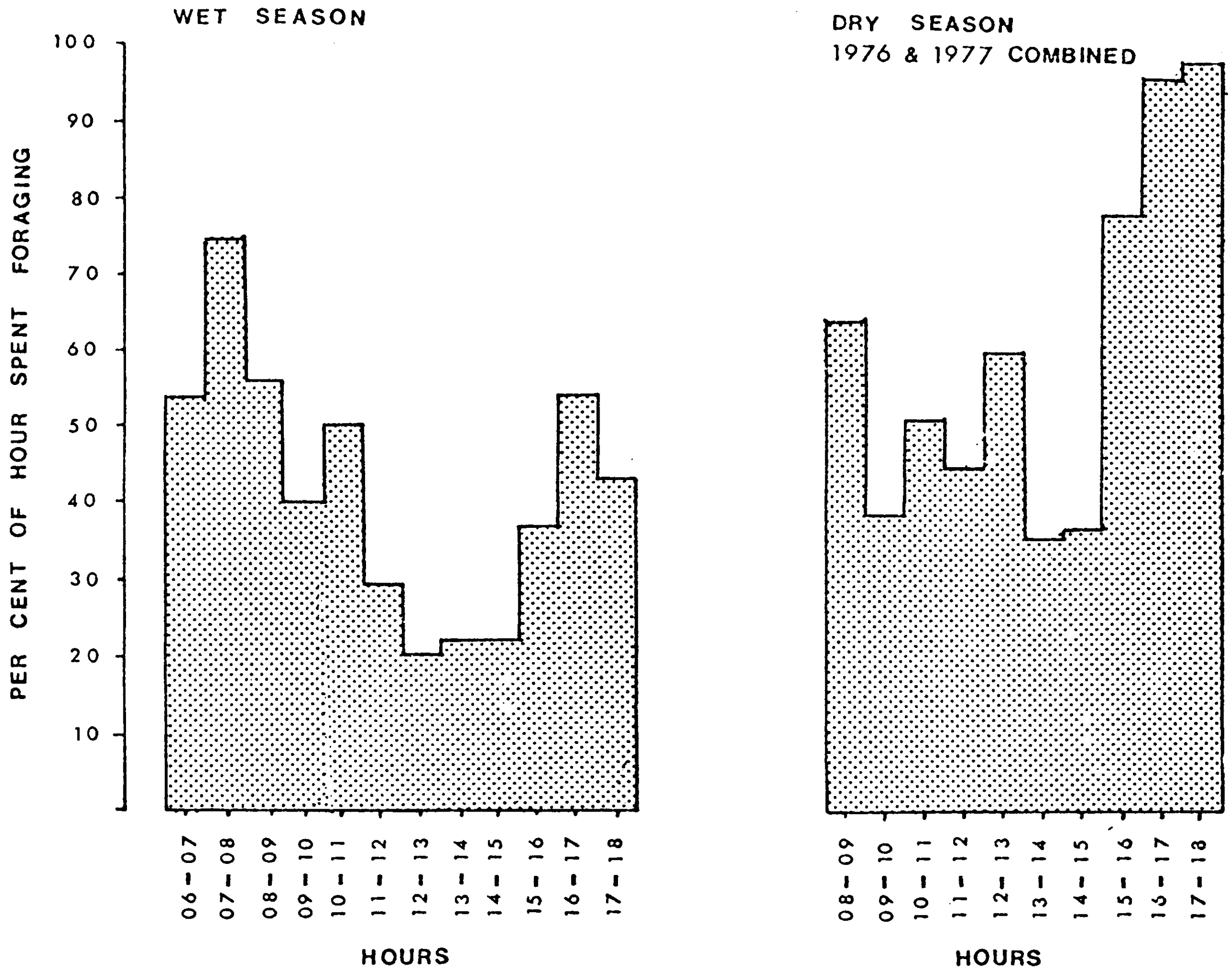

FIG. 35 DIURNAL VARIATION IN THE PROPORTION OF TIME SPENT FORAGING

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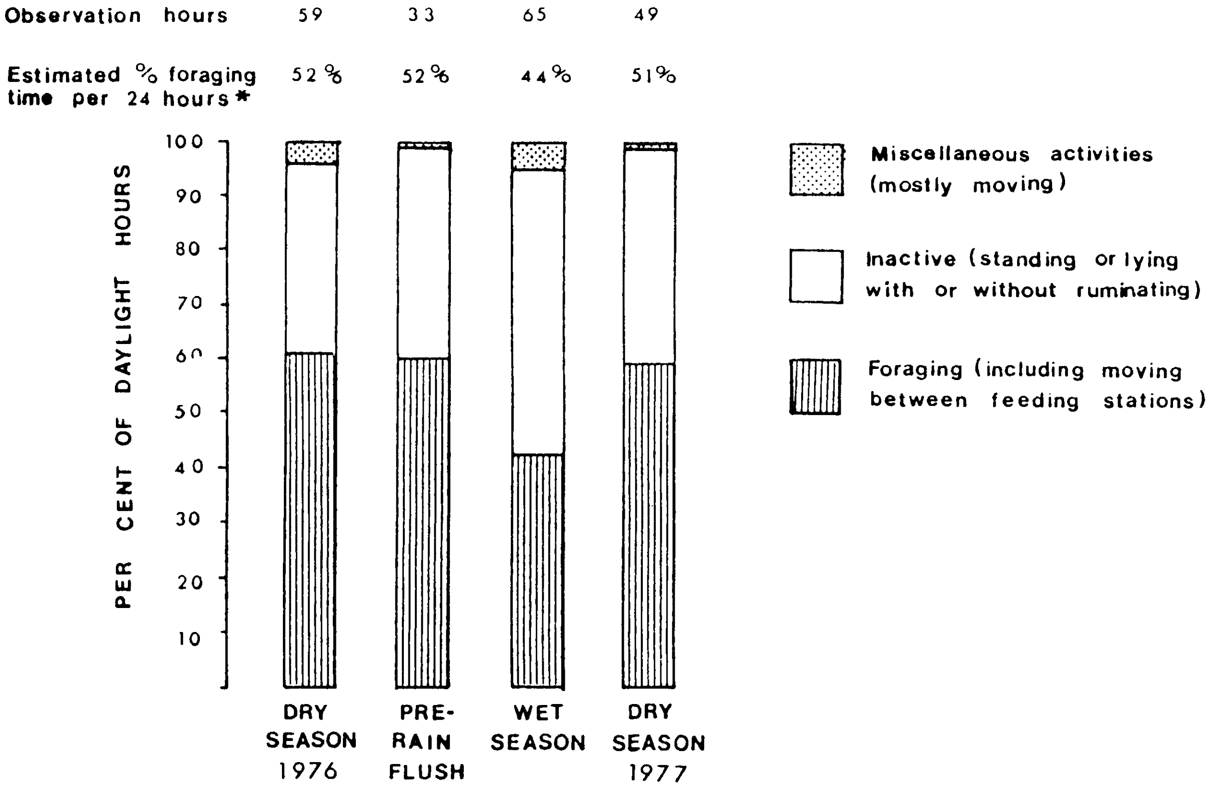
Seasonal changes in activity budgets

The proportion of daylight hours spent foraging varied seasonally, being lower in the wet season than in the pre-rain flush and dry seasons (Fig. 36). This result is in accord with Owen-Smith's (1979) finding that foraging time per day is lowest in the wet season. Reliable data on night activity was more difficult to obtain. Owen-Smith (1979) did two all night watches in the wet season and two in the late dry season. These showed no evidence of seasonal differences and an overall mean of 45 per cent of the night was spent foraging. I was able to complete one all night watch during the wet season of 1977, which also gave a value of 45 per cent foraging. The estimates of foraging time per 24 h in Fig. 36 were derived assuming 45 per cent of the night devoted to foraging with no seasonal variation.

DISCUSSION

Although the magnitude of seasonal variation in the index of accepted food abundance was not as great as that of potential food abundance the general seasonal trend was the same for both measures. However when feeding time per pace is partitioned into woody plant and forb components it is evident that only the latter followed the same seasonal trend as potential food abundance; feeding time per pace on woody plants was highest in the pre-rain flush, the season of lowest potential food abundance. This is in accord with the evidence (Chapter 2) that forbs were preferred, and feeding time spent on woody plants increased only when forbs were scarce.

In general, variations between habitats in accepted food abundance correspond with variations in potential food abundance. The most marked discrepancy between the two measures was on the hill slopes during the dry seasons, where the feeding time per pace spent on woody plants was high in relation to the biomass



* Assuming 45% of the night spent foraging with no seasonal variation

FIG. 36 SEASONAL VARIATION IN THE PROPORTION OF DAYLIGHT HOURS SPENT FORAGING, INACTIVE AND ON MISCELLANEOUS ACTIVITIES

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of woody plant leaves. Data on the seasonal variations in diet composition (Chapter 2) show that in the dry seasons the kudus tended to favour the common woody species on the hill slopes relatively more than woody plants in other regions, thus supporting the evidence that acceptable food abundance was higher on the slopes than elsewhere.

The general correlation between leaf biomass and the index of accepted food abundance shows that the index is sensitive to variations in habitat conditions. This supports the idea that the index would be useful in assessing long term relationships between food availability and the population performance of kudus. However, the index can be employed with confidence only if estimates of variations in the average eating rate are available. This is particularly true in assessing seasonal variations in acceptable food abundance because, as stressed by Dunham (1982), seasonal variations in eating rate can be marked. Monro (1979) found that the weight of food eaten per unit feeding time by impala in the dry season was only 60 per cent of that in the wet season. Thus as food abundance declines from the wet season to the dry the eating rate of kudus is also likely to decline. As a result feeding time per pace would underestimate the true magnitude of variation in accepted food abundance. To determine seasonal changes in the proportion of potential food that is accepted by kudus it would be necessary to estimate the magnitude of seasonal variation in eating rate.

Both this study and that of Owen-Smith (1979) established that the kudus decrease the proportion of foraging time spent on miscellaneous activities in the dry season. This has the effect of compensating for the dry season increase in the proportion of foraging time spent walking, so that the proportion spent feeding varies little between seasons. Feeding time per foraging time, the index of food intake rate, was therefore less sensitive to variations in habitat conditions than was feeding time per pace.

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It was evident from the diurnal variation in time spent foraging that the kudus preferred to forage in the cooler hours of the day and to rest in the early afternoon. Nevertheless throughout the year some foraging took place during the hot midday hours, and the question arises of whether foraging behaviour is modified to cope with the heat load. For example the kudus could move more slowly and pause more frequently during foraging at midday to reduce heat production due to activity. This would amount to sacrificing food intake rate while foraging for the sake of temperature regulation. Diurnal modifications in foraging behaviour could affect the indices of acceptable food abundance and food intake rate while foraging. However there was no significant diurnal variation in feeding station duration, in mean steps per set or in foraging time apportionment, so there seems no reason to suspect any marked temperature effect on these parameters.

The rainfall during this study (651 mm in 1975-76, and 668 mm in 1976-77) was higher than during 1974-75, the years covered by Owen-Smith (1979) (542 mm). Despite this difference in rainfall there was little difference in the foraging parameters. As discussed above the pattern of seasonal variation in the parameters was similar in both studies. The year round averages were also similar. The proportion of foraging time spent feeding was reported as 72 per cent by Owen-Smith (1979) and 75 per cent in this study. Time spent on miscellaneous activities was 11 per cent in Owen-Smith's study and 9 per cent in this one. Sampling procedure for feeding time per unit distance moved (the index of accepted food abundance) differed between the two studies; Owen-Smith (1979) sampled it as feeding time per 50 paces walked, whereas in this study feeding time per pace was derived from mean feeding station duration and mean steps per set. Nevertheless if both are expressed as feeding time per pace the values are close, 5,8 seconds from Owen-Smith (1979) and 5,4 seconds in this study. Feeding time per 24 hours was slightly lower in this study, 50 per cent as opposed to 54 per cent. The small differences between these means are unlikely to be significant, suggesting that habitat conditions

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remained fairly similar over the years covered by the two studies.

Foraging behaviour of kudus compared with that of other antelope

Jarman (1974) postulated that typical group size in African antelope is determined in part by the spatial dispersion of their food. He argued that selective feeders could not associate in such large groups as unselective feeders because the group members would soon become scattered as they foraged for their relatively rare and widely dispersed food items. In most African savannas grass plants are more continuously dispersed than browse plants, and Jarman suggested this as one reason why browsers do not associate in such large groups as do some grazers, such as the wildebeest.

Apart from kudus, patterns of foraging behaviour have been studied quantitatively in blesbok and springbok (Novellie 1978) and impala (Dunham 1982). Kudus are browsers, blesbok are exclusively grazers, while springbok and impala are mixed feeders, accepting both grass and browse. As would be predicted by Jarman's (1974) hypothesis the typical group size of kudus is smaller than those of the other three species.

According to Jarman's hypothesis the average distance between food items should be highest for browsers and lowest for grazers, with the mixed feeders intermediate. The average number of steps per set should thus be highest for the kudus and lowest for the blesbok. Grazers would be expected to have the highest feeding time per foraging time because they need to spend less time moving between food items than browsers or mixed feeders.

The year round averages of the foraging parameters are compared between the four species in Table 36. As predicted, the mean number of steps per set is highest for the kudus and lowest for the blesbok. The mean feeding station duration is much higher

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TABLE 36 : COMPARISON OF FEEDING STATION DURATION, NUMBER OF STEPS PER SET, FEEDING TIME PER PACE WALKED WHILE FORAGING AND FEEDING TIME PER FORAGING TIME BETWEEN FOUR ANTELOPE SPECIES. THE VALUES SHOWN ARE AVERAGED OVER A SEASONAL CYCLE

FORAGING PARAMETER	SPECIES			
	Kudu	Springbok	Impala[×]	Blesbok
Feeding station duration (seconds)	19	6	-	9
Number of steps per set	3,6	3,0	-	1,7
Feeding time per pace (seconds)	5,4	2,0	5,8	5,3
Feeding time per foraging time (per cent)	75	68	83	87

[×] From Dunham 1982

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for the kudus than for the other species. This suggests that on average woody browse plants offer more food per feeding station than grass plants.

Also as expected, the feeding time per foraging time is highest for the blesbok. As already noted by Dunham (1982) feeding time per foraging time for impala is higher than for kudus. However mean feeding time per foraging time is unexpectedly low for the springbok. The mean feeding time per pace differs little between the kudus, impala and blesbok, but is again much lower for the springbok.

Thus because of their short average distance between feeding stations the grazing blesbok are able to feed continuously, taking mostly single steps at comparatively frequent intervals. Unlike the kudus they seldom interrupt feeding to walk between feeding stations and this accounts for their high feeding time per foraging time. The high feeding station duration for the kudus compensates for their high average steps per set, and hence the time they spend feeding per pace does not differ much from the other species. The low feeding time per pace and feeding time per foraging time of the springbok may reflect the fact that the area where they were studied (the sour Transvaal Bankenveld, see Novellie 1978) was unsuitable habitat for springbok.

The differences between these four species in patterns of foraging behaviour are as would be predicted by Jarman's (1974) hypothesis. Similar data on a wider variety of species are needed to further evaluate the hypothesis.

For impala Dunham (1982) noted a four-fold seasonal variation in feeding time per unit distance covered while foraging, with a peak in the wet season and a low point in the dry season. This is slightly greater than the magnitude of seasonal variation in feeding time per pace from the wet season to the dry in kudus (3,6 times). Dunham (1982) also noted only a small decrease from the wet season to the dry in the proportion of foraging time spent feeding by impala. As was the case for kudus this was

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achieved in part by a reduction in the proportion of foraging time devoted to miscellaneous activities in the dry season.

For both impala and kudus the proportion of foraging time spent moving increased from the wet season to the dry (Owen-Smith 1979, Dunham 1982, this study), indicating that time spent searching for acceptable food increases as food becomes scarcer. The opposite tendency was reported in reindeer foraging on tundra by Trudell and White (1981). The reindeer increased the proportion of foraging time spent searching as food abundance increased, evidently feeding more selectively as the abundance of favoured food plants increased.

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CHAPTER FOUR : ESTIMATING NUTRIENT REQUIREMENTS AND NUTRIENT INTAKE

The importance of food as a factor limiting the kudu population could be directly assessed if it were possible to measure nutrient intake rate in relation to nutrient requirements for maintenance and production. Nutrient requirements of African wild ruminants have not been determined, but from published data on domestic ruminants and North American deer (Moen 1973) it is possible to make an approximation of the protein, energy, phosphorus and water requirements of kudus. For comparison with the estimated requirements rough approximations of daily protein, phosphorus and water intakes of kudus are calculated from the data given in the previous chapters. Estimates of energy intake are derived from the values for protein (see below). These estimates are too rough to reliably assess the adequacy of nutrient intake. They are nevertheless useful in identifying shortcomings in the data at present available and in indicating the information that is needed to determine the nutritional status of free-ranging kudus. The exercise is also useful in suggesting which of the nutrients analysed in this study is most likely to be limiting, and the times of the year when limitations are likely to occur.

Nutrient requirements for maintenance, pregnancy and lactation for an adult female kudu are estimated according to Moen's (1973) scheme. The female is assumed to weigh 180 kg, to con= ceive on 1 May (the conception peak is through April-May, Owen-Smith unpublished) and to give birth on 15 January (gestation period 260 days). Observations in this study are in accord with Wilson's (1965) observation that the birth peak for kudu is January to March. The mass of the calf at birth is assumed to be 15 kg (from Wilson 1965). The nutrient requirements of a weaned calf (weighing about 95 kg) in the late dry season are also estimated. Relatively few data were obtained on the foraging behaviour, diet and activity cycle of adult males and so no attempt is made to assess their requirements.

Protein requirements

Protein is required for production (growth of hair, body tissue, foetal tissue and milk production) and for the maintenance of basic life processes. Even if an animal receives a completely nitrogen-free diet a certain quantity of nitrogen appears in the urine and faeces, demonstrating that a proportion of the nitrogen in the excreta is of endogenous rather than dietary origin (McDonald et al. 1973).

The endogenous urinary nitrogen (EUN) is derived from the catabolism of body tissue and is related to the metabolic weight of the animal (Crampton and Harris 1969). Approximately 2 mg nitrogen is excreted in the urine daily for every kcal energy expended for basal metabolism. The EUN can thus be estimated as

$$\frac{2 \times 70\ (W^{0,75})}{1\ 000} \text{ g/day}$$

where W is the weight of the animal in kg (Moen 1973).

The nitrogen of endogenous origin in the faeces, known as metabolic faecal nitrogen (MFN), arises from microbial cells, tissue abraded from the digestive tract, and spent enzymes. MFN is related to the quantity of food eaten, approximately 5 g of nitrogen are excreted per day per kg of dry matter intake by cattle and sheep (ARC 1965). If digestion inhibitors such as phenolics are present within the plant cells they can form irreversible complexes with digestive enzymes, with microbial proteins or with the protein of epithelial cells in the digestive tract, thus markedly increasing MFN (Mould and Robbins

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1981). Since phenolics are more prevalent in browse than grass MFN is likely to be higher for kudus than for grazing cattle and sheep. Because of this the MFN estimate for deer fed on browse diets (7,55 g N/kg dry matter intake) reported by Robbins _et al_. (1974) is used to estimate MFN for kudus rather than the ARC value for cattle and sheep.

The loss of metabolic faecal nitrogen and endogenous urinary nitrogen must be replaced by nitrogen from the diet. Protein requirements for maintenance can thus be estimated as 6,25 (MFN + EUN), assuming that the protein contains 16% nitrogen (Moen 1973).

Protein is also required for the growth of hair and replacement of tissue abraded from the skin surface but this amounts to a very small proportion of total protein requirements (ARC 1965) so for the approximations made here it can be ignored.

The protein requirements for pregnancy and lactation remain to be considered. From data given by the ARC (1965) Moen (1973) derived the following equation for estimating protein requirements for gestation in cattle:

$$Y = e^{(-3,1206 + 0,0298 t)}$$

where Y is the protein requirement for gestation in grams per day, t is the time pregnant in days, and e is the base of natural logarithms.

The formula can be modified to calculate the requirement for pregnancy in a wild ruminant as follows:

$$Qpp = \{e^{-3,1206 + 0,0298 (t/c)}\}/W$$

where Qpp is the quantity of protein required in grams per day per kg of foetus weight at birth, and c is a conversion factor for the gestation period (260/280 = 0,92857 in the case of the kudu). W is the birth weight of the average domestic calf in

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kg (45 kg) (see Moen 1973). The absolute requirement is cal= culated by multiplying the grams per kg foetus weight by the birth weight of the wild ruminant (in the case of the kudu 15 kg).

To establish the protein cost of lactation Moen estimated the protein requirements of the growing offspring and the fraction of those requirements which are met by the mother's milk as opposed to forage. This fraction declines, as the fawn grows, from 100% at birth to zero at weaning. It is assumed that the protein in the milk is sufficient to meet the requirements of the offspring. If the protein content of the milk is known the quantity of milk produced per day to satisfy the offspring can be calculated. The cost to the mother in terms of protein of producing the required quantity of milk can then be estimated from data on lactation in domestic ruminants.

Data required for these estimates include:

(i) the growth rate of the offspring
(ii) the protein requirement of the offspring per unit body weight
(iii) the development of the rumen in the growing offspring (which gives an indication of the percentage of protein requirements that are derived from the milk)
(iv) the protein content of the milk.

For kudu information on these factors is lacking, but some estimates can be made. The birth weight and gestation period of the American elk is similar to that of kudu and so the age-weight relations derived by Murie (1951), quoted by Moen (1973), for female elk are used for kudu calves:

$$W = e^{(2,529 + 0,385 \ln t)}$$

where W is the weight of the calf in kg and t is its age in days.

Moen (1973) estimated that the protein requirements of white-tailed deer fawns range from 3,3 to 6,6 grams of crude protein

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per kg per day during the nursing period. Kudu calves are larger than white tailed deer fawns (which are only 3 kg at birth) and so the protein requirement of kudu calves per unit body weight would be lower. As a rough estimate kudu calves are assumed to require 3 g protein per kg during the nursing period.

On the basis of rumen development in growing white tailed deer Moen derived a linear regression relating the percentage of nutrients met by milk to the weight of the fawn. As noted the percentage declines from 100% at birth to 0% at weaning. From observations in the field it was evident that kudu calves seldom suckled after they were about 4 to 5 months old. Age at weaning is thus assumed to be 150 days (5 months), at which time the calf weighs 85 kg (estimated from the formula for elk given above). A linear regression relating milk dependance to weight in kudu is then:

$$\%MD = 121{,}5 - 1{,}43\ W$$

where %MD is the percentage of nutrients met by milk and W is the weight of the calf in kg (adapted from Moen's formula).

The protein content of kudu milk is assumed to be the same as that of eland (7,6%, Van Zyl and Wehmeyer 1970). The assumed duration of lactation of 5 months is shorter than Simpson's (1968) estimate of 6 months for kudu. The difference does not materially alter conclusions.

The milk production necessary to meet the protein needs of the offspring can be calculated using the equation given by Moen (1973):

$$Qmp = \frac{(W)(MD)(^{Qpf}/_{6,25})}{(0{,}01216)(0{,}85)}$$

where Qmp is grams milk produced per day, W is the weight of the offspring in kg, MD is the fraction of the offspring's protein requirements met by the milk, Qpf is the protein required by the offspring (for kudu 3 g per day per kg), 0,01216 is the nitrogen fraction in eland milk, and 0,85 is the net protein coefficient for milk, 6,25 is the protein : nitrogen ratio for body tissue. As estimated by this formula the milk production increases from birth as the requirements of the growing offspring increases, then reaches a peak and declines as an increasing proportion of requirements are met by forage instead of milk (see Moen 1973). As recommended by Moen the protein requirement for lactation by the mother was estimated by multiplying the nitrogen in the milk by 6,38 to convert it to a protein equivalent and then by 1,3 which represents the protein cost to the mother over the protein in the milk alone.

For calculation of metabolic faecal nitrogen estimates are required of the seasonal variation in dry matter intake. Arman and Hopcraft (1975) reported that eland ingested 2,6 to 3,4% of their body weight of pelleted ration per day. The kudu cow is assumed to eat 3% of her bodyweight in dry matter per day during the wet season, i.e. 5,4 kg. If this quantity is eaten in 8 hours feeding time per day (see Chapter 3) then the mean eating rate is 11 g min^{-1}. On the basis of Monro's (1979) observations on seasonal variation in bite size taken by impala Owen-Smith and Novellie (1982) assumed that the eating rate of kudu in the dry season is 60% of that in the wet season. If this assumption is followed here then the eating rate in the dry season would be 7 g min^{-1}. In the dry season the kudus spent an average of 9,1 hours feeding per day so that at the assumed eating rate of 7 g min^{-1} the dry matter intake would be about 3,7 kg per day.

The eating rate and hence the amount ingested per day in the pre-rain flush is difficult to estimate. For calculation of metabolic faecal nitrogen the kudus are assumed to eat the same quantity per day in the pre-rain flush as in the dry season. In summary then, a 180 kg kudu cow is assumed to eat 5,4 kg per day from December to April and 3,7 kg per day from May to November. There is likely to be a gradual seasonal change in the quantity ingested per day rather than such an abrupt change, but in view of the approximate nature of these estimates refinements are not justified.

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The protein requirements for growth and maintenance of a weaned calf in the late dry season (August) are also estimated. The calf is assumed to be 7 months old and weighing 95 kg (estimated from the elk growth rate equation given above). The dry matter intake of the calf is taken as 2,5% of body weight (2,4 kg). The nitrogen requirement for growth can be estimated as about 2,5% of the gain in body weight per day (ARC 1965). From the elk growth rate equation the calf would be gainingabout 0,18 kg per day. The figure seems reasonable since the average gain per day of wildebeest from birth to one year is about 0,25 kg per day (Berry 1980).

The seasonal cycle in protein requirements of the cow calving in January and the requirements of the weaned calf in August are shown in Table 37. In the late dry seasons, July to September, the cow is in the early stages of pregnancy, and the protein requirement for pregnancy makes up only a small proportion of total requirements. Only in the last two months before parturition, December and January, do the demands of the foetus contribute significantly to total protein requirements. As shown by Moen (1973) the requirements at peak lactation (for the kudu in mid-February) are considerably higher than at the late stage of pregnancy just before parturition. The total protein requirement of the cow is thus at its peak in mid-February, and thereafter declines. The calving season, January to March, is the period of maximum biomass of potential food, so that peak requirements coincide with the peak availability of protein (see Figs. 17 and 18).

Estimating protein intake

The extent to which dietary protein meets requirements can now be estimated. From the data on diet composition (Chapter 2), the protein contents of the various food species (Chapter 1), and

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TABLE 37a : ESTIMATED DAILY PROTEIN REQUIREMENTS OF A 180 KG KUDU COW GIVING BIRTH TO A 15 KG CALF ON 15 JANUARY (GESTATION PERIOD 260 DAYS). THE CALF IS ASSUMED TO BE WEANED IN MID JUNE, WEIGHING 85 KG. REQUIREMENTS ARE ESTIMATED FOR THE 15TH OF EACH MONTH, GIVEN IN GRAMS PROTEIN PER DAY.

Date	Maintenance		Pregnancy		Lactation		
	EUN X 6,25	MFN X 6,25	Days pregnant	Protein	Days Lactating	Protein	Total
15/7	43 g	175 g	76	0,2 g			218 g
15/8	43 g	175 g	107	0,5 g			219 g
15/9	43 g	175 g	137	1,2 g			219 g
15/10	43 g	175 g	168	3,2 g			221 g
15/11	43 g	175 g	198	8,5 g			227 g
15/12	43 g	255 g	229	22,9 g			321 g
15/1	43 g	255 g	Parturition	62,0 g			360 g
15/2	43 g	255 g	-	-	30	121 g	419 g
15/3	43 g	255 g	-	-	61	101 g	399 g
15/4	43 g	255 g	-	-	91	60 g	358 g
15/5	43 g	175 g	-	-	122	25 g	243 g
15/6	43 g	175 g	-	-	152	0	218 g

Assumed daily dry matter intake of cow: December to April 5,4 kg per day
May to November 3,7 kg per day

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TABLE 37b : ESTIMATED DAILY PROTEIN REQUIREMENTS OF A 95 KG WEANED KUDU CALF IN THE LATE DRY SEASON (AUGUST). THE GROWTH RATE IS ASSUMED TO BE 0,18 KG PER DAY

Maintenance		Growth	Total
EUN X 6,25	MFN X 6,25		
27 g	114 g	29 g	170 g

Assumed daily dry matter intake of calf = 2,4 kg

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the presumed daily dry matter intakes given above it is possible to estimate the daily intake of crude protein. In making these estimates it has been assumed that feeding time provides an accurate indication of the relative quantities of the different species in the diet, in other words that there are no differences between the rates at which the various plant species are eaten. The possible effects of variations in eating rates on daily nutrient intake are discussed later. Monthly variations in the daily protein intake are compared with requirements in Fig. 37.

Not all dietary nitrogen is used by the animal, a proportion passes out in the excreta. The true digestibility of nitrogen is generally between 90 and 100%. For white-tailed deer Robbins et al. (1974) report a true digestibility of 94%, i.e. on average 94% of dietary nitrogen is absorbed from the digestive tract and 6% remains undigested, passing out in the faeces.

The percentage of the nitrogen absorbed from the digestive tract that is retained by the animal (i.e. not excreted in the urine) is defined as the biological value (McDonald et al. 1973). The biological value is variable, depending on the level of protein in the diet, the amino acid composition and whether protein is catabolised to provide energy (Crampton and Harris 1969, McDonald et al. 1973). The concentration of protein in the diet that is available to meet the requirements of the animal can be estimated by multiplying the dietary crude protein concentration by the true digestibility and the biological value expressed as fractions (Mould and Robbins 1981).

For the kudus true digestibility of protein is assumed to be 95% and the biological value 70% (as suggested by the ARC, 1965, for rough estimates). These values were used to convert the estimated daily crude protein intake to available dietary protein (Fig. 37).

Fig. 37 indicates that the protein intake of a kudu cow is well in excess of her requirements throughout the year. The surplus

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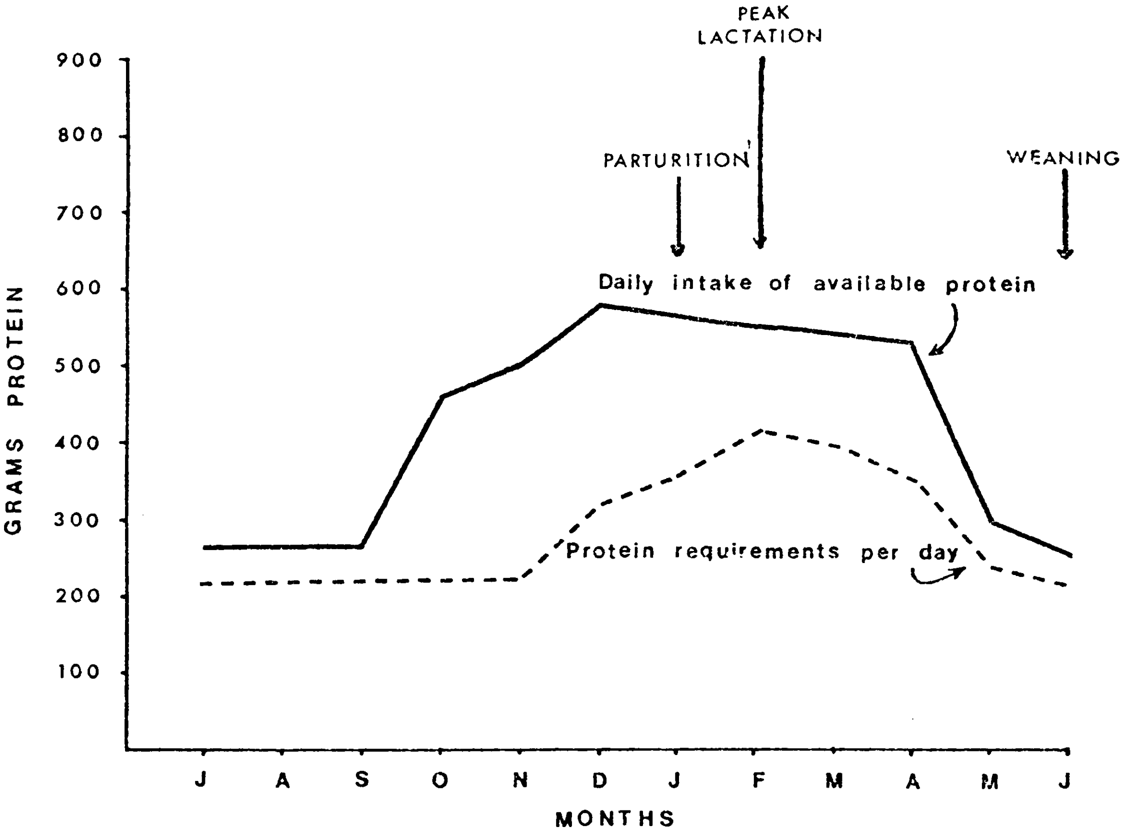

FIG. 37 ESTIMATED INTAKE OF AVAILABLE PROTEIN (CRUDE PROTEIN X TRUE DIGESTIBILITY X BIOLOGICAL VALUE : SEE TEXT) COMPARED WITH PROTEIN REQUIREMENTS FOR A 180 kg KUDU COW CALVING IN JANUARY. REQUIREMENTS ARE FOR MAINTENANCE (ENDOGENOUS URINARY NITROGEN PLUS METABOLIC FAECAL NITROGEN), PREGNANCY AND LACTATION (FROM TABLE 37a)

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is relatively greater in the wet season than the dry. The intake of available dietary protein by a 95 kg weaned calf in the late dry season is estimated to be about 165 g per day. This is close to the estimated daily requirement of 170 g to support a growth rate of 0,18 kg per day (Table 37b). This suggests that protein deficits are more likely to occur in growing calves than adult cows.

Energy requirements

The energy requirements of the kudu cow and growing calf can be estimated in a similar way. The net energy requirement for maintenance is given by the sum of expenditure for basal metabolism and the expenditure for activity. The expenditure for basal metabolism in MJ per day can be estimated from the standard formula of 0,293 times the body mass in kg raised to the power of 0,75. The expenditure for activity was estimated from the daily activity budget (Chapter 3) using the estimates of the energy cost of various activities given by Moen (1973).

As discussed in Chapter 3 a complete record of the 24 h activity budget was not obtained. For the daylight hours activities were categorised as foraging, 'inactive' (which included standing, lying and rumination) and 'miscellaneous activities' (which included mostly moving; little time was spent on social interactions or play). At night it was possible to record the kudu only as being either 'active' or 'inactive'. The following assumptions were therefore made in deriving the energy cost of activity:

(i) Miscellaneous activity includes only moving.

(ii) There is no moving at night, i.e. all 'active' records at night were counted as foraging. This assumption is reasonable because, as reported by Owen-Smith (in press), kudus move very little at night.

(iii) More resting time was spent standing than lying, so standing is assumed to comprise 75% of 'inactive' time and lying 25%. The difference in energy expenditure between standing and lying is not great (Moen 1973) so errors in this assumption would be of little consequence.

The energy expended on rumination has been ignored but this would make up only a small proportion of total expenditure (Graham 1964).

The energy requirement for gestation was estimated using the relationship derived by Moen (1973) from data given by the ARC (1965):

$$\text{Qep} = 0{,}004184 \{e^{(2{,}8935 + 0{,}0174 \frac{t}{c})}\}/45$$

where Qep is the energy required for pregnancy in MJ metabolizable energy per day per kg of foetus weight at term, e is the base of natural logarithms, t is days pregnant and c is the conversion factor to correct for the difference in gestation period between kudu and cattle (0,92857). The absolute energy requirement for kudu is found by multiplying the above equation by the birth mass of the kudu calf (15 kg). This estimates the energy retained by the developing foetus and adnexa but there are likely to be additional costs associated with pregnancy. The basal metabolism is assumed to increase by 20% in the last month of pregnancy (ARC 1965). The extra weight carried by the pregnant cow adds slightly to the cost of activity. The cow is estimated to weigh 190 kg one month before parturition and 200 kg just before parturition.

The procedure and assumptions for estimating energy requirements for lactation are similar to those described for protein above (see Moen 1973). The estimates for percentage dependence on milk and growth rate are as given above. Moen quotes Nordan, Cowan and Wood (1970) as finding that the energy requirements of black tailed deer fawns are about 2,1 times basal metabolism, and the requirements of kudu calves during the nursing period are assumed to be the same.

The quantity of milk produced by the kudu cow to meet the energy requirements of the calf was then calculated from these data using the formula given by Moen (1973):

$$Qmp = \{(2,1)(0,293)(W^{0,75})\}\{(MD)\,{}^{1}/_{Enet}\}/GE$$

where Qmp is milk production in grams per day based on energy requirements of the offspring, W is the mass of the offspring in kg (growing as predicted by the elk-formula), MD is the fraction of the offspring's requirements met by the milk as opposed to forage, Enet is the net energy coefficient of milk (0,8) and GE is the energy in milk. The energy cost to the mother of producing the required quantity of milk can be estimated as 1,6 times the energy contained in the milk (Moen 1973). As noted, the calf is estimated to be weaned at five months old at a weight of 85 kg. The change in milk production from birth to weaning is thus similar to that described above for protein. The energy in the milk is estimated as 6,4 kJ g^{-1}, assuming that the composition of kudu milk is the same as that of eland (Van Zyl and Wehmeyer 1970). The energy value of the milk was derived from the formula : energy kJ = 0,3817 (% fat) + 0,2455 (% protein) + 0,1655 (% lactose) (from Sadleir 1980).

The estimated energy expenditure for maintenance is shown in Table 38. Adult kudu cows spend very little time on the more strenuous activities such as running and playing, and the activity which accounts for much the greatest part of energy expenditure is foraging. Year round the energy expenditure for maintenance averages just over 1,4 times the basal metabolism. Because of the seasonal variation in the activity budget energy expenditure for activity varies seasonally, expenditure is lower in the wet season than in spring or the dry season. However the magnitude of the seasonal difference is not great. Although

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TABLE 38 : ESTIMATES OF THE ENERGY COSTS OF MAINTENANCE (BASAL METABOLISM PLUS ACTIVITY) FOR A 180 KG KUDU COW. THE ENERGY EXPENDITURE ON EACH ACTIVITY IS GIVEN IN MJ ABOVE BASAL METABOLISM, ESTIMATED FROM DATA PRESENTED BY MOEN (1973)

Activity	Dry Season (1976 & 1977 combined)		Pre-rain Flush		Wet Season	
	Hours per day	Energy MJ per day	Hours per day	Energy MJ per day	Hours per day	Energy MJ per day
Basal metabolism	24	14,4	24	14,4	24	14,4
Foraging	12,5	5,1	12,5	5,1	10,6	4,3
Standing	8,2	0,5	8,3	0,5	9,2	0,6
Lying	2,7	0	2,8	0	3,0	0
Walking*	0,6	0,4	0,5	0,3	1,2	0,8
Total daily energy for maintenance		20,4		20,3		20,1
Total as a multiple of basal		1,42		1,41		1,39

*All walking is assumed to be on level ground at a speed of 2km h^{-1}

foraging time per day decreased from the dry season to the wet more time was spent walking in the wet season. This is partly the reason for the lack of marked difference between the seasons in energy expenditure, but even if walking is disregarded seasonal differences are not great.

The energy intake per day will be estimated in terms of metabo= lizable energy, and so requirements must be expressed in the same way. The requirements in Table 38 are for net energy (metabolizable energy minus the heat increment, Crampton and Harris 1969). According to the ARC (1965) the efficiency of utilization of metabolizable energy for maintenance and mus= cular work is about 68% for good all-roughage rations with an energy content of about 8,4 MJ per kg. The energy expenditure for maintenance was therefore converted to requirements for metabolizable energy assuming an efficiency of utilization of 70%. For roughage diets the efficiency of utilization of meta= bolizable energy for lactation is about 66% (ARC 1965), so this value was used here to convert net energy requirements for lac= tation (calculated from the formula given above) to metaboliza= ble energy. For pregnancy the above formula derived by Moen gives requirements in terms of metabolizable energy (assuming an efficiency of utilization of 40%, see ARC 1965) so no adjust= ment is necessary. Seasonal changes in requirements for metabo= lizable energy of the 180 kg cow calving in January are shown in Table 39. The pattern of seasonal variation is the same as described for protein, with highest requirements occurring in February at peak lactation.

Estimating energy intake

A gross energy determination of a forage gives no indication of its nutritional value because a large part of the energy measured is obtained by oxidising compounds which cannot be digested or metabolized by the animal. Direct determination of metabolizable

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TABLE 39 : ESTIMATED REQUIREMENTS IN MJ DAY^{-1} FOR METABOLIZABLE ENERGY FOR A 180 KG KUDU COW CALVING ON 15 JANUARY

	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June
Maintenance (Basal Metabolism & Activity)	29,2	29,2	29,2	29,2	29,1	33,0*	33,4+	28,7	28,7	28,7	29,2	29,2
Pregnancy	0,1	0,2	0,3	0,6	1,0	1,8	3,3	-	-	-	-	-
Lactation	-	-	-	-	-	-	-	18.7	13,2	5,4	4,3	-
Total	29,3	29,4	29,5	29,7	30,1	34,8	36,7	47,4	41,9	34,1	33,5	29,2

*Basal metabolism assumed to increase by 20% in last month of pregnancy. Mass of cow in December assumed ot be 190 kg.

+Mass of cow just before parturition assumed to be 200 kg.

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or net energy through trials is time consuming and costly, and therefore attempts have been made to derive predictive equations relating energy values of forages to the concentrations of various chemical components (Stallcup et al. 1976). The latter study tested the accuracy of predictive equations for a number of feeds. No regressions were found which would be of value in predicting the energy contents of forages in general - different kinds of forages require separate equations.

Since there is a general correlation between the energy value of a forage and its crude protein content it is reasonable to derive a predictive equation relating the two nutrients. Crampton and Harris (1969) give tables showing the nutrient contents of lucerne, Medicago sativa, at different stages in the growth cycle. The following regression was derived from the data in these tables (see Fig. 38):

$$Y = 9{,}025 + 0{,}092X, \ R^2 = 0{,}42$$

where X is the per cent crude protein and Y is the digestible energy content in MJ kg^{-1} dry matter. This equation derived from lucerne data is used in preference to others reported in the literature (e.g. Stallcup et al. 1976, Anon. 1975) because it is more likely to reflect the protein: energy ratio of browse than would an equation derived for other forages. Using this regression the digestible energy content of the diet was estimated from the protein content. The metabolizable energy content was estimated as 0,82 times the digestible energy content (Crampton and Harris 1969).

The daily intake of metabolizable energy was then estimated for the 180 kg kudu cow, assuming that daily intake of dry matter was the same as discussed above for protein requirements. Intake of metabolizable energy is the same as or slightly higher than requirements in the dry season and at peak lactation in February (Fig. 39). For the remainder of the year estimated intake is considerably higher than requirements.

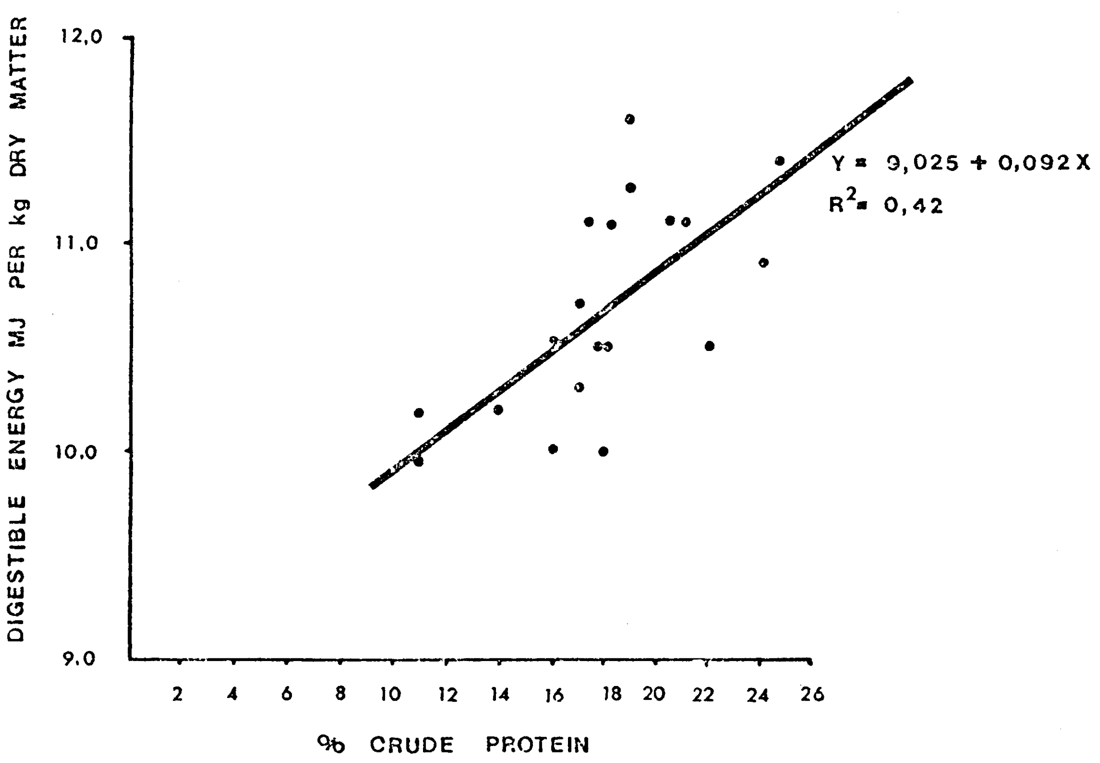

FIG. 38 REGRESSION RELATING CRUDE PROTEIN CONTENT TO DIGESTIBLE ENERGY IN LUCERNE (MEDICAGO SATIVA), FROM DATA GIVEN BY CRAMPTON AND HARRIS (1969).

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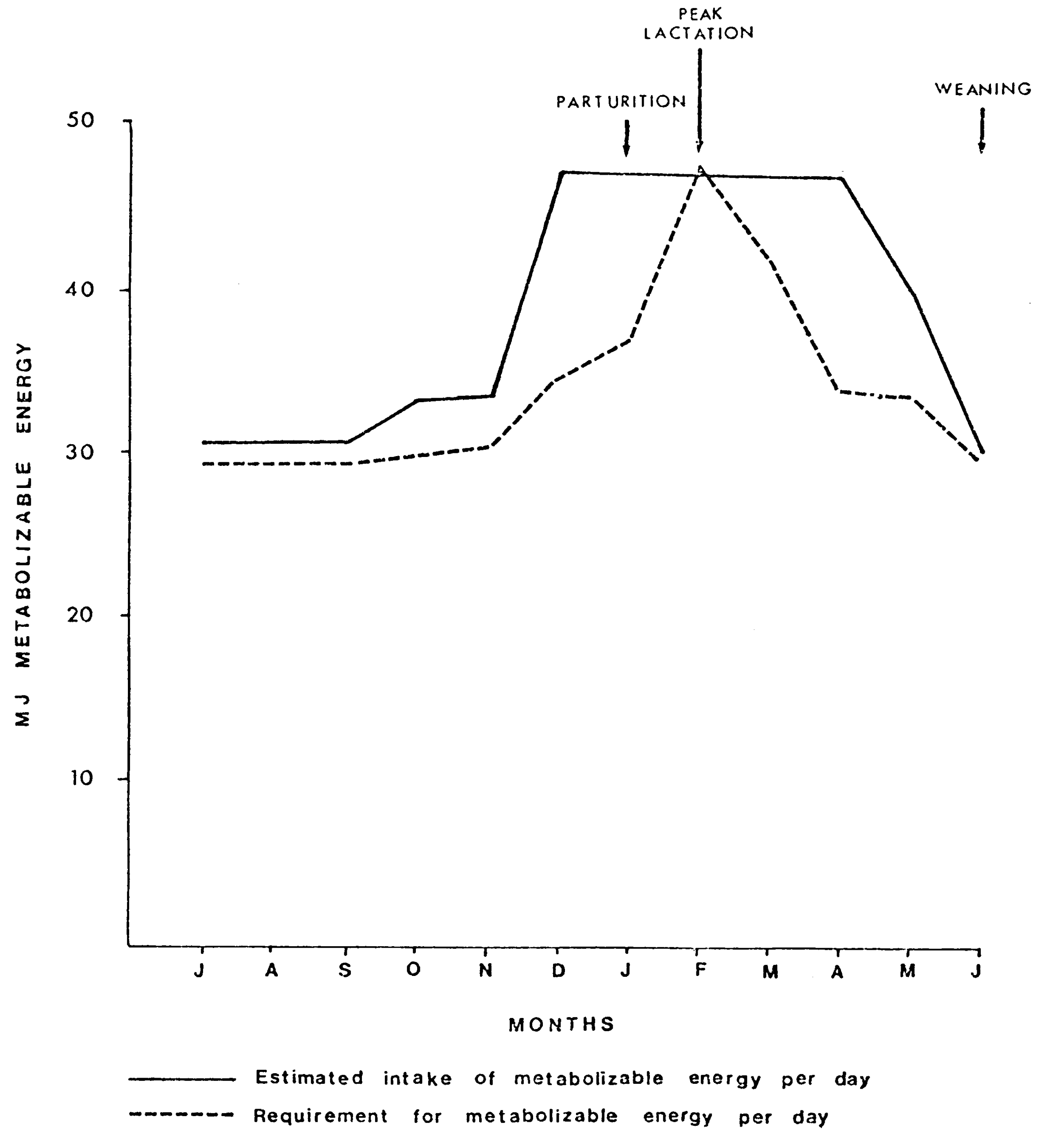

FIG. 39 ESTIMATED DAILY INTAKE OF METABOLIZABLE ENERGY COMPARED WITH TOTAL DAILY REQUIREMENTS FOR A 180 kg KUDU COW CALVING IN JANUARY. REQUIREMENTS ARE FOR MAINTENANCE (BASAL METABOLISM PLUS ACTIVITY), PREGNANCY AND LACTATION

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For the 95 kg weaned kudu calf growing at 0,18 kg per day in the late dry season requirements for maintenance are estimated at 17,4 MJ metabolizable energy per day. The energy value for gain in young growing cattle is 14,7 MJ per kg and the effi= ciency of utilization of metabolizable energy for gain is about 40% (ARC 1965). For the kudu calf requirements for the daily gain in terms of metabolizable energy can then be estimated as 6,6 MJ, and the total requirement is then 24,0 MJ per day. If the calf eats 2,5 per cent of its body weight in dry matter per day then the estimated intake of metabolizable energy is 19,9 MJ which is less than requirements for growth but sufficient for maintenance.

Phosphorus requirements

From tables given by Crampton and Harris (1969) the ratios of daily phosphorus to protein requirements for domestic cattle were calculated for:

(i) non-reproductive adult cows
(ii) pregnant cows
(iii) lactating cows, and
(iv) growing calves.

Using these ratios the daily requirements of kudus for phosphorus were derived from the estimated requirements for protein dis= cussed above. Phosphorus requirements for the cow calving in January and the growing calf in the late dry season are shown in Table 40.

Daily intake of phosphorus was estimated from the phosphorus contents of the food plants (Chapter 1) and the diet composition in the same way as described above for protein intake. Phos= phorus intake and requirements are compared in Table 40. Intake is in most cases in excess of requirements, except for the cow at peak lactation. Low dietary intake of phosphorus is sometimes associated with low milk yield in dairy cows (ARC 1965).

TABLE 40 : ESTIMATED PHOSPHORUS REQUIREMENTS COMPARED WITH PHOSPHORUS INTAKE FOR A 180 KG KUDU COW CALVING IN JANUARY, AND A 95 KG WEANED KUDU CALF

	Phosphorus Requirements g/day	Phosphorus Intake g/day
Cow August (107 days pregnant)	7	10
Cow January (parturition)	10	16
Cow February (peak lactation)	17	16
Calf August	5	7

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However this does not necessarily imply that the apparently low phosphorus intake of the lactating kudu cow would limit milk production. Particularly during lactation domestic ruminants liberate phosphorus and calcium from the bones. Since phosphorus intake is evidently adequate for the kudu cow over most of the year phosphorus in the bones could be mobilized to meet the extra requirements at peak lactation.

Pope (1971) recommended a minimum dietary concentration of 0,16 per cent phosphorus for sheep. It is noteworthy that the leaf phosphorus contents of all woody species analysed, except Securinega virosa, declined below this value at some time during the year (Table 17). However the phosphorus contents of forb leaves were much higher than most woody plants, seldom declining below 0,2 per cent of dry matter at any time of the year (Fig. 12).

Calcium requirements

The calcium content of browse is generally higher than that of grass, and the calcium : phosphorus ratio tends to be higher for browse than for grass (Roth and Osterberg 1971, Dougall et al. 1964). Louw (1969) suggested that a calcium content of about 0,22 - 0,46% is adequate for optimal production of domestic livestock. The calcium contents of browse plants analysed in this study are all very much higher than this (1,3 - 3,8% see Table 19) so a deficiency of calcium for kudus seems very un= likely. It is interesting that the calcium : phosphorus ratio of browse is very much higher than the values of 1:1 to 2:1 generally recommended for domestic livestock (Table 19). However evidence suggests that domestic ruminants can tolerate much higher ratios than those usually recommended (Du Toit et al. 1940, McDonald et al. 1973).

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Water requirements

Taylor (1968) estimated the minimum total water requirements (including metabolic water) of eland to be 3,74% of body weight at a constant environmental temperature of 22°C, and 5,48% with 12 h at 22°C and 12 h at 40°C. These values are assumed to hold for kudu. The metabolic water obtained by a 180 kg kudu cow can be estimated roughly as 1 litre (from Taylor's (1969) data on eland), and this is subtracted from the total requirement to give required daily intake of drinking water plus preformed water from the food. The water requirements of a 180 kg cow are shown in Table 41. The wet season values in Table 41 include an estimate of extra water required at peak lactation. Assuming that the energy content of kudu milk is the same as that of eland (see above) about 1,2 litres of milk would be required at peak lactation to meet the daily energy requirements of the calf. According to the ARC (1965) 0,87 litres of water are required per litre of milk produced, so that the water requirement at peak lactation would be 1,04 litres.

The intake of water from the food was estimated from the moisture contents of the various food species (Chapter 1). The assumed quantity of food ingested in each season is as described above under protein requirements. As a result of the greater heat load and the demands for lactation water requirements are much higher in the wet season than in the dry season. In spite of this, however, the water obtained from the diet appears adequate to meet requirements in wet season, and probably also in the pre-rain flush, but not in the dry season (Table 41). This result suggests that the kudus would have no need for surface water except during the dry season.

It was evident in the field that kudus could go for several days without drinking; even in the dry season cow groups were sometimes contacted on up to four consecutive days, during which time they remained away from surface water. They did make occasional trips to the Nwaswitsontso River to drink in the dry season but the exact frequency of this is unknown. In summer they were observed

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TABLE 41 : ESTIMATED WATER REQUIREMENTS OF A 180 KG KUDU COW COMPARED WITH WATER OBTAINED FROM THE FOOD

SEASON	Estimated Requirement ℓ/day	ℓ/day Obtained from food
Dry Season	5,7*	4,3
Pre-rain Flush	5,7* - 8,9^{+}	8,4
Wet Season	8,9^{+} - 9,9^{x}	13,5

Estimated requirements of the kudu cow are assumed to be the same as for eland (Taylor 1968).

*Estimated assuming a constant temperature of 22°C

$^{+}$Estimated assuming 12 hours at 40°C and 12 hours at 22°C

^{x}As above but including water requirements for milk production at peak lactation

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drinking from pools of rainwater or from pools in the Nkongwana drainage line. The high intake of water from the food in summer is largely due to the high proportion of forbs in the diet; the average moisture content of forb leaves in the wet season was 76%, considerably higher than that of woody plant leaves.

It seems that the kudus could be independent of surface water in the wet season and would drink only if water is readily available. Unless they specifically select food with a higher water content than the 'average' values measured (see Chapter 1) it would seem that surface water is obligatory in the dry season.

DISCUSSION : NUTRIENT REQUIREMENTS IN RELATION TO INTAKE

The preceding results indicate no serious deficiency of protein, phosphorus or energy for adult female kudus at any stage during the study period. In the dry season the water content of the diet appears insufficient to meet the total requirement for water but the deficit could be easily made up by drinking surface water. Relatively low energy intake may restrict the growth rate of weaned calves in the late dry season to below their physiological maximum. However the estimated energy intake of the weaned calves in the dry season is in excess of their maintenance requirement, and more abundant food the following wet season would allow growth to be made up. Thus the growth rate of the calves in the late dry season would be at most temporarily retarded. The kudu population was increasing during the study period and preceding years (Owen-Smith 1979), which shows that conditions were favourable. The above indication that nutrient requirements were relatively easily met is in accord with this. However even in the favourable years the kudus in the study area lost condition and became thinner in the late dry season (Owen-Smith pers. comm., personal observation), especially the older animals. This suggests that the above calculations have overestimated nutrient intakes.

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The estimated daily nutrient intakes contain numerous potential sources of error, possibly the most serious being that eating rates, and hence daily dry matter intake, could not be measured. It is therefore possible that the daily quantities of food eaten were overestimated. There are also reasons for believing that the concentrations of usable nutrients in the diet were overestimated. In calculating the dietary nutrient contents it was assumed that the kudus eat only leaves, whereas in fact they accept an unknown proportion of shoot ends with the leaves. Shoot ends are usually more lignified than the leaves and their nutrient contents would be lower. Also the foliage of the unarmed woody species can probably be eaten faster by kudus than that of the armed species. The unarmed species would then comprise a relatively greater fraction of the diet than indicated by the proportion of feeding time spent on them. Since the unarmed species averaged lower in protein content than armed species (Chapter 2) the error would lead to an overestimate of dietary nutrient content. Thirdly the digestibility reducing effect of plant secondary compounds have not been considered. Mention has been made of the fact the phenolics can increase the loss of endogenous nitrogen in the faeces by forming complexes with digestive enzymes, protein from the digestive tract and microbial protein. These compounds also complex with dietary proteins thus reducing the digestible fraction of ingested protein (Cates and Rhoades 1977).

The estimated energy intake by kudus is relatively closer to requirements than is the case for protein and phosphorus. This is in accord with Owen-Smith's (in press) observation that because of the high protein content of browse it seems unlikely that browsers would fail to achieve sufficient protein intake, and energy is more likely to be the major limiting nutrient. The intake of protein seems greatly in excess of requirements but, as noted, this depends on the digestibility reducing effect of plant secondary compounds.

The above estimates indicate two seasons when adult female kudus could experience nutrient deficiencies under conditions of food scarcity. Firstly the estimated energy intake is closest to the maintenance requirement of the female in the late dry season, apparently even under the good conditions which prevailed during the study period. The second critical period occurs at the time of peak lactation in the mid-wet season, when requirements for energy and phosphorus are again close to estimated intake.

It has so far been implied that there is a specific quantity of milk required for the growth and maintenance of the calf. More accurately the fitness of the calf is dependent on the quantity and quality of the milk it receives, and even a small reduction in the nutrient intake of the calf could influence its growth rate and vulnerability to predators and parasites. Owen-Smith's (unpublished) records do in fact suggest a relationship between food availability and calf survival in kudus. There were consistent increases in the population each year from 1974 to 1978 but in 1979, after the first year of below average rainfall, the population declined by about 10%. This was associated with a drop in calf survival from 52-85% over previous years to 25%.

However whether or not the cow experiences critical nutrient deficiencies during the periods of peak lactation or the late dry season depends on the extent to which nutrients could be stored during those seasons when intake exceeds requirements. When the diet is insufficient tissue can be catabolized to provide protein, phosphorus can be liberated from the skeleton, and fat reserves can provide energy. Critical nutrient deficits would only occur if overall conditions deteriorated to the extent that accumulated reserves in favourable seasons were insufficient to cover the deficits in the unfavourable seasons. The energy intake of the kudu cow over the early wet season appears to considerably exceed requirements and it is possible that she could accumulate fat reserves over this period to be used at peak lactation.

Signs of weight loss by the kudus were noted only in August and early September. As discussed in Chapter 1 some woody plants begin leaf production in mid-September irrespective of whether rain arrives. The approximations made above suggest that even if total daily food intake is assumed to remain the same in the pre-rain flush as in the late dry season the nutrient content of the flushing leaves is so high that intake seems greatly in excess of requirements for all nutrients analysed. Despite the late arrival of the rain in both study years no mortality occurred, and the pre-rain flush was sufficient to carry the population from the middle of September to November. The start of the pre-rain flush thus seems likely to mean the end of the critical period of inadequate energy intake. A combination of circumstances that might cause mortality among adult kudus is delayed rain together with a reduced or retarded pre-rain flush. The abundance of the pre-rain flush is likely to depend on the quantity of reserves of moisture and nutrients sorted by the woody plants during previous seasons, and a number of successive dry years might lead to depletion of these reserves.

In summary, the preceding estimates permit only a tentative conclusion that the intake of protein, energy and phosphorus by kudus during the study period was sufficient to meet their requirements. Data needed for more reliable assessment of the nutritional status of the kudus can now be considered.

Estimation of the nutrient requirements of kudus from data on cervids and domestic bovids is unsatisfactory because digestive and metabolic capabilities can vary between species (Mould and Robbins 1981, 1982). Extrapolation from one species to another adapted to a widely different environment could be misleading. More information is needed on the nutrient requirements of African wild ruminants, the following aspects in particular deserving attention:

(i) Maintenance requirements of adults for energy, protein, phosphorus and other nutrients.

(ii) Nutrient requirements of females during pregnancy - the relationships between female nutrition during pregnancy and the survival chances of her offspring (see Thorne, Dean and Hepworth 1976, Robbins and Moen 1975a).

(iii) Nutrient requirements for growth in young animals - the change in the relative contribution of milk as opposed to forage to meeting the calf's requirements from birth to weaning (Robbins and Moen 1975b).

(iv) The nutrient cost to the female of producing the required quantity of milk.

(v) Nutrient costs of parasite infestation - the relationship between nutrient intake and the capacity of the animal to maintain immunity towards pathogens.

As already indicated an important difficulty experienced in the present study was that the average rate at which the kudus ingest each dietary component could not be measured. Estimates of dry weight eaten per unit feeding time are necessary to convert feeding time spent on each food type to dry weight eaten, and to calculate daily dry matter intake from the total daily feeding time. Another difficulty was that observation distances were too great to determine selection among plant species growing in the herb layer or to estimate the relative contribution of different plant parts to the diet. The average leaf nutrient contents of forbs and woody plants used in estimating nutrient intake provide only a rough indication of diet quality and, as discussed above, are likely to overestimate the actual nutrient concentration of the diet.

These difficulties can only be overcome by studying food selection in tamed kudus. If the animals were sufficiently tame to allow frequent handling the most accurate results could be obtained by means of oesophageal fistulation, which would allow measurement to eating rate (Trudell and White 1981), and analysis of the nutrient content of the ingested material. Alternatively eating rates of the tame animals could be estimated by counting the rate of bites and duplicating by hand the amount of the different vegetation components taken per bite (e.g. Deschamps, Urness and Austin 1979, Pellew in prep.). The relative quantities of shoots and leaves accepted could also be determined in this way. The nutrient content of the ingested food could be estimated by hand collecting vegetation components in the same proportions as they occur in the animals' diet and subjecting this simulated diet to analysis for chemical composition (Pellew in prep.). Another approach could be to analyse the nutrient contents of indivudual food types and to calculate overall nutrient content of the diet according to the relative proportion of each type in the diet.

A potential problem in using tamed animals is that food habits depend partly on experience and learning (Leuthold 1971, Frost 1981) and food selection by hand-reared animals may differ from wild ones. Comparisons of food selection between tamed and wild animals would be necessary to assess the reliability of the method.

In addition, information is required on the fraction of ingested nutrients that are physiologically available to meet the animals' requirements, as well as the rate of digestive assimilation of the available nutrients. Of particular importance is the extent to which nutrients are rendered unavailable to the animal by plant defensive chemicals. The digestibility and energy content of the diet can be determined by conventional in vivo digestion trials, but these are expensive and require impractically large quantities of forage (Palmer and Cowan 1980). Digestibility and energy content are therefore frequently predicted from equations developed by comparison of food chemical composition and in vivo digestibility (e.g. Stallcup et al. 1976) or alternatively derived from in vitro trials provided relationships between in vivo and in vitro digestibilities is known (Palmer and Cowan 1980, Mould and Robbins 1982).

Nutrient requirements need not be met entirely by dietary nutrients; as indicated above stored reserves can make an important contribution in unfavourable seasons. For assessment of year-round nutritional status it would be necessary to estimate the animals' capacity to accumulate reserves in favourable seasons, and also

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the extent to which these are used to meet requirements in unfavourable seasons.

A considerable number of factors need to be measured in order to estimate nutrient intake in relation to requirements. Never=theless methods of obtaining these measurements need to be developed and refined, since this is important for determining the likely effect of food as a factor limiting wild ungulate populations, and also for nutrition-based estimates of carrying capacity (Moen 1973). Moen's basic framework for modeling carrying capacity involves relating the nutrient requirements of the animals to the supply of nutrients available in the habitat. Two studies have used the considerable information on nutrient requirements of cervids to calculate carrying capacities accor=ding to this model (Wallmo, Carpenter, Regelin, Gill and Baker 1977; Hobbs, Baker, Ellis, Swift and Green 1982). Hobbs *et al*. (1982) showed that relatively small errors in estimation of nutrient requirements or the quantity of nutrients available in the habitat can result in large variations in estimates of carrying capacity. Clearly a close understanding of the interrelationships between habitat characteristics, nutrient intake rates, and animal fit=ness is required before meaningful estimates of carrying capacity are possible.

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CONCLUSIONS

The aim of the present study was to investigate aspects of the feeding ecology of kudus that might have a bearing on their population performance. If the measurements assessed in this study can in fact provide a sensitive reflection of the quantity and quality of available food, they could be used to monitor long-term changes in the nutritional status of the kudu population. Such monitoring may eventually be useful for determining the levels of food availability at which the kudu population is likely to decline. It remains, finally, to evaluate the potential usefulness of the estimates of abundance and nutritional value of potential food, and the index of accepted food abundance.

The sensitivity of the indices of accepted food abundance and food intake rate while foraging was evaluated by comparing them with seasonal and between-habitat variations in potential food abundance. The results confirmed Owen-Smith's (1979) finding that the index of food intake rate while foraging did not closely reflect seasonal variations in food abundance. On the whole the index of accepted food abundance and the estimates of potential food abundance showed similar patterns of variation between seasons and habitat subdivisions, but two major discrepancies between them were noted. The first was that the magnitude of seasonal variation in the index of accepted food abundance was less than that of potential food abundance, which suggests that the kudus accepted a greater fraction of potential food in the dry season than in the wet season. This indication was supported by observations on diet composition: There were some woody species that were accepted in the dry seasons but rejected in the wet season (Chapter 3). The tendency to expand the diet when the abundance of favoured food types declines is in accord with the predictions of optimal foraging models (see Owen-Smith and Novellie 1982).

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But, as discussed in Chapter 3, the index probably underestimated seasonal variations in dry weight of food accepted per unit distance moved while foraging because of the likely decline in eating rate from the wet season to the dry. Thus estimates of eating rates are required before the true seasonal variation in the fraction of potential food that is accepted could be determined.

The second major discrepancy between the index of accepted food abundance and potential food abundance was observed in both dry seasons of the study period when comparing the hill slope and pediment. The index of accepted food abundance showed higher values for the slopes than the pediment whereas potential food abundance did not differ between the two habitat subdivisions. The difference was evidently due to the higher acceptance of the woody plants on the slopes than those on the pediment. Again this was supported by the observations on food selection: During the dry seasons the kudus favoured the dominant woody species on the slopes (Combretum apiculatum) to a much greater extent than the dominant species on the pediment.

The mid-summer fire offered the opportunity to compare potential and accepted food abundance between burnt and unburnt regions. The fire caused the kudus to leave the burnt areas, but they returned within three months once the vegetation had recovered. After their return there were no marked differences between burnt and unburnt regions in either potential or accepted food abundance that could be attributed to the fire. However, the forb leaves which grew on the burn after the fire had a lower average nutrient content than the unburnt forb leaves, a difference possibly caused by the fire. This difference in forb nutrient content may have been the reason why the acceptance of forbs on the burnt regions by kudus was slightly lower than that of the unburnt regions.

Thus the index of accepted food abundance generally corresponded with estimates of potential food abundance, but where discrepancies between the two occurred supporting evidence indicated that these were due at least in part to differences in the fraction of potential food that was accepted. Therefore although the index may have been distorted by variations in eating rate it was successful in detecting the main seasonal and between-habitat differences in accepted food abundance. There is reason for confidence then, that the index could be used to monitor long-term changes in food abundance as experienced by the kudus. However because the eating rate is likely to decrease with declining food availability the index may underestimate the true magnitude of a decline in food abundance, such as might occur under drought conditions. The reliability of the index would therefore be increased if it were accompanied by measurements of eating rates.

The index of accepted food abundance alone gives no indication of the nutritional value of the diet. As discussed in Chapter 4, the average nutritional value of potential food does not provide a reliable measure of dietary nutrient content, but it can serve as a general index of food quality. The estimates of potential food abundance and leaf nutrient contents made in the present study provide a reflection of habitat conditions during the favourable period of the late 1970's when the kudu population was expanding. Comparison with future data obtained during a population decline phase could reveal the extent to which population changes are associated with habitat changes.

An important aspect of the study was the identification of staple and favoured dietary components, because the abundance of these is likely to have a more important effect on kudu population dynamics than total potential food abundance. Favoured and avoided woody species were identified (Chapter 2), but further observations are needed to determine the most important food plants in the herb layer.

A feature of the diet composition of kudus at the Nwamuriwa study area was the predictable seasonal change, certain plant species regularly increased in prominence in the diet during specific seasons. In part this seasonal change was related to the differences among the various plant species in phenology. There were differences among woody species in the time of commencement of leaf production in the early growing season, and also in the extent of leaf loss in the dry season. This meant that the relative differences between woody species in leaf abundance and nutritional value varied over the seasonal cycle according to a fairly consistent pattern. Thus the early flushing woody species such as Acacia nigrescens, and Combretum hereroense offered high quality food when little else was available, and therefore comprised a large proportion of the kudus' diet in the early growing season (September to November). Later flushing species such as Securinega virosa and Dichrostachys cinerea tended to increase in importance in the diet later in the season (December to March). The seasonal differences in the relative contribution of forbs and woody plants to the diet was also rela=ted to the difference between them in phenology: The low accep=tance of forbs in the early growing season was the result of their tendency to flush later than the woody plants.

On the other hand the variation over the seasons in the relative contribution of armed and unarmed woody species to the diet could not be traced to variations in relative nutrient content or abun=dance. Armed species averaged higher in leaf protein content than unarmed species throughout the year. There was no general diffe=rence between armed and unarmed species in the magnitude of sea=sonal variation in leaf abundance, so that the relative quanti=ties of each available to the kudus did not vary much between seasons. Thus neither nutrient content nor relative availability could account for the dry season increase in the contribution of unarmed species to the diet. Although other explanations of the change in diet are possible the hypothesis that the inhibiting effect of thorns is relatively greater in the dry season than the wet seems the most plausible. The influence of the thorns would also account for the observation that the selectivity ratings of the various food species were significantly correlated with their nutrient contents in the wet season (when the high quality unarmed species were preferred) but not in the dry season (when the lower quality unarmed species were favoured). To test this hypothesis observations are required on the effects of structural defences on the rate at which browse can be harvested by kudus, as well as the way in which this is modified by changes in shoot age and leaf density.

The methods used in this study had certain limitations and the following refinements could be introduced in future studies:

(i) Improved estimates of woody plant leaf biomass. The frame method used to determine leaf weight per unit canopy volume yeilded overestimates for some species. Detection and correction of the bias proved laborious and could be done only for the dominant woody species in the study area. The leaf biomass estimates are therefore more reliable for Acacia nigrescens and Combretum apiculatum than for the other species. As discussed in Chapter 1 improved methods of biomass estimation for woody plants would be valuable.

(ii) Estimates of the abundance of leaves and shoots at different growth stages. In this study leaf abundance of woody plants was categorized by species, and each species was regarded as having a certain characteristic average nutrient content. This does not consider the within-species variation in nutrient content between leaves and shoots of different ages. To provide a more realistic indication of the array of food types available browse biomass could be categorized by plant part (leaves and shoot ends) and by growth stages (e.g. new, mature and falling leaves) as well as by species.

(iii) Additional analyses of nutritional value. The analyses of leaf protein content gave a rough indication of relative nutritional value, but to further evaluate the factors underlying diet selection it would be necessary to analyse for contents of plant secondary chemicals and also digestible energy content. The latter is important because the results of Chapter 4 suggest that energy is more likely to be a limiting nutrient for kudus than protein.

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(iv) Identification and survey of vegetation subcommunities within the study area. The availability of different food types as experienced by the kudus depends on the proportion of foraging time they spend in the various vegetation subcommunities. This needs to be taken into account in calculating selectivity ratings. The study area was divided into broad subcommunities (Chapter 2), but further surveys aimed at identifying finer scale vegetation subcommunities of relevance to the kudus are required.

(v) Statistical tests of the selectivity ratings. The methods used in this study to test the statistical reliability of the selectivity ratings had two drawbacks: Firstly some of the assumptions made in applying the analyses of Neu _et_ _al_. (1974) were unrealistic for the data (see Chapter 2) and secondly sampling errors in the estimates of food availability were not taken into account (i.e. it was assumed that availability was measured without error). Alternative approaches to assessing the reliability of utilization-availability data (Johnson 1980, Hobbs and Bowden 1982) require independent, replicated samples of diet composition which could not be obtained in this study. Sampling procedures and methods of statistical analysis of selectivity ratings suitable for the kudu study need to be developed.

(vi) Estimation of dry matter intake per unit feeding time. It would be difficult to measure eating rates for free-ranging kudus at Nwamuriwa, but work on captive animals, using the method of Dunham (1980), could determine the rate at which food is harvested from the most important food plants. As noted, this would be necessary to test the hypothesis put forward to explain the seasonal varia= tion in acceptance of armed and unarmed woody species.

Data requirements for determining the nutritional status of the kudu population were identified in Chapter 4. This information would allow direct assessment of whether the population is likely to be limited by its food supply. The data needed for such an evaluation would be time consuming and expensive to obtain, and it would not be practical to monitor nutrient intake rate of the kudu population over long periods. The approach evaluated in this study, using the index of accepted food abundance supported by estimates of the nutrient content and abundance of potentially available food, offers a feasible means of determining the importance of the food supply as a population limiting factor. It remains for future research to reveal whether long-term variations in these indices are in fact associated with variations in the performance of the kudu population.

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SUMMARY

The feeding ecology of kudus was investigated with the aim of developing and assessing indices of their nutritional status. Aspects measured were (i) an index of potential food abundance, given by the biomass of forb and woody plant leaves per unit ground area (ii) the nutritional value of potential food (protein, phosphorus and water contents) (iii) an index of accepted food abundance, given by the feeding time achieved per unit distance moved while foraging (iv) an index of food intake rate, given by the proportion of foraging time spent feeding (v) diet composition (vi) differences among food plants in acceptance, assessed by comparing the proportion of each in the kudus' diet with its relative availability in the habitat.

Potential food abundance was highest in the late wet season (February-March) at 60 g dry weight per m^2, and lowest in the late dry season (August-September) at 12 g per m^2. The nutrient content of potential food was highest in the early growing season (September to November) and lowest from June to August.

The kudus generally favoured forbs over woody plants. Forbs comprised about 65 per cent of the diet during most of the year, but declined to below 20 per cent in the early growing season. At this time the woody plants _Acacia nigrescens_ and _Combretum hereroense_ made up the major part of the kudus' diet. These two species constituted an important food resource as they began leaf production early, thus offering high quality food when little else was available. The third dietary staple among the woody plants was _Combretum apiculatum_ which was favoured in the dry season. Rarely accepted woody plants were _Acacia tortilis_, _Cissus lonicerifolia_, _Dombeya rotundifolia_, _Pterocarpus rotundifolius_, _Grewia monticola_, _Peltophorum africanum_ and _Euclea divinorum_.

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The acceptance ranks of the various food types were positively correlated with their leaf protein, phosphorus and water contents in the wet season, suggesting that the kudus selected for plants with a high nutrient content. However, in the dry season there was no significant relationship between leaf nutrient content and acceptance. This may have been because plant morphological defences, thorns and spines, tended to outweigh leaf nutrient content as a factor influencing selection during the dry season. The kudus tended to favour woody plants armed with thorns in the growing seasons and unarmed species in the dry seasons, despite the fact that armed species averaged higher in nutrient content throughout the year. The suggested explanation is that the soft thorns on new shoots in the growing seasons inhibit browsing to a lesser extent than hard thorns on mature growth in the dry seasons.

The index of accepted food abundance was compared with seasonal and between habitat variations in potential food abundance. The results suggested that the index provided a satisfactory reflection of variations in accepted food abundance. However a disadvantage of this approach is that feeding time is assumed to accurately reflect the quantity of food eaten, whereas in fact the amount of food eaten per unit time spent feeding may vary. To be used reliably the index would need to be corrected for differences in eating rate. Despite this reservation the index of accepted food abundance, supported by estimates of the abundance and nutrient content of potential food, shows promise as a method of demonstrating whether long-term fluctuations in food availability are associated with kudu population performance.

Rough approximations of the protein, phosphorus, energy and water intakes of kudus were compared with their estimated requirements. These comparisons indicated no nutrient deficiencies at any stage of the seasonal cycle, which was in accord with the observation that the population was expanding during the study period. Data requirements for more reliable measurements of nutrient intake rate in relation to requirements are discussed.

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OPSOMMING

Die oogmerk met die studie was om 'n indeks te ontwerp en te evalueer wat die koedoe se voedingstatus sal reflekteer. Derhalwe is die volgende aspekte bepaal:

(i) 'n indeks van die potensiële hoeveelheid voedsel beskik=baar, uitgedruk as die biomassa van blare van kruidag=tige - sowel as houtagtige plantsoorte per eenheid oppervlakte.

(ii) die nutriëntinhoud (proteïen-, fosfor- en waterinhoud) van potensiële voedselbronne

(iii) 'n indeks van die aanvaarde hoeveelheid voedsel, uit=gedruk i.t.v. die tyd gespandeer aan voeding per een=heid afstand wat die dier beweeg gedurende die weidings=periode.

(iv) 'n indeks van die voedselinnametempo, uitgedruk i.t.v. die tyd wat die dier aan voeding per eenheid weidings=tyd spandeer

(v) dieëtsamestelling

(vi) die aanvaarbaarheid van verskillende plantsoorte; bepaal deur die verhouding tussen die proporsie van die plant=soort in die koedoe se dieët, en die relatiewe beskik=baarheid van die plantsoort in die habitat.

Die potensiële hoeveelheid voedsel beskikbaar het 'n maksimum bereik gedurende die laat-reënseisoen (Februarie-Maart) met 'n droëmassa van 60 g per m^2, en 'n laagtepunt in die laat-droë=seisoen (Augustus - September) teen 12 g per m^2 . Die voedings=waarde van potensiële voedsel het ook seisoenaal gevarieer, met die hoogste nutriëntinhoud in die vroeë-groeiseisoen en die

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laagste waardes vanaf Junie tot Augustus.

Oor die algemeen het koedoes kruide bo bome en struike verkies. Die oorgrootte tyd van die jaar het die koedoes se dieët uit sowat 65 persent kruide bestaan, behalwe in die vroeë-groeiseisoen, waartydens dit gedaal het tot minder as 20 persent. Gedurende hierdie tyd was dit veral jong blare en spriete van die boomsoorte Acacia nigrescens en Combretum hereroense wat die grootste bydrae tot die koedoes se dieët gemaak het. Hierdie twee spesies is 'n belangrike voedselbron vir die koedoes: Tydens 'n kritiede tydperk, wanneer daar min ander bronne beskikbaar is, het hul blaarproduksie al in aanvang geneem en verskaf hulle daarby ook 'n hoë voedingskwaliteit. Wat boomsoorte betref is Combretum apiculatum 'n derde stapelvoedselplant. Dit was hoofsaaklik in die droë-seisoen benut. Acacia tortilis, Cissus lonicerifolia, Dombeya rotundifolia, Pterocarpus rotundifolius, Grewia monticola, Peltophorum africanum en Euclea divinorum is boomsoorte wat selde deur koedoes benut was.

Die selektiwiteitsrangorde vir verskillende voedselsoorte toon 'n positiewe korrelasie met die blare se proteïen-, fosfor- en waterinhoud gedurende die reënseisoen. Dit impliseer dat die koedoes selekteer vir plante met 'n hoë nutriëntinhoud. In die droë-seisoen bestaan daar egter geen noemenswaardige verband tussen die nutriëntinhoud en voorkeur nie. Dit kan moontlik toegeskryf word aan die teenwoordigheid van sekere morfologiese verdedigingsmeganismes soos dorings en stekels, wat dan 'n seleksie vir hoër nutriëntinhoud oorheers. Gedurende die groeiseisoen het koedoes hoofsaaklik voorkeur gegee aan plantsoorte met dorings en stekels. Ten spyte daarvan dat bewapende spesies 'n hoër nutriëntinhoud gedurende die hele jaar handhaaf, het die koedoes wel plantsoorte sonder verdedigingsmeganismes in die droë-seisoen verkies. Dit kan moontlik daaraan toegeskryf word dat die sagte dorings wat op jong takkies in die groeiseisoen gevorm word, weiding nie soseer sal strem as in die geval van harde dorings op ouer takke in die droë-seisoen nie.

Die indeks vir die aanvaarde hoeveelheid voedsel is, volgens habitat en seisoen, vergelyk met die potensiële hoeveelheid

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voedsel beskikbaar. Volgens die vergelykings blyk dit dat dié indeks 'n redelik betroubare beeld gee van variasies in die aanvaarde hoeveelheid voedsel. 'n Tekortkoming van hierdie tegniek is dat dit aanvaar dat die tyd wat die dier aan voeding spandeer 'n akkurate weergawe is van die hoeveelheid voedsel wat ingeneem is. Bepalings van die voedselinnametempo sal egter die betroubaarheid van die indeks verhoog. Ten spyte van hierdie beperking is die indeks vir die aanvaarde hoeveelheid voedsel, gerugsteun deur bepalings van biomassa en nutriëntinhoud van potensiële voedsel, 'n belowende metode om langtermyn variasies in beskikbare voedsel te koppel aan die koedoe se populasiesukses.

'n Benadering van die koedoe se proteïen-, fosfor-, energie- en waterinname is vergelyk met hulle berekende behoeftes. Volgens hierdie bepalings blyk dit dat daar geen nutriëntgebrek gedurende enige tyd van die jaar bestaan nie. Dit sluit ook aan by die gevolgtrekking dat die koedoes gedurende die studieperiode 'n populasiegroei ondervind het. Die noodsaaklikheid vir meer betroubare bepalings van nutriëntinname in vergelyking met behoeftes, is ook in die teks bespreek.

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APPENDIX I

LIST OF FORB SPECIES IDENTIFIED AT THE NWAMURIWA HILLS, KRUGER NATIONAL PARK WITH FREQUENCY OF UTILIZATION BY KUDUS INDICATED

* One feeding record

** Two to five feeding records

*** More than five records

Unmarked species are not known definitely to be utilized by kudus

FAMILY ACANTHACEAE

Asystasia gangetica
Asystasia subbiflora
*Barleria lancifolia****
*Barleria prionitoides**
*Blepharis integrifolia**
Crabbea hirsuta
*Crabbea velutina**
Dyschoriste spp.*
*Justicia flava****
*Justicia kraussii**
*Ruellia cordata***
*Ruellia patula**
Thunbergia dregeana

FAMILY BORAGINACEAE

*Heliotropium steudneri***
Heliotropium strigosum

FAMILY CAPPARACEAE

Cleome monophylla
*Maerua cafra***

FAMILY COMMELINACEAE

*Commelina africana****
*Commelina benghalensis****

FAMILY COMPOSITAE

*Aspilia mossambicensis****
*Epaltes gariepina****
*Vernonia fastigiata***

FAMILY CONVOLVULACEAE

Evolvulus alsinoides
Hewittia sublobata
*Ipomoea crassipes****
*Ipomoea obscura****
*Merremia palmata**
Seddera capensis
Seddera suffruticosa

FAMILY CRASSULACEAE

Kalanchoe lanceolata

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APPENDIX I (CONTINUED)

FAMILY CUCURBITACEAE

*Coccinia rehmannii***
*Corallocarpus bainesii**
*Cucumis africanus*** (fruit & leaves)
Cucumis metuliferus fruit***
leaves**
Momordica clematidea

FAMILY EUPHORBIACEAE

*Acalypha indica***
*Acalypha segetalis***
*Dalechampia galpinii***
Jatropha variifolia
Phyllanthus maderaspatensis
*Tragia rupestris****

FAMILY LABIATAE

Endostemon obtusifolius
Hemizygia spp.
Leucas glabrata
Ocimum canum
*Ocimum urticifolium***
Orthosiphon australis

FAMILY LEGUMINOSAE

*Indigofera schimperi***
Indigofera viciodes
Neorautanenia amboensis
*Rhynchosia caribaea**
*Rhynchosia densiflora***
*Rhynchosia minima**
*Rhynchosia totta****
*Tephrosia rhodesica***
*Vigna decipiens**

FAMILY LILIACEAE

Scilla spp.**
Schizobasis intricata

FAMILY MALVACEAE

*Abutilon austro-africanum**
*Hibiscus cannabinus**
*Hibiscus engleri**
*Hibiscus micranthus****
*Hibiscus pusillus***
Sida dregei

FAMILY NYCTAGINACEAE

*Boerhavia bracteata***

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APPENDIX I (CONTINUED)

FAMILY OLEACEAE

Jasminum fluminense

FAMILY PORTULACACEAE

*Talinum caffrum***

FAMILY SOLANACEAE

Solanum coccineum

*Solanum incanum***

Solanum panduraeforme	fruit***
	leaves***

FAMILY VERBENACEAE

*Lantana rugosa****

FAMILY VITACEAE

Cissus rotundifolia

*Cyphostemma schlechteri**

FAMILY ZYGOPHYLLACEAE

Tribulus terrestris

FAMILY ADIANTACEAE

Pellaea viridis

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APPENDIX I (CONTINUED)

ADDITIONAL FORB SPECIES IDENTIFIED ON THE NWAMURIWA HILLS BY COETZEE (1977)

FAMILY ACANTHACEAE
Barleria obtusa

FAMILY AMARANTHACEAE
Achyranthes aspera
Hermbstaedtia odorata

FAMILY ARACEAE
Stylochiton natalense

FAMILY COMMELINACEAE
Commelina livingstonii

FAMILY COMPOSITAE
Bidens bipinnata
Vernonia oligocephala
Vernonia posheana

FAMILY CONVOLVULACEAE
Convolvulus farinosus
Ipomoea sinensis
Merremia tridentata

FAMILY CYPERACEAE
Kyllinga alba

FAMILY EUPHORBIACEAE
Euphorbia neopolycnemoides
Phyllanthus incurvus
Tragia diocca

FAMILY LABIATAE
Becium cnyanum

FAMILY LEGUMINOSAE
Tephrosia burchellii

FAMILY MALVACEAE
Sida chrysantha

FAMILY MOLLUGINACEAE
Corbichonia decembens

FAMILY PEDALLIACEAE
Ceratotheca triloba

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APPENDIX I (CONTINUED)

FAMILY POLYGALACEAE
Polygala sphenoptera

FAMILY SANTALACEAE
Thesium gracilarioides

FAMILY VITACEAE
Cyphostemma subciliatum
Rhoicissus tridentata

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