The diet, habitat selection and body condition of impala *Aepyceros melampus* and nyala *Tragelaphus angasi* in Zululand.

by

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ABSTRACT

The habitat selection, diet and body condition of impala and nyala were investigated in Mkuzi and Ndumu Game Reserves.

Impala and nyala, separated into different habitats within Mkuzi Game Reserve: impala preferring the western and nyala the eastern regions of the reserve. A degree of overlap in habitat preference existed within the centre of the reserve.

Impala preferred a grass diet but following lignification and a decline in protein during winter, dicotyledon intake increased. Nyala also preferred grass after the first rains. Breeding impala females were in a positive protein balance during the early stages of gestation although, following an increase in protein intake during the later stages of gestation and early lactation their requirements exceeded intake.

Pregnant females of both species had higher kidney fat indices than non-pregnant individuals which suggests that fat deposition was enhanced, even when food quality was low. Territorial male impala lost condition during the rut due to a reduction in food intake whilst bachelors was unaffected. KFI of nyala bulls remained low throughout the study period.

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CHAPTER 1

Introduction

I. General Introduction.

The ultimate aim of the individual is to reproduce. This ensures the transmission of the individual's genes into the genepool and thereby enhances its own fitness. To do this the individual must first survive to an age at which it can reproduce, then gather enough energy to sustain its normal metabolic needs and have enough energy spare to invest in reproduction.

To study only what the animal ingests in a study of diet will therefore be purely descriptive and of very little use. Food is converted into energy, and energy is the driving force behind the transmission of genes. However, the food that provides the energy is influenced by an array of factors. If the individual is a herbivore, certain factors determine the availability of food (eg. rainfall and habitat) while sex, age, reproductive status o.a. will determine the demand for the specific quantity and quality of food to be taken in.

The subject of the present study is two similar sized African ungulates, both utilising similar food sources (intermediate feeders) but with different social organisations. They adapted differently to survive. Impala are associated with open woodlands and nyala with thickets and dry forests. The former congregating in larger groups dispersing seasonally, while nyala are found singly or in small family groups (which are not territorial).

Seasonal changes in food availability and quality have a marked influence on herbivores. Rainfall and temperature have a direct influence on both quantity and quality of forage. Changes in energy availability have led some species to adapt by becoming seasonal breeders. Habitat also provides cover against the elements and predators as well as space to exert social activities. These components also change with the seasons.

The present study considers only some of these factors. Diet which is the energy intake, body condition which is a measure of energy in reserve and the habitat which will influence the diet as the individuals of each species are adapted to a particular habitat.

II. Introduction to the study animals.

Impala.

In South Africa impala are common in the Transvaal bushveld and in the northeastern parts of Natal and KwaZulu as far as the Mhlatuze river (Smithers 1983) (Figure 1).

Impala are gregarious, found in groups of up to 100 in the dry season, but more commonly in groups of less than 30. They breed seasonally (Skinner 1971) in response to changing environmental cues (Skinner & van Jaarsveld 1987) and social relationships within the species centre on the autumn rut. Territories are defended by territorial rams only during the rut in southern Africa (Dasmann & Mosssman 1962, Anderson 1972, Mason 1976, Murray 1982) but are held throughout the year close to the equator (Leuthold 1970). Territorial rams have exclusive mating rights (Jarman 1974) and bachelors are excluded from territories. Females entering the territories are herded by the resident males which defend them against other males.

Bachelors may be forced to occupy sub-optimal habitat, and they may be joined by the territorial males after the rut. This spatial segregation of females is said to reduce intraspecific competition (Anderson 1972, Mason 1976). The group structure changes dramatically after the rut. Male herds break up and more single males are seen. Lambs are separated from their mothers as a result of the rut activities and they congregate into herds. Yearling males now aggregate with the bachelor herds.

After the rut the territorial system deteriorates and mixed groups are formed. Towards the end of pregnancy females aggregate into huge herds either with or without males. Births are synchronised within a short period (Skinner, Nel & Millar 1977) and ewe-lamb herds are formed.

Nyala

Nyala occur in the southeastern parts of the continent and because of their habitat requirements have a localised distribution (Figure 2). In southern Africa nyala occur in Zimbabwe in the northeast in the Zambezi valley and the lower reaches of the river's tributaries. In the south nyala are found around the Limpopo river and its tributaries as far west as Swartwater. South of this they are found along the Mozambique border in the Kruger National Park to about 24° 30'S. Currently their distribution in Natal is limited to the Ndumo and Mkuzi Game Reserves, the Hluhluwe-Umfolozi complex and the vicinity of Lake St Lucia (Smithers 1983). Nyala occur on farms in northern Natal down to the Umhlatuzi river. Their distribution in Mozambique south of the Zambezi is limited to the southern parts of Beira and Vila Pery Districts, north of the Save river. South of this they occur in the northern and western parts of the Gaza and Inhambane districts.

Nyala are gregarious, occurring in groups of up to 30 but more often in two's and three's (Anderson 1980). Nine types of social groups are described by Anderson (1980) ranging from single calves to mixed herds. Male groups are not stable as in impala and associations are of short duration (Tello & van Gelder 1975, Anderson 1980). Adult males are solitary as a result of being avoided by younger males as the latter will be prevented from mating in the presence of an older male. The basic social group is the family unit which consists of an adult female and her offspring. Family units may aggregate to form female groups (Anderson 1980).

Unlike impala, nyala are not territorial, probably as a result of their habitat selection as it is too costly to maintain a territory in a closed habitat (Anderson 1980).

Nyala males do not exhibit any seasonal sexual cycle (like impala); although conceptions take place throughout the year, a bimodal pattern is evident in spring and autumn (Anderson 1979). Births thus occur throughout the year (in seclusion) and young have a lying-up period of about two weeks.

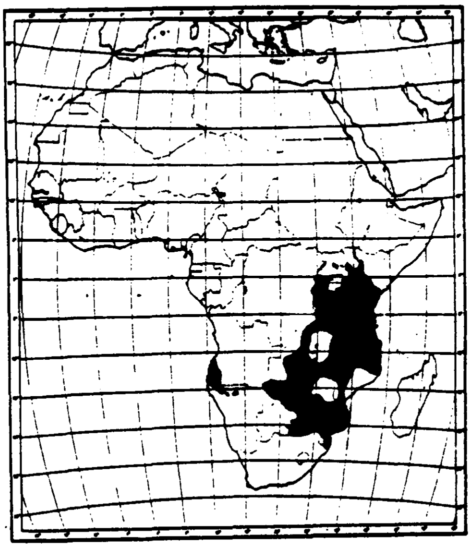


Figure 1. The distribution of impala in Africa (Smithers 1983).

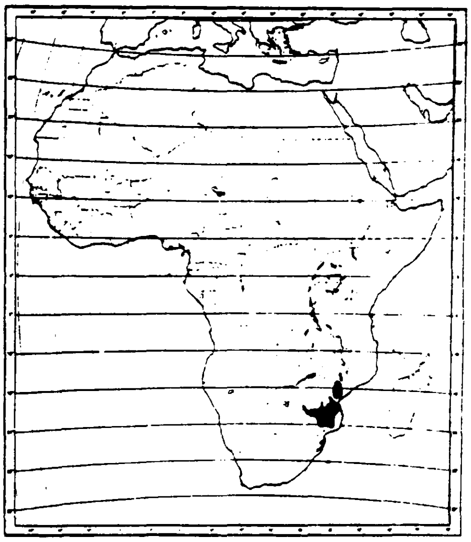


Figure 2. The distribution of nyala in Africa (Smithers 1983).

CHAPTER 2

Study areas

Introduction

This study was carried out in two reserves in the northern part of Natal. All data except those concerned with the diet of nyala were collected in the Mkuzi Game Reserve. A detailed description of the Mkuzi Game Reserve is given below and a brief description of the Ndumu Game Reserve.

The Mkuzi Game Reserve has been described in detail by Goodman (1990). This chapter is a condensed version of the relevant parts as described by Goodman (1990).

Mkuzi Game Reserve

Location

The Mkuzi Game Reserve in Zululand, Natal is located between latitude 27° 30' south and 27° 45' south; and longitude 32° 05' east and 32° 25' east. Altitude varies from 30m in the southeast to a maximum of 480m in the northwest. The reserve is situated on the coastal plain east of the Lebombo Mountains, an average of 40km from the coast (Figure 3).

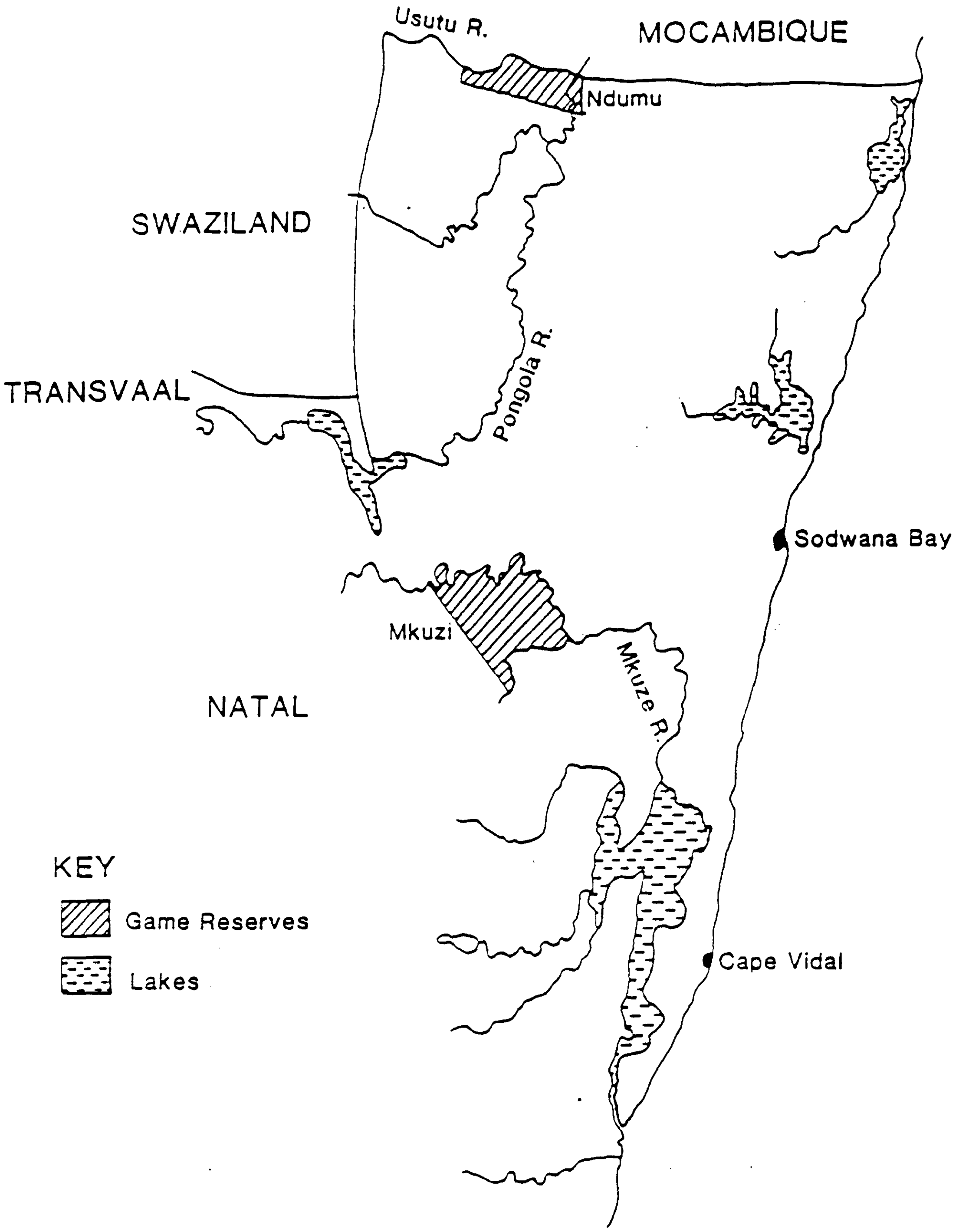


Figure 3. The location of the study areas in Zululand, Natal.

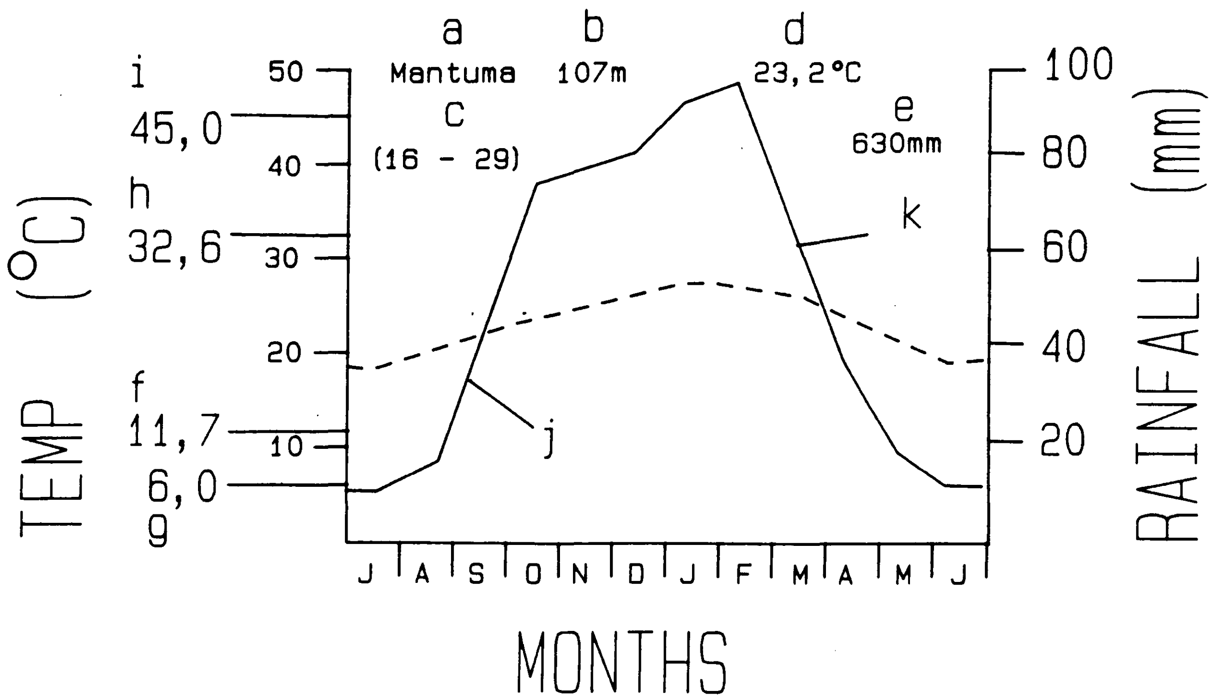
This 28 638ha reserve is bounded in the north and east by the Mkuze river, in the south by the Msunduzi River while in the west it is bounded by a fence along the Lebombo Mountains.

Climate

A climatic diagram (Figure 4) summarizes the climatic features (after Walter 1971). The reserve is warm to hot, humid sub-tropical and falls into Koppen's arid zone steppe climate group with a mean annual temperature greater than 18°C. The reserve is also semi-arid with little or no moisture surplus in any season.

The rainy season occurs in the hot humid summer (mid-September to mid-March), winter being warm and dry. The rainfall is strictly seasonal, peaking in February, while June is on average the driest month. The rainy season (all months with > 50mm of precipitation) begins in October and lasts until March. Spatial variation in rainfall is not great. Mean annual rainfall (measured at the weather station at Mantuma camp) is 631mm, but as the frequency histogram is positively skewed it is better expressed by the median of 610mm.

The mean annual temperature is 23,2°C. Summers are hot. The mean temperature for the hottest month, January, is 27,1° C and the mean maximum is 32,5° C. Winters are warm with a mean



a. Station name

b. Altitude

c. Nuber of years of observation; temperature - precipitation

d. Mean annual temperature

e. Mean annual precipitation

f. Mean daily minimum of coldest month °C

g. Absolute minimum °C

h. Mean daily maximum °C

i. Absolute maximum °C

j. Arid period

k. Humid period

Figure 4. Climate diagram of Mkuzi Game Reserve.

daily temperature of 18,8^{o} C in the coldest month, July, with a mean minmum of 11,7^{o} C. No frost has been recorded at the weather station.

Prevailing winds occur in September and October and are north-easterly or north-westerly.

Topography, geology and geomorphology

The topography is related to the physiography and geology. Five land units are evident, ocurring from east to west (Fig 5.):

1.) the hilly Lebombo Mountains (Jr),

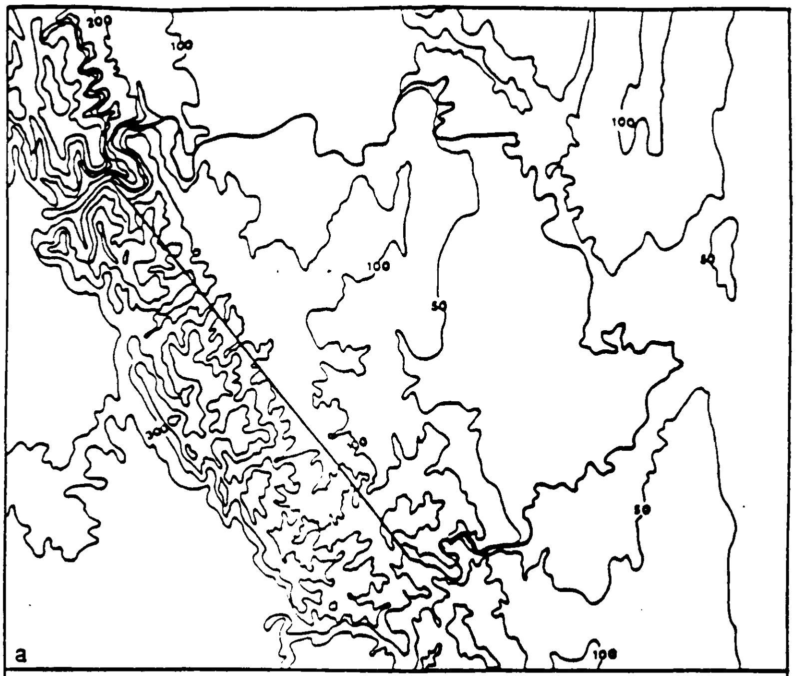
2.) a gently undulating region underlain by Early Cretaceous sediments (Cr_3),

3.) a gently undulating, slightly elevated Quarternary dune complex (Pl),

4.) a low lying essentially flat region underlain by Late Cretaceous sediments (Cr_2) and

5.) a low lying flat alluvial floodplain (Al) of recent origen which occurs adjacent to the two rivers.

The Lebombo Mountains consists predominantly of the Jozini Rhyolite formation which overlies and post-dates the more westerly occurring Sabi River Basalts. The Jozini formation is composed mainly of massive flows of rhyolite and rhyodacite interbedded with basaltic flows. Several dykes occur in this



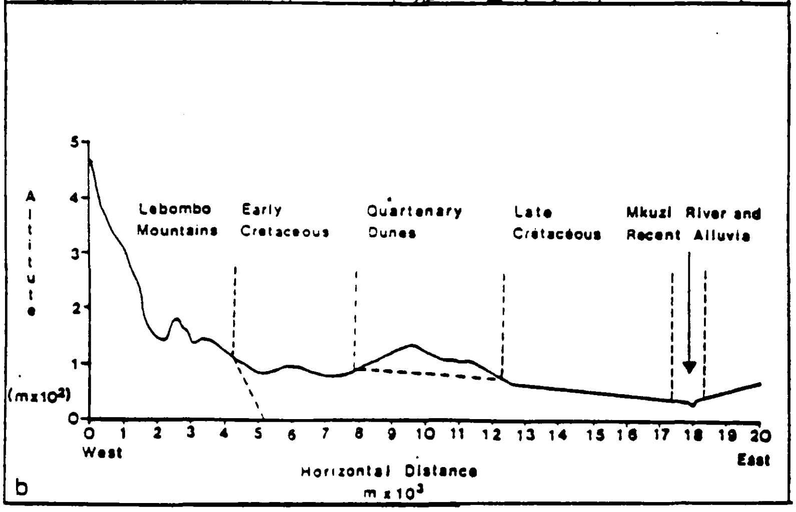


Figure 5a. The topography of the Mkuzi Game Reserve (Goodman 1990).

Figure 5b. A cross-section through the game reserve to illustrate the gross strategraphic relationships and major topographic features (Goodman 1990).

with dolerite being the most common. The rhyolite and rhyodacite gave rise to the Lebombo Mountains due to their extreme resistance to erosion. The Bumbeni Complex and the Mpilo Member Basalts are two futher volcanic bodies occurring to the south of the reserve.

The break-up of the protocontinent Gondwanaland gave rise to both the actions of the Lebombo volcanics and their closure. This break along the continental rift together with the influx of seawater resulted in the deposition of Early and Late Cretaceous conglomerates and sediments, in Mozambique and Zululand. These deposits probably originated in the beds of high gradient, anastomising, torrential streams.

A series of epierogenic uplifts associated with concomitant down-flexing of margins together with world-wide changes in sea level due to glacio-eustatism followed the break-up of Gondwanaland. The coastal plain thus underwent a complex history of sedimentation and erosion from the end of the Cretaceous through the Tertiary and Quartenary periods. These actions of land and sea resulted in the north - south trending dune ridges evident today as conspicuous topographic features on the present day coastal plain. These dune ridges consist of red or yellow-brown sand and two can be seen in the reserve. The first dune cordon is the oldest (Plio-Pleistocene) and occurs adjacent to the Lebombo volcanics, a result of the most westerly shoreline. This ridge is poorly preserved, with well developed soil profiles. The second, lower but better preserved, is approximately 2km east. This cordon forms a prominent ridge bisecting the reserve, with generally poorer soil profiles than the first. A third dune cordon exists 11km to the east and is situated outside the reserve. The Mkuze and Msunduzi rivers cut through this ridge east of the reserve and thus during the upper Pleistocene the low lying eastern area of the reserve would have been estuarine, with marine and river borne deposits.

The last glacial, with three interglacial peaks in sea level, was followed by a deep regression. This lowering in sea level caused deep valley incision. It is postulated that all valley fill was eroded. During the upper Pleistcene a rise in sea level took place causing an inflow of alluvial material along the incised drainage lines and created pans, reed swamps and vleis where these drainage lines became submerged.

Soil

Soils generally correspond closely to the underlying geology and topography. The Lebombo mountains in the west of the reserve, with its steep slopes and high resistance to erosion have given rise to lithosoils of various depths. The area of alluvial deposition in angular valley floors is very limited. These alluvia are predominantly shallow gritty clays with the clay complex dominated by kaolinite.

Soils in the Early Cretaceous are derived from conglomerates, sandstones and siltstones (derived from a variaty of rock types: basalt, dolerite, rhyolite, granite, banded ironstone and quartzite) are of varying depths, texture and mineral composition. A gently undulating (slope angles 2 - 5°) landform with moderate relief (valley depth 30 - 100m) and moderate drainage spacing (400 - 1500m) resulted in this landtype as a result of weathering and erosion. Soil depth and clay content increase from west to east. Upland sites in the west are characterised by lithic soils, while those in the east are ferruginous soils. Bottomlands are generaly calcimorphic, characterised by brown to dark calcimorphic soils in the west and vertisoils in the east. Upland soils are more leached with less clay than bottomlands.

In the east the Late Cretaceous deposits consist primarily of glauconitic sandstone and resulted in a uniformly deep soil mantle throughout the area. The landform is level to very gently sloping (0 - 2°) with a very low relief (<10m), wide drainage spacing (1 500 - 3 000m) orientated north to south. Calcimorphic clay dominates this area, with angular valley floors containing more clay than the flat interfluves with brown calcimorphic clay loams.

Quartenary sand deposits occur as two north-south parallel dune cordons. Soil profiles of the westerly cordon are deep, red, and well developed displaying advanced mineral diagenesis. Soil in the upland areas in the dunes are ferruginous arenosols while those in the bottomlands are of higher kaolinitic clay content beig ferruginous soils. The eastern dune cordon soil profiles are poorly developed yellow to orange arenosol.

In the Mkuzi Game Reserve there are a large number of soils derived from alluvium that are no longer subject to flooding and an appreciable amount of horizon developement has taken place in some of these "older alluvia". Large expanses of alluvial soil occur along the two major rivers in the reserve (the Mkuzi and Msunduzi Rivers) and along the major streams, the Nhlonhlela and Nsumu. Apart from the lower sections of the two major rivers no flooding of alluvia occurs and horizon developement continues.

Surface hydrology

Geomorphological factors and climate (low rainfall and high evaporation) have resulted in an area with no naturally occurring permanant surface water within the boundaries of the reserve. The two rivers wich form the boundaries in the north, east and south have most of their catchment area to the west of the reserve. Both of these rivers are strictly seasonal. Subsurface water is available throughout the year in the Mkuzi River. The reserve itself is drained through numerous streams running east to flow into the Nhlonhlela and Nsumu streams and then drain into the Mkuzi River via the Nhlonhlela and Nsumu pans.

Several small (> 0.25ha), shallow, seasonal clay floored pans occur in the reserve, but are more common in the eastern half. Larger pans are found along the Mkuzi River floodplain, filled through channels from the river or from streams as in the case of Nsumu (the largest) and Nhlonhlela. The only permanent water in the reserve is in the piped pans Bube and Msinga close to each other in the centre of the reserve.

Vegetation

The Mkuzi Game Reserve falls into two major phytochorological regions: the Tongaland - Pondoland Regional Mosaic (a subdivision of the Indian Ocean Coastal Belt) and the Sudano-Zambezian Region. Acocks (1975) ascribes three vegetational types in the reserve, Coastal Forest and Thornveld, Lowveld and Zululand thornveld.

Goodman (1990) divided the reserve into nine major vegetation types which overlap along environmental gradients and are thus not in all instances distinct.

1.) Dry Mountain Bushveld and Grassveld.

This is open woodland to grassveld with dominant species being

Combretum apiculatum, *Acacia nigrescens*, *Themeda triandra*, *Heteropogon contortus* and *Cymbopogon excavatus*, and is associated with the lithosols on the Lebombo Mountains.

2.) Microphyllous Thorny Plains Bushveld.

This vegetation type is represented by *Acacia nigrescens* Tropical Plains Thornveld. It is associated with the vertic and ferruginous clay soils in the west and vertic clays in the east. *Acacia nigrescens* dominates the tree layer while *Dichrostachys cinerea* is common in the sub-storey. Dominant grasses in the diverse herbaceous layer are *Themeda triandra*, *Panicum maximum*, *Digitaria eriantha*, *Urochloa mosambicensis* and *Bothriochloa insculpta*.

3.) Mixed Bushveld.

This vegetation type consists of a mosaic of woodland types on soils ranging from brown calcimorphic sandy clay loams to vertic clays and hydromorphic gley soils. This is generally an open to closed woodland dominated by *Acacia tortilis*, *A. nilotica*, *A. grandicornuta* and *A. senegal*. Associated trees and shrubs are *Spirostachys africana* and *Schotia brachypetala*. The herbaceous layer is not well developed, the main grasses being *Dactiloctinium australe*, *Cholris virgata*, *Eragrostis rigidior* and *Aristida spp.*.

4.) Thicket

Thickets occur on vertic clays and hydromorphic gley soils where topography is flat and soils poorly drained. Thickets are in some places impenetrable and 3 - 4m high. Dominant trees are Acacia luederitzii and Euclea divinorum. Important grasses are Dactyloctinium australe, Enteropogon monostachyos, Panicum maximum and P. deustum. In places Spirostachys africana, Shotia brachypetala, Pappea capensis, Syderoxylon inerme, Berchemia zeyheri, Albizia anthelmintica and Cassine spp. emerge above the thicket forming a dense, multilayered woodland.

5.) Red Sand Bushveld.

This open to closed vegetation type occurs on the ferruginous arenosols of Quarternary origin and is approximately 7m tall. Combretum molle, Acacia burkei, Sclerocarya caffra, Ziziphus mucronata and Terminalia sericea are the most common trees. The herbaceous layer is sparse with the grasses Dactyloctinium australe, Aristida spp., Panicum maximum, Eragrostis pallens, E. rigidior, Pogonarthria squarrosa and Hyperthelia dissoluta being common.

6.) Sand forest.

A distinctive type of dry, semi-deciduous forest which occurrs on the poorly developed yellow-orange arenosols of Quarternary origin. This vegetation type consists of a mosaic of forest patches 10 to 25m high in a matrix of open woodland. Important tree species are Newtonia hilderbrandtii in localized pure stands, Cleistanthus schlechteri, Hymenocardia ulmoides, Pteleopsis myrtifolia, Dialium schlechteri, Croton gratissimus and Strychnos henningsii. A well developed sub-canopy of small trees and shrubs consisting of Salacia leptoclada, Croton pseudopulchellus and Hymenocardia ulmoides is present. The herbaceous layer is extremely poorly developed.

7.) Riparian fringing forest and woodlands.

These may be divided into two principal parts:

a.) Streambed and drainage line woodland, along minor streams and drainage lines. Schotia brachypetala, Acacia robusta, Spirostachus africana, Euclea schimperi, Sideroxylon inerme, Thespesia acutiloba and Cassine spp. are present.

b.) Riverine forest and woodland. This vegetation type varies from a well developed forest to an open woodland up to 35m high. Main tree species on the alluvia along the two rivers in the reserve are Acacia xanthophloea, Rauvolfia caffra and Trichilia ametica. Acacia schweinfurthii, Azima *tetracantha* and the alien specie *Eupatorium odoratum* form a well developed sub-canopy, in some places impenetrable. Again the herbaceous layer is underdeveloped consisting of a wide variety of forbs and creeping grasses.

8.) Floodplain grasslands.

These grasslands occur on the inundated flats adjacent to the Mkuzi and Msunduzi floodplains. This tall grassland is characterised by *Phragmites australis*, *Echinochloa pyramidalis*, *Eriochloa spp.*, *Sorgum spp.*, and *Cyperus spp.*.

Fauna

Zoogeographically the Mkuzi Game Reserve falls into the East African Province of the Ethiopian Region, the fauna in many respects having tropical affinities. The mammals of the region, Maputaland were listed and discussed by Rautenbach, Skinner & Nel (1980) and for the reserve by Dixon (1964). The large herbivores are listed in order of descending numerical importance in Table 1. Major herbivores that no longer occur in the reserve are buffalo *Synceros caffer* and elephant *Loxodonta africana*.

Large predators include leopards *Panthera pardus*, cheetahs *Acinonyx jubatus*, black-backed jackals *Canis mesomelas* and spotted hyaenas *Crocuta crocuta*, lions *Panthera leo* and wild dogs Lycaon pictus do not occur in the area anymore.

Impala are the most common herbivore in the reserve followed by nyala. In the west of the reserve impala are the most important ungulate as they consume the greatest amount of energy while nyala dominate and consume the greatest amount of energy in the east (Goodman 1990).

Table 1. The large herbivores of the Mkuzi Game Reserve in order of descending numerical importance.

Impala	*Aepyceros melampus*
Nyala	*Tragelaphus angasi*
Warthog	*Phacochoerus aethiopicus*
Blue wildebeest	*Connocheatus taurinus*
Kudu	*Tragelaphus strepsiceros*
Zebra	*Equus burchelli*
Grey duiker	*Sylvicapra grimmia*
Bushpig	*Potamochoerus porcus*
Giraffe	*Giraffa camelopardalis*
Reedbuck	*Redunca arundinum*
Mountain reedbuck	*R. fulvorifula*
Red duiker	*Cephalopus natalensis*
Steenbok	*Raphicerus campestris*
Suni	*Neotragus moschatus*
Hooked lipped rhinoceros	*Diceros bicornis*
Bushbuck	*Tragelaphus scriptus*
Square-lipped rhinosceros	*Ceratotherium simum*
Hippopotamus	*Hippopotamus amphibius*
Eland	*Taurotragus oryx*
Waterbuck	*Kobus ellipsiprymnus*
Klipspringer	*Oreotragus oreotragus*

The Ndumu Game Reserve

The Ndumu Game Reserve is situated just south of the Usutu River, which forms the boundary between Natal, South Africa and Mozambique. The reserve is topographically fairly flat. The two perennial rivers, the Usutu and the Pongola, together with the pan system form a source of water. The summers are hot and humid with temperatures reaching up to 40°C, while winters are cool with temperatures seldom falling below 5°C. The annual rainfall is 547mm and the rainy season lasts from October to March.

The vegetation was described in detail by de Moor, Pooley, Neville & Bowbrick (1977). Tinley (1964) described three physiographic features; river floodplains, the higher *Sclerocarya- Terminalia- Acacia burkei* woodland on sandy soils and the large, low lying secondary mosaic dominated by *Acacia grandicornuta*, *Albizia evansii* and *A. anthelmintica.* The hygrophilous floodplain grasses *Echinichloa pyramidalis* and *Hemarthia latissima* are available to nyala during the dry period when other food is scarce (Anderson 1979).

CHAPTER 3

Habitat selection of impala and nyala in the Mkuzi Game Reserve, Natal.

Introduction.

The meaning of the terms habitat selection, distribution and preference in this chapter are those attributed to them by Fretwell & Lucas (1970) i.e.

Habitat. "The habitat of a species is any portion of the surface of the earth where the species is able to colonize and live. The total area available to a species can be divided into different habitats. The area of any one habitat can be large or small, and different habitats of the same species may be of different sizes. A given habitat can consist of several subdivisions which are not contiguous. We will define habitats so that all of the area within each habitat is, at zero density of the species, essentially homogeneous with respect to the physical and biological features which we believe to be most relevant to the behaviour and survival of the species. .... habitats are not identical with respect to those same physical and biological features." (Fretwell & Lucas 1970 p.180).

The habitat distribution of a species is represented as the number of individuals in each habitat; when the area available to the species is subdivided into different habitats. This can also be expressed as the proportion of the population in different habitats, or as the density of the species in each habitat (Fretwell & Lucas 1970). The latter removes the physical size of the habitat from the expression of distribution and will be used.

Habitat preference or selection is the frases by which habitat distribution is achieved. It is a combination of behavioural phenomena involving stimuli and reponses. Individuals in certain habitats will experience certain stimuli (positive or negative) to which they will react by either staying in the habitat or moving out to seek better conditions in another habitat type. These two words relate to the same phenomena and will be used interchangeably.

No community is stable, no vegetation type stays the way it is for ever. Changes do occur, some small and inconspicuous while others are dramatic and occur over a short period of time. It is the latter that we observe in a seasonal environment. Vegetation may be dry, nutritionally poor, and scarce. After rains grasses sprout and dicotyledons bud. Flowers grow into fruit and an overabundance of nutritios food is available to ungulates. After this overabundance food quality and quantity decrease slowly until the dry period sets in, when grass becomes lignified, high in fibre and low in protein. Tannins increase in dicotyledons which influences digestibility, so that the animal is forced to change either habitat or diet or both.

Vegetation types are different and react differently to climatic changes because of altitude, soil type, slope and other similar factors. A whole array of vegetation types is available to ungulates in most areas set aside for conservation. The use of these vegetation types depends on the species itself (eg. its size, nutritional demands, social organisation and type of predator avoidance).

The study of habitat selection will lead to insight into the distribution of ungulates in given environmental cirumstances. In order to understand the behavioural responses, we should consider the environmental factors which exerted the natural selection leading to the evolution of the behaviour (Fretwell & Lucas 1970). This understanding is of utmost importance in the conservation of any species. No animal can successfully be conserved in the long term without provision of suitable habitat.

An individual (solitory ungulate) or herd (social species) thus has the opportunity to select a habitat type that best suits its demands. Feeding style, as described by Jarman

(1974) is the most important factor determining the habitat selected by any ungulate.

Both nyala and impala form part of Jarman's (1974) class C ungulates. These intermediate feeders select between monocotyledons and dicotyledons, depending on availability and nutritional demand. They feed very selectively whether grazing or browsing and fairly large homeranges are used.

Impala prefer open woodland (Dassman & Mosmann 1962, de V. Pienaar 1974, Lamprey 1963, Schenkel 1966, Rodgers 1976) avoiding open grassland, but frequent the ecotone between the two (Mason 1976, Pettifer & Stumpf 1981) Acacia and Colophospermum mopane woodlands are used extensively. In addition surface drinking water and protection from weather and predators are limiting factors.

Anderson (1972) described the social organization and distribution of impala in Hluhluwe (Natal) and stated that the social behaviour influences the habitat used by the males. Males concentrate in the poorer habitats outside the rut. Anderson (1972) and Mason (1976) interpreted this differential habitat selection in impala as a way of reducing intersexual competition for food.

Impala are selective feeders and are able to switch from browse to graze in a short period (Hoffman & Stewart 1972).

Mason (1976) and Murray (1982) described the shift in habitat utilisation between the wet and dry seasons. These changes were associated with changes in diet, from a predominantly grass diet in the wet season to a predominantly browse diet of up to 65% at the end of the dry season in a semi-arid mixed tree savanna (Skinner, Monro & Zimmerman 1984).

Impala are dependant on surface drinking water, remaining in close proximity to rivers in arid regions (Young 1972, Stewart & Stewart 1963). More than half of Young's (1972) records show that herds remained within 1,6km of water. Impala will drink daily where water is available but become more dependant on water during the dry season. About 3*l* of drinking water per 100kg body mass per day is needed (Maloiy & Hopcroft 1971). On the other hand drinking water is apparently not essential to nyala as they occur in areas where it is only seasonally available (Davison 1971). Nevertheless, when freely available they drink daily (Tello & van Gelder 1971). In the Mkuzi Game Reserve both impala and nyala were found to drink at all hours of the day but mostly around midday (Villet & Woodiwiss 1986).

Evans (1979) described the habitat used by nyala as more specialized than impala. Nyala select dry forest, thicket and dense woodlands (Davison 1971, de V. Pienaar 1974) while Vincent, Hitchens & Bigalke (1968) state that nyala select densely bushed areas. Most authors report however that nyala often wander into open habitat but run straight for cover when disturbed.

Anderson (1980) calculated the community percentage composition of thirteen nyala home ranges in the Hluhluwe Game Reserve, Natal. Forest was the most consistent, all home ranges contained more than 10%. Tall _Acacia karroo_ and grassland communities occurred to varying extents within each home range. He did not regard the presence of these communities as important. Forest however is important as it provides cover. He also found that certain parts of the home range are only used at night; "Grassland and short _Acacia karroo_ shrubland comprised a significantly greater percentage of the nocturnally occupied part of the home range than that occupied by day..." (p.120). These habitat types must thus have some significance and should not be regarded as unimportant (see diet).

Materials and methods

In order to estimate the large herbivore densities in the Mkuzi Game Reserve, officials have been conducting censusses since 1980. The primary means of estimation was the use of line transects of indefinite width as reviewed by Burnham, Anderson & Laake (1980). Thirteen line transects are walked each year during the dry season. These transects are placed in such a way that all land types and vegetation types are sampled.

The density of each species was determined in each of the land types separately and then combined to produce a total figure for the reserve as a whole. This method has been used since 1980, (excluding 1981), and all data up to 1988 were made available for this study. As densities were available for each species in each land type for a number of consecutive years, in which ungulate densities and rainfall varied, it presented an excellent opportunity to determine not only long term habitat selection but also the dynamics thereof.

The method described by Pettifer & Stumpf (1981) was used to determine the habitat selection of nyala and impala for each year. The following formulae were used:

$$x_i = y_i/y$$

$$y_i = n_i/d_iA_i$$

Where x_i is the preference index

y_i is the mean number of animals observed/census/hectare in unit$_i$ for a specific season,

y is the total number of animalsobserved

n_i is the total number of animals observed in unit$_i$ during a specific season

d is the number of censuses conducted in the i'th unit for a specific season,

A_i is the area in hectares of unit_i

and $i = 1,2,3, \ldots, z$ where z represents the number of units utilised by the animals.

$$\bar{y} = \text{Sigma}(n_i/d_iA_i)/z$$

i.e. $\bar{y}$ is the mean number of animals counted/census/hectare in all the units utilised by the animals.

$$\bar{x} = \text{Sigma}(y_i/\bar{y})/z = 1$$

so that $x_i > 1$ indicates an above average preference for unit_i a complete even distribution will be indicated by $x_i = 1$ and below average selectivity by $x_i < 1$.

From the densities given in Table 2a & b, it was possible to determine the Pettifer & Stumpf Habitat Selection Index (PSHPI). The relative energy consumption (expressed as AU, animal units) of nyala and impala were determined after Goodman (1990). The AU for each species was calculated as $(455/m)^{0,75}$. The relative energy consumption was then related to the density of each species in each land unit and expressed as AU per unit area; Km^2.

Table 2a. The densities of impala in the five land units from 1980 to 1988, as well as the relative energy consumption in AU/km^2.

Yr	Jr	Cr_3	Pl	Cr_3	Al	Overall	Pop. Size
1980	0,4639	0,3495	0,5647	0,4956	--	0,4192	9755
1982	0,5002	0,3138	0,2758	0,3642	--	0,3642	8475
1983	0,3458	0,4598	0,0881	0,3429	--	0,3117	7382
1984	0,2931	0,1740	0,2421	0,1617	0,0808	0,2079	5900
1985	0,3048	0,1245	0,2162	0,1171	0,0878	0,1839	5268
1986	0,2259	0,2089	0,1651	0,1298	0,1001	0,1780	5098
1987	0,2248	0,1587	0,2140	0,1626	0,1054	0,1967	5634
1988	0,3052	0,2128	0,4350	0,1984	0,0964	0,2440	6993
$\bar{x}$	0,3330	0,2502	0,2751	0,2465	0,0937		
AUkm^2	5,379	4,042	4,444	3,982	1,514		

Mass 40kg

AU 6,19

Table 2b. The densities of nyala in the five land units from 1980 to 1988, as well as the relative energy consumption in AU/km^2.

Yr	Jr	Cr_3	Pl	Cr_2	Al	Overall	Pop. Size
1980	0,0388	0,0611	0,1322	0,1439	--	0,0866	2015
1982	0,0354	0,0878	0,2410	0,2009	--	0,1204	2801
1983	0,0185	0,1451	0,2744	0,1880	0,1901	0,1257	2926
1984	0,0231	0,0727	0,2884	0,1284	0,2915	0,0897	2570
1985	0,0202	0,0611	0,1471	0,1608	0,0762	0,0841	2409
1986	0,0348	0,0770	0,3580	0,2430	0,2430	0,1484	4251
1987	0,0275	0,1008	0,1744	0,1578	0,1145	0,1004	2875
1988	0,0373	0,0936	0,1727	0,1793	0,4752	0,1343	3846
$\bar{x}$	0,0295	0,0874	0,2235	0,1752	0,2318		
AUkm^2	0,644	1,912	4,890	3,834	5,072		

Mass 60kg

AU 4,57

Results

The PSHSI for impala and nyala are given in Table 3a & b. The mean in each land unit is given and this was used to express the two species' long term habitat distribution. From Figure 6a it can be seen that impala use the Lebombo Rhyolites and Pleistocene sands more than expected at an even distribution. The Late and Early Cretaceous and Alluvium are used less than expected at an even distribution.

Nyala occur at above average densities in the Pleistocene, Alluvium and Late Cretaceous land units while the Lebombo Rhyolites and Early Cretaceous are utilised well below the averages expected at an even distribution (Figure 6b).

Figure 7a shows the density distribution of impala and nyala in the reserve, which corresponds closely to the relative energy consumption of impala and nyala (Figure 7b) in the Mkuzi Game Reserve.

The only land unit which is selected by both species is the Pleistocene sands in the centre of the reserve. On average nyala densities are the highest (1,557 anim./ha) in this land unit while impala occurred on average at 1,338 anim./ha in their most preferred habitat and at 1,096 anim./h in the Pleistocene sands. Figure 8 illustrates this well where the

Table 3a The Pettifer and Stumpf Habitat Preference Index of impala, in the Mkuzi Game Reserve from 1980 to 1988 and the mean thereof.

Yr	Jr	Cr_3	PL	Cr_2	Al	y
1980	0,990	0,746	1,205	1,058	--	0,4684
1982	1,376	0,863	0,758	1,002	--	0,3635
1983	1,118	1,487	0,285	1,109	--	0,3092
1984	1,540	0,914	1,272	0,849	0,425	0,1903
1985	1,792	0,732	1,271	0,688	0,516	0,1701
1986	1,361	1,259	0,998	0,782	0,603	0,1660
1987	1,299	0,923	1,236	0,939	0,609	0,1731
1988	1,225	0,854	1,745	0,796	0,380	0,2492
$\bar{x}$	1,338	0,972	1,096	0,903	0,507	
Rank:	1	3	2	4	5	

Table 3b. The Pettifer and Stumpf Habitat Preference Index of nyala, in the Mkuzi Game Reserve from 1980 to 1988 and the mean thereof.

Yr	Jr	Cr_3	Pl	CR_2	Al	y
1980	0,413	0,650	1,406	1,531	--	0,0940
1982	0,250	0,621	1,706	1,422	--	0,1413
1983	0,113	0,888	1,681	1,152	1,165	0,1632
1984	0,144	0,152	1,793	0,798	1,813	0,1608
1985	0,217	0,656	1,580	0,727	0,818	0,0931
1986	0,182	0,403	1,873	0,271	1,271	0,1912
1987	0,239	0,876	1,516	1,372	0,996	0,1150
1988	0,195	0,488	0,901	0,936	2,480	0,1916
$\bar{x}$	0,219	0,629	1,557	1,026	1,424	
Rank:	5	4	1	3	2	

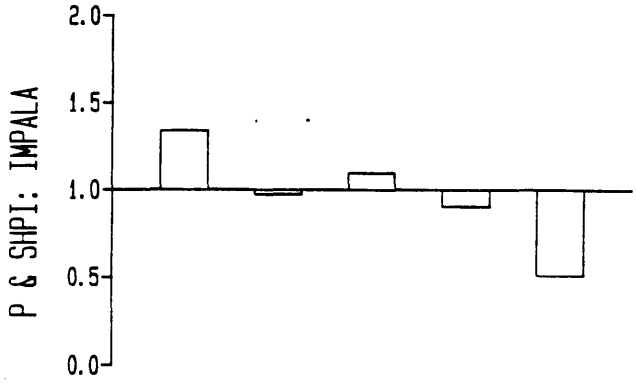


Figure 6a. The mean PSHPI of impala for the five land units in the Mkuzi Game Reserve

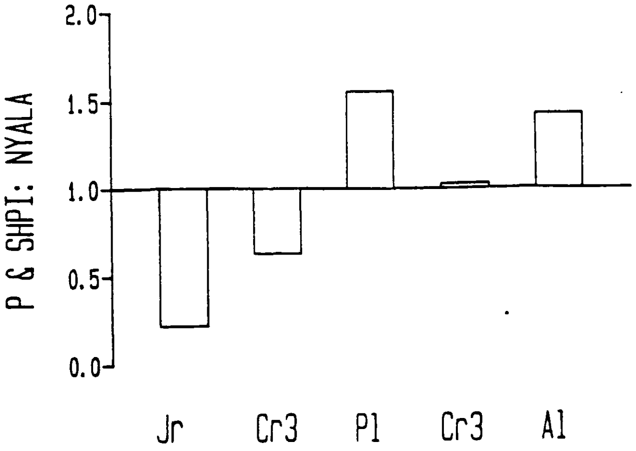


Figure 6b. The mean PSHPI of nyala for the five land units in the Mkuzi Game Reserve.

land units are ranked in order of preference for the two species and are plotted against each other. It is apparent from this figure that a negative correlation does exist between the ranked land unit distribution of the two species, the Pleistocene sands being the only land unit which does not follow this pattern as it is preferred by both species.

Tables 2a & b reveal the energy consumption of impala and nyala in each land unit. These figures represent an average from eight years to produce the long term relative energy consumption. Figure 9 shows that a negative correlation exists between the relative energy consumption of the two species in each land unit, illustrates the same pattern as in Figure 8. Again the Pleistocene sands (and possibly the Cr3) are the only exception/s, where both species consume relatively high amounts of energy per unit area.

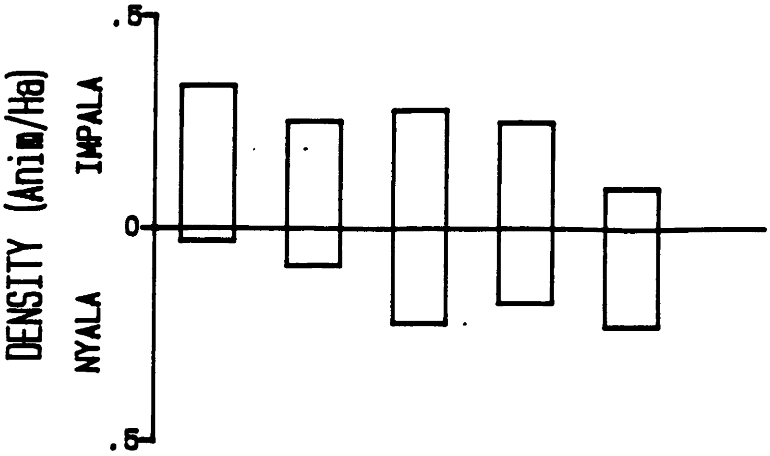


Figure 7a. The average density of impala and nyala in the five land units.

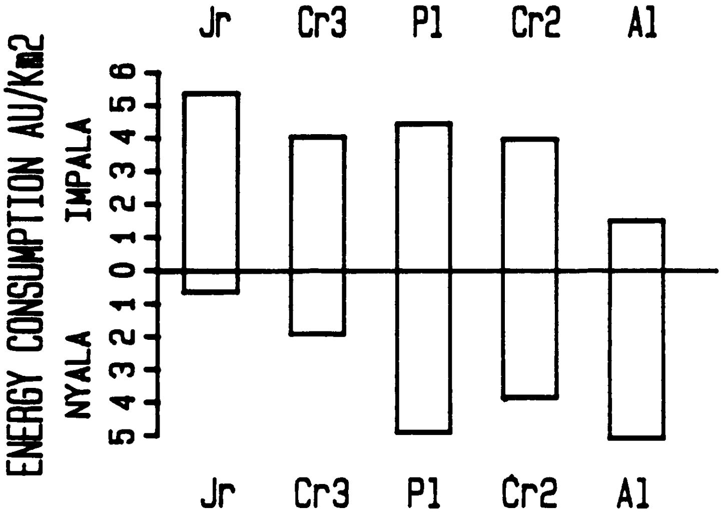


Figure 7b. The relative energy consumption of impala and nyala in the five land units.

Discussion

Impalas' most preferred habitat is the Lebombo Rhyolites followed by the Pleistocene sands. Both the lower and upper Cretaceous land units are selected against (though close to a even distribution) while the Alluvial soils next to the rivers and pans are strongly selected against (PSHPI = 0,507). The vegetation on the Lebombo Rhyolites is described by Goodman (1990) as a Dry Mountain Bushveld and grassveld. The dominant species are; *Combretum apiculatum*, *Acacia nigrescens*, *Themeda triandra*, *Heteropogon contortus* and *Cymbopogon excavatus*.

This land type offers good grass stands throughout the year with a fair amount of woody material. A further attraction in this hilly land type is probably the vegetation occurring in the stream beds and drainage lines. This not only offers cover and shelter in adverse weather conditions but also good quality food.

The available food in the open woodland, drainage lines and stream beds, together with the open structure of this land unit allows impala to congregate in large groups. Group size in the Lebombo rhyolites are significantly bigger than groups in other land types ($p < 0,05$). These large groups have well known advantages concerning predator detection and a decrease in time spent on vigilance.

Evans (1979) described the habitat requirements of nyala as specialized. Nyala select densely bushed areas in the form of dry forest, thicket and dense woodlands (Vincent, Hutchens & Bigalki 1968, Davison 1971, Pienaar 1974). Anderson (1980) calculated the community percentage composition for nyala and concluded that forest is the most important community as it provides cover. Various authors stress this point and the vegetation in the drainage lines and stream beds is limited. Thus the Lebombo rhyolites do not provide the habitat requirements of nyala.

The preferred land unit of nyala, the alluvial floodplain is more suited for nyala as it provides this ungulate with dense bush in the form of Riparian forest and woodland. The presence of the tall <u>Acacia</u> <u>karroo</u> and grassland communities were not regarded as important by Anderson (1980). Nyala do however wander into open habitat to graze when succulent grass is available. Monocotyledons comprise a fair amount of the diet of nyala (see chapter on diet). As little or no grass cover exists in these dense woodlands and forests, the floodplain grasslands are thus very important.

Two hypotheses are proposed to explain why impala reject the alluvial floodplain; vegetation may not be suitable for impala (the grass on the floodplain being tall) and very wet conditions during the rainy season may be a deterrent, or impala are excluded from this habitat type by interferance competition by nyala.

Impala avoid the Cretaceous land types although these are close to what can be expected from an even distribution, while nyala select strongly against the Lower Cretaceous (Cr_3) and prefer the Upper Cretaceous (Cr_2) (the latter preference is also close to what is expected from an even distribution).

From these results it is evident that impala and nyala are segregated clearly on the basis of habitat. Nevertheless Figure 8 shows that the Pleistocene sands are preferred by both the species which is confirmed by their relative energy consumption (Figure 9).

Highest densities of impala occurred in the west with lowest densities in the eastern part of the reserve as confirmed by their habitat preference. In contrast, nyala occurred at highest densities in the east (their preferred habitat) with lowest densities are in the west (the rejected habitat). The Pleistocene sands in the centre of the reserve was the area of greatest overlap. The only two permanent water holes in the reserve occur here and together with the vegetation type induced both species to aggregate here in high densities. Impala, could be attracted to this land unit by the available drinking water, whereas nyala, which are apparently less dependant on water may be attracted by specific habitat requirements other than surface water. Vegetation in this land unit is made up of a mosaic of Red Sand Bushveld, Mixed Bushveld and Sand Forest (Goodman 1990) (for a description of each vegetation type see Chapter 1: Study Area).

Conclusions

Impala and nyala utilise different land units, only occurring in substantial numbers together in the Pleistocene sand land unit. Impala prefer the western while nyala prefer the eastern part of the reserve. Possible competition is minimized by the differential habitat preference. Both species occur together at high densities in the Pleistocene sands but probably resources are not limited in this land unit.

CHAPTER 4

The effect of habitat, rainfall and density on group size of impala.

Introduction

The life history patterns among African ungulates are explained by Jarman (1974) and Estes (1974) by two non-exclusive theories relating feeding style and habitat selection to body size, group size and behaviour (Wirtz & Lorscher 1983). These are the major determinants of group size, other ecological factors have a secondary effect.

The function of ungulate groups has been studied by various authors in both the Cervidae and Bovidae (Hamilton 1971, Jarman 1974, Brown 1982, Lipetz & Bekoff 1982, Giraldeau 1984, Lagory 1986). Most authors regard vigilance as the driving force behind forming bigger groups. Optimal group size, however, is described by Brown (1982) as a compromise between advantages gained by sharing costs and disadvantages arising from resource depletion.

Large variations in group size are documented both within and between species (Jarman 1974, Wirtz & Lorscher 1983). The underlying proximate and ultimate forces behind these variations are not clear (Pulliam & Caraco 1984). Several causes have been documented. The group size in open areas is bigger than in more dense habitat (Jarman 1974, Estes 1974, Lagory 1986), the theory being that because of their conspicuousness in open habitat animals group together, while in dense vegetation animals are more concealed. Underwood (1982) however suggested that animals in dense vegetation are more vigilant. This may well be because of their smaller group sizes in the thicker vegetation. Visual contact between individuals is hampered in thick vegetation so that groups disperse (Walther 1972) and smaller groups are formed.

Jarman (1974) described how feeding style through competition for food can negate group size. Concentrate selectors (Jarman's class A ungulates) are solitary or associate in cpules because of their selection for high quality food items. Individuals following others will find that preferred food items have already been taken and will then have to forage further away from each other. In the same way the vegetation type may induce smaller or larger groups. A habitat type with a high concentration of preferred food items will sustain a bigger group without the individuals in the group experiencing competition by depletion. Ferguson (Unpubl.) proposed a theory of optimal group size in which he illustrated an optimum group where survival from predation through vigilance stimulates bigger groups and food ingestion limited by competition or depletion will prevent groups from growing too big.

It is apparent that several factors affect group size. Feeding style, behaviour and body size are the ultimate factors involved here while density and food abundance are proximate factors. Several authors have reported a positive correlation between group size and density for African ungulates, for example Uganda Defassa waterbuck *Kobus defassa ugandea* (Spinage 1969), Bohor reedbuck *Redunca redunca* (Wirtz & Lorscher 1983), zebra *Equus burchelli bohmi*, and kongoni *Alcelaphus buselaphus cokei* (Leuthold & Leuthold 1975) all had bigger groups at higher densities.

The aim of the present study was to investigate the influence of habitat (forage availability), rainfall (a proximate factor influencing forage availability) and density (number of animals per unit area) on the observed group size of impala.

Rainfall improves vegetation in both quality and in quantity. Therefore the hypothesis can be advanced that bigger groups will be found in a species' preferred habitat, and an increase in rainfall will stimulate aggregation. The density of the animals should however not effect the group size as it does not interfere with any of the factors affecting group size.

Material and Methods

Transects were walked in the Mkuzi Game Reserve in order to estimate ungulate densities following Burnham, Anderson &

Laake (1980). Thirteen transects are walked each year towards the end of the dry season. These transects are placed in such a way that animals in all land types are sampled. The following relationship was used to estimate density:

$$D = n.f(o)/2L$$

Where D is a group density estimate

n is the number of groups seen

f(o) is the probability density function at zero distance from the line

L is the length of the transect walked.

The estimation of f(o) was based on the Fourier series expansion of the probability density function following Burnham _et al_ (1980). Impala density was determined annually in each land unit from 1980, except in 1981.

The method of Pettifer & Stumpf (1981) was used to determine the habitat selection of impala. The method is based on the formula:

$$\bar{x} = \text{Sigma}(y_i/\bar{y})/z = 1$$

where $\bar{y}$ is the mean number of animals counted/ census/ hectare in all the units utilised by the animals,

y_i is the mean number of animals counted/ census/

hectare in unit$_i$

z is the number of units utilised by the animals.

$\bar{x} > 1$ indicates an above average selection for unit$_i$, a completely even distribution by $\bar{x} = 1$ and a below average selection by $\bar{x} < 1$.

Impala were reduced in the reserve from 0,419 animals/ha in 1980 to 0,178/ha in 1986, impala then increased to 0,244/ha in 1988 (Figure 10). Group sizes in each habitat could be extracted from the main data base. Spatial variation of rainfall in the reserve is not great (Goodman 1990) and data measured at the Mantuma camp were used.

Data were analysed using the SAS Linear Models Procedure.

Results

Table 4 contains the data used to determine the Pettifer & Stumpf habitat preference depicted in Figure 11. It is apparent that impala select habitat in the west of the reserve in preference to to that in the east. The mean group sizes at average rainfall and density are given in Table 5. The Bonferroni test was used to determine differences in the group size when corrected for density and rainfall (Table 5). The group sizes in the Lebombo Rhyolites and Lower Cretaceous differred significantly from the rest ($p < 0,05$). Rainfall

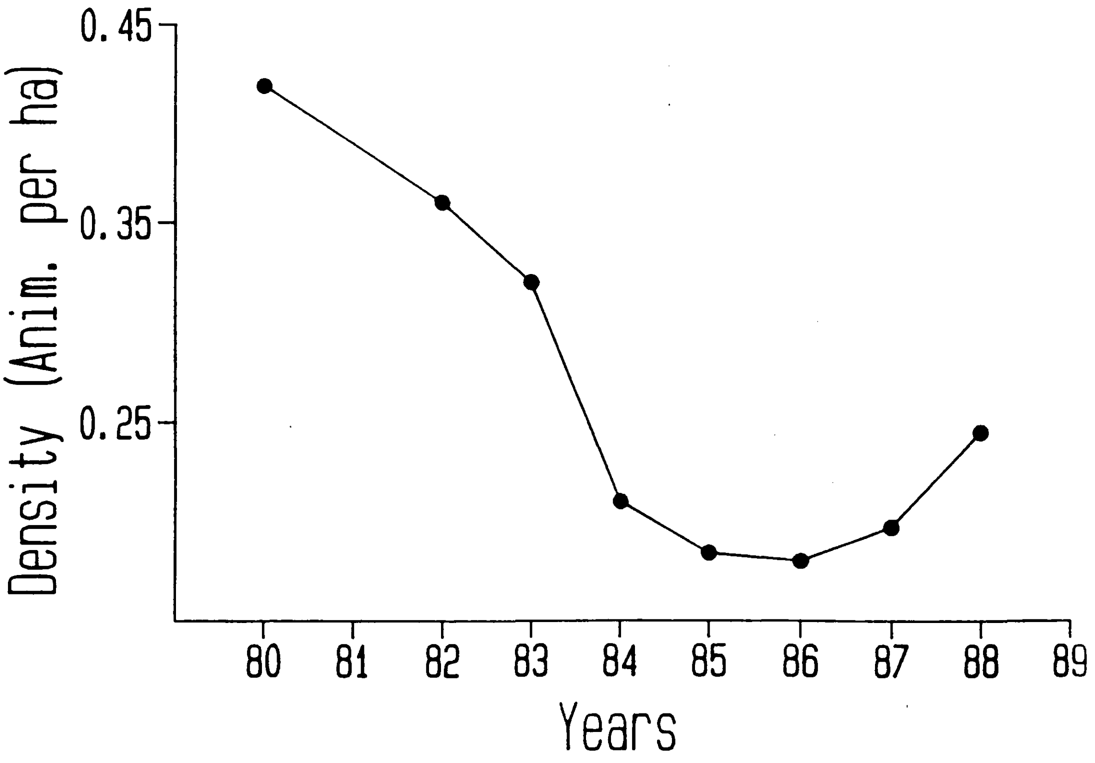


Figure 10. The density (Anim. per ha) of impala in the Mkuzi Game Reserve, from 1980 to 1988.

Table 4. The Pettifer and Stumpf Habitat Preference Index of impala, in the Mkuzi Game Reserve from 1980 to 1988 and the mean thereof.

Yr	Jr	Cr_3	Pl	Cr_2	y
1980	0.990	0.746	1.205	1.058	0.4684
1982	1.376	0.863	0.758	1.002	0.3635
1983	1.118	1.487	0.285	1.109	0.3092
1984	1.134	0.799	1.112	0.742	0.2177
1985	1.599	0.653	1.134	0.614	0.1906
1986	1.238	1.145	0.905	0.711	0.1824
1987	1.183	0.835	1.126	0.856	0.1900
1988	1.060	0.739	1.511	0.689	0.2878
$\bar{x}$	1.212	0.908	1.005	0.847	

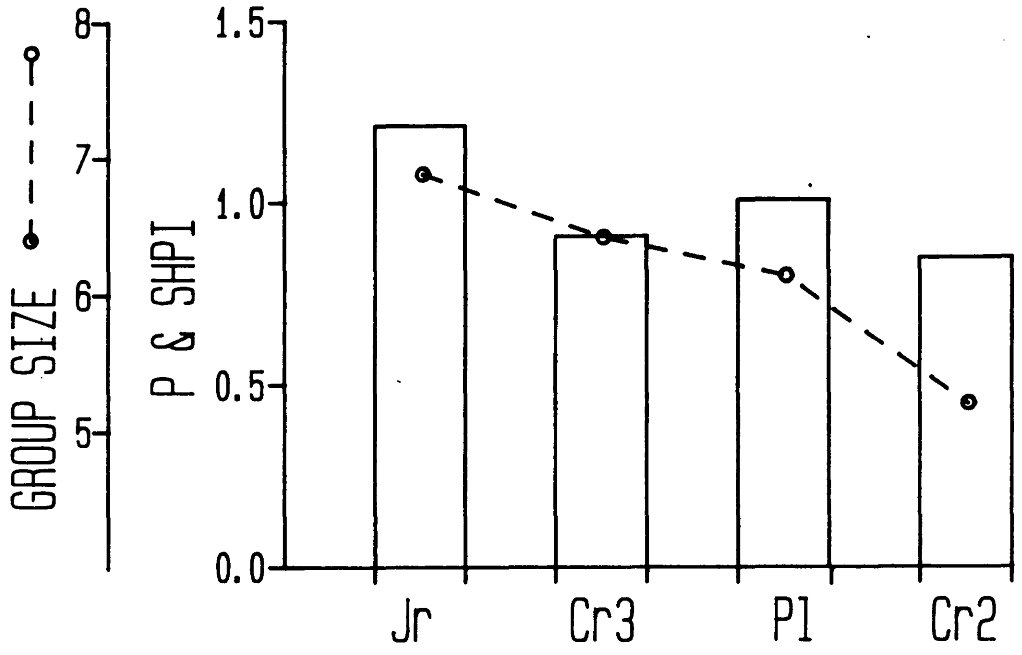


Figure 11. The Pettifer and Stumpf Habitat Preference Index of impala and the group sizes in the four land units considered.

Table 5. Group sizes of impala in the Mkuzi Game Reserve, means and at average rainfall and density in the four different habitat types.

HABITAT	CORRECT. GRP SIZE	DIFFERENCE
Lebombo R.	6,873	***
Upper Cret.	6,435	n.s.
Pleist. sands	6,143	n.s.
Lower Cret.	5,219	***

*** P = 0,0312

n.s. = not significant.

significantly influenced group size ($p < 0,01$). A 1mm increase in rainfall increases group size by 0,0023 animals per group.

Land units (and therefore vegetation) influence group size significantly ($p < 0,05$). Density of ungulates however does not have any effect on the group size ($p = 0,8476$).

Discussion

Various authors have reported on the influence of environmental factors (other than those described by **Jarman** (1974)) on ungulate group size, but none of these explains the mechanism or driving force behind these changes. Most of these reports examined only one or two of these factors at a time which makes comparison between them very difficult. The data used in the present paper were collected in one game reserve over a period of eight years, during which the rainfall varied from 316 to 1003 mm per annum and density of impala were reduced from a peak of 0,419/ha. to a nadir of 0,178/ha. by means of culling. Four different habitat types were examined and censuses were done during the same time of year to minimize the effect of seasonal changes on social behaviour that could affect group size.

Rodgers (1977) found that species with an open social structure have more flexible group sizes than those with more closed social structures. Impala are described as having an open social system (Schenkel 1966, Rodgers 1977). The group size of impala should thus vary according to ecological factors.

From Figure 11 it is clear that the Lebombo Rhyolites are strongly preferred by impala while the Lower Cretaceous in the east of the reserve is rejected. The two land units in the centre of the reserve are used by impala almost as expected at an even distribution. The Lebombo Rhyolites are thus accepted as the best habitat for impala in the reserve, while the Lower Cretaceous is considered the most unsuitable habitat. Following this hypothesis that the Lebombo Rhyolites should thus provide the best food resources for impala per unit area and group sizes in this habitat conform with the hypothesis. Furthermore, the lowest mean group size was observed in the Lower Cretaceous, while group sizes in the two land units in the centre of the reserve (Upper Cretaceous and Pleistocene sands) do not significantly differ (these habitats are also used close to an even distribution, $\bar{x} = 1$). These differences may also be attributed to the openness of the habitat. The Lebombo Rhyolites are largely open woodland, while in the rest of the reserve the canopy is more closed.

group sizes at different densities (see above). Higher population densities should however not increase group size as the forces behind group formation are not altered. At average rainfall and habitat conditions intra-herd competition will prevent additional individuals from entering the group. The additional individuals will then have to group together which results in more groups rather than bigger groups. Wirtz & Lorscher (1983) compared the group sizes of Bohor reedbuck from different studies and concluded that the different group sizes observed were due to the influence of density differences. However they did not consider habitat as a factor influencing group size, while this variable may have been responsible as shown in the present study.

Leuthold & Leuthold (1974) describe significant differences between group sizes of zebra and kongoni north and south of Tsavo East National Park. They consider both habitat and density to be factors controlling group size (densities in the north differred from those in the south) and specifically state the uncertainness of the effect of density; "Whether this relationship is a direct one, or whether it is a secondary consequence of habitat conditions just discussed, is impossible to decide." Spinage (1969) also found a positive relationship between group size and density for waterbuck, the different densities were however also from different areas and again the effect of habitat is not considered. As suggested by Leuthold & Leuthold (1974) the bigger groups at high densities may be a consequence of the habitat. The better habitat will sustain more individuals per unit area allowing bigger groups which will ultimately result in a higher density.

Conclusions

Group sizes in ungulates with an open social system are influenced not only by the specific feeding style of a species but also by certain environmental factors. Food availability correlates positively with group size (Dunham 1979). Habitat and rainfall are determinants of food availability and variation in these correlate with group size. Openness of habitat may also increase group size through vigilance. Density on the other hand does not alter the main forces behind optimal group formation for ungulates (food availability and predation) and as indicated by results from this study does not influence group size in impala.

CHAPTER 5

Isotopic evaluation of a microscopic method to determine the monocotyledon : dicotyledon ratio of impala rumen contents.

Introduction

The accurate assessment of ungulate diets is vital in both research and management. Various methods have been used to determine the monocotyledon:dicotyledon ratio of rumen contents and faeces. The aim of the present study was to evaluate the accuracy of a method used to determine the monocotyledon : dicotyledon ratio during a previous study (viz. van Rooyen & Skinner 1989) with a view to using the same method in the present study.

Various authors sieved rumen contents before analysis (Dirschl 1962, McCaffery, Tranetki & Piechura 1974, Owaga 1978) thus removing all small particles. With most small particles removed from the sample identification of particles can be done more rapidly with fewer unidentified items. This may however introduce a bias in the method which must be assessed for and corrected. Owaga (1978) used two mesh sizes and sieved the rumen contents from seven ungulate species in order to detemine the effect of mesh size on the results. Samples that were screened through the two mesh sizes produced different results in the case of some species and similar results in others.

The main problem, however, is that the accuracy of the method cannot be tested by conventional methods. The results from the same rumen contents when analysed after screening with two or more mesh sizes may be similar, but this does not necessarily prove that the result will be the same as the actual ratio in the whole sample.

Not all plants assimilate carbon dioxide from the atmosphere via the Calvin-Benson photosynthetic pathway. In the Calvin cycle the initial product of carbon dioxide fixation is the three-carbon molecule, phosphoglyceric acid (PGA), while a four carbon molecule, oxaloacetic acid, constitutes the first carboxylation product in the Hatch-Slack mechanism (Hatch & Slack 1970). Thus the designations C_3 and C_4 to distinguish between plants utilising the two different pathways. Most monocotyledons are of the C4 type while most dicotyledons are of the C_3 type. C_3 grasses do occur in southern Africa but are generally geographically separated from the C_4 grasses (Vogel, Fuls & Ellis 1978).

This phenomenon enables one to use the difference in the $^{13}C/^{12}C$ isotope ratio between C_3 and C_4 plants to distinguish between grazers and browsers (Vogel 1978). The isotopic assessment of a rumen sample will thus give an unbiased estimation of the monocotyledon:dicotyledon ratio. This method is expensive and time consuming but is nevertheless accurate and can be used to evaluate a quicker, less expensive method.

Materials and methods

Rumen samples from impala collected in the Mkuzi Game Reserve were separated; one half was dried for isotopic assessment and the other half was sieved for microscopic determination of the monocotyledon : dicotyledon ratio. Two mesh sizes, 3mm and 1mm were used to obtain particles of between $1mm^2$ and $9mm^2$ in size. Samples were then stained using Saphranine-O dissolved in acetic acid and distilled water. The samples were placed in a Buchner funnel on top of a sheet of filter paper. The samples were then suspended in water until evenly distributed, after which the water was removed by suction. Samples were then analysed using a dissection microscope at six times magnification. A grid with 100 points was projected over the sample using a drawing arm. Five hundred particles were counted on a multicounter and placed in one of the following categories: monocotyledon leaf, monocotyledon sheath or stem and dicotyledon leaf, stem or fruit.

Isotopic assessment of the samples was done by the National Physical Research Laboratory, CSIR, using the limestone standard (PDB). The isotope ratio is given relative to a limestone standard. Thus a sample with a relative $^{13}C/^{12}C$ ratio, of -25 parts per thousand (^{o}/oo) contains 25 ^{o}/oo less ^{13}C than the standard PDB carbon.

The average relative $^{13}C/^{12}C$ ratio of C^{3} plant foliage is -26,5 ^{o}/oo, while that of grasses is -12,6 ^{o}/oo (Craig 1953). By using these values as a standard the C3 content of the sample can be determined.

Results

Figure 12 shows the dicotyledon content determined with the microscopic method plotted against the isotopic method. When values are converted to percentages a significant correlation ($r = 0,988$; $p < 0,005$) exists between the two methods. It is however clear that in three samples the dicotyledon proportion was underestimated by the microscopic method.

Discussion

Although in most samples the two methods correlated well the dicotyledon proportion of three samples was underestimated by the microscopic method. On closer investigation it was revealed that samples 2007, 2016 and 2019 each contained more than 8% seeds.

Therefore it may be assumed that the seed content of the sample is either under estimated and/or that seeds contribute more to the weight of the sample than dicotyledonous leaves because of their volume. Differences in all other samples did not exceed 11%.

The microscopic method described in this thesis has been proved accurate for analysing impala rumen contents. It is however realistic to assume that the dicotyledon content could be underestimated when animals consume large quantities of pods. However this occurs only during the short period when pods are shed. Then dicotyledon intake of impala would in any case be high. Furthermore, the importance of seeds in the diet of impala has still not been quantified. Jarman (1976) found less than 6% of seeds remaining in the faeces of impala after feeding them on known amounts of seeds, and concluded that most seeds are broken up and digested by these animals. On the other hand it has been suggested that ruminants eject seeds while chewing pods and during rumination (Coe & Coe 1987). Furthermore seeds that passed through the digestive tracts of kudu and eland were not digested, and subsequently were successfully germinated (Coe & Coe 1987). It is therefore assumed that only the pod is eaten and utilised as a source of protein. Should this be the case, then the underestimation of dicotyledons in samples by the microscopic technique containing a high proportion of seeds results in a more realistic interpretation of available food in the rumen.

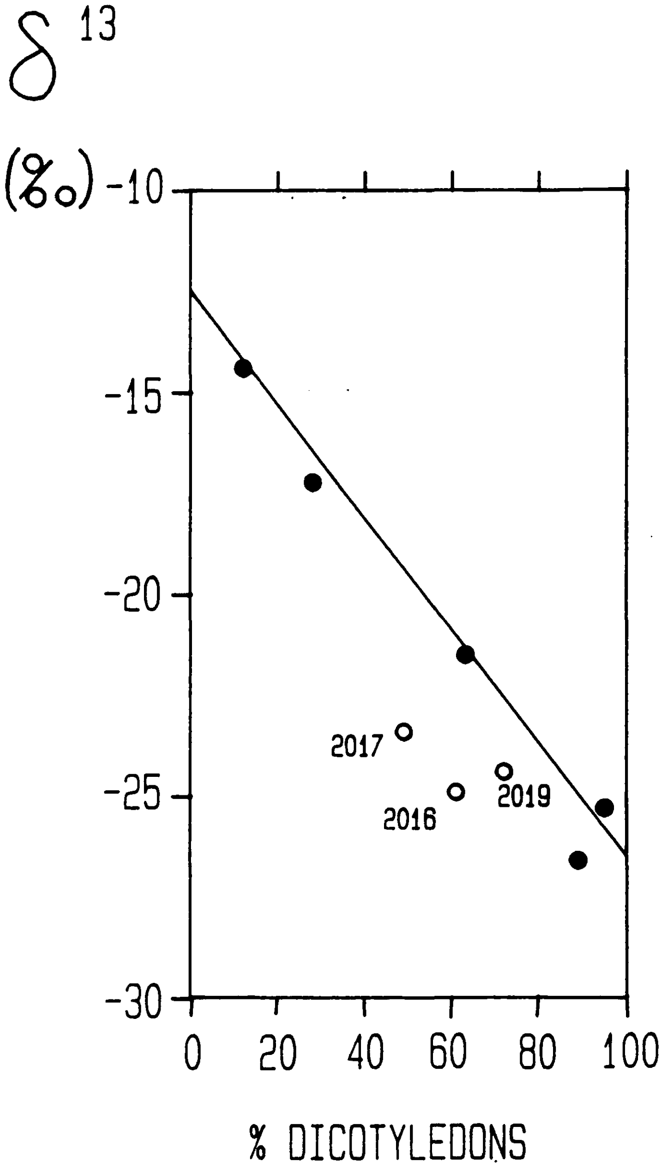


Figure 12. The relationship between the isotopic and microscopic techniques for assesment of rumen contents.

CHAPTER 6

The diet of impala and nyala in Zululand.

Introduction

The proccess of diet selection by ungulates is fundamental to understanding many aspects of ungulate ecology (Hobbs, Baker & Gill 1983). Body size and morphology limit the range of foods they can efficiently eat (Hoffman 1973), while food selection affects the social structure, patterns of dispersal and predator avoidance (Jarman 1974). A sound knowledge of the diet as well as the factors affecting it are thus crucial in the understanding of ungulate ecology and management.

Impala and nyala occur in substantial numbers in the Zululand game reserves. The aim of this chapter was to determine the diet (composition and quality) of these two ungulates.

Jarman (1974) described the feeding habits of impala as flexible, feeding selectively on a wide variety of grasses and browse within a number of vegetation types over a large home range. He further stated that their diet changes seasonally, as does their preference for vegetation types. Dicotyledon content in the diet of between 60% and 65% was found by Talbot & Talbot (1962), McAllister & Bornman (1972), Monro (1979) and

Dunham (1980) while Jarman (1971) recorded the lowest dicotyledon percentages of less than 10%. Impala are selective feeders, selecting low fibre high protein plant parts. This is made possible by their relative narrow muzzles compared to grass/roughage feeders (Janis & Ehrhard 1988).

In order to accommodate such a catholic diet Hofmann (1973) reported that impala exhibit reversable stomach linings. These changes refer to the surface enlargement of the rumen, this being due to pappillary growth or recession and mucosal alterations in the rumen and the abomasum (Hofmann & Stewart 1972). These changes in the rumen and abomasum are related to the fibre content of the diet (Hofmann 1973).

Jarman & Sinclair (1979) reported that impala attempt to meet nutritional requirements by seasonal selection of habitat, plant species and plant parts, futhermore van Rooyen & Skinner (1989) reported on differences in the composition of the diet between territorial rams, bachelors and ewes. Such differences could be attributed to habitat selection (bachelors), time available for foraging (territorial rams) and the possible nutritional requirements of ewes. Dunham (1980) found ewes to have a significantly higher quality diet than rams, probably as a result of habitat selection.

Detailed data on the diet of nyala have not been published. Several authors have described nyala as primarily or predominantly browsers, although they note that nyala do include a fair amount of grass in their diet when this is available (Vincent, Bigalke & Bass 1968; Anderson & Pooley 1977). Anderson (1979) refers to nyala as intermediate feeders.

Materials and Methods

Impala and nyala were collected monthly in the Mkuzi and Ndumu Game Reserves respectively. Rumen samples were taken from adjacent to the oesophagus and stored in 10% formalin for later analysis.

All rumen samples were sieved following the method of Monro (1982) and Owaga (1978). Particles of sizes $1mm^2$ - $3mm^2$ were placed on a grid under a dissecting microscope, and identified as either monocotyledon or dicotyledon (see Chapter 5).

Nitrogen content of samples was determined by the Kjeldahl method (A.O.A.C. 1975). Crude protein was estimated by multiplying the nitrogen value by 6,25. Rumen microorganisms can however also contribute to the nitrogen and this was tested by washing rumen contents under running water and the crude protein content compared to unwashed samples.

Results

The monocotyledon:dicotyledon ratios for impala and nyala are illustrated in Figures 13 and 14. Dicotyledon content in the rumens of impala and nyala increase as winter progresses and grass lignifies. Soon after the first rain when sprouting grass becomes available, monocotyledon content increases rapidly to a maximum. Dicotyledon content then slowly increases again in the case of nyala and decreases in the case of impala.

Significantly less nitrogen was contained in washed samples than in unwashed rumen contents (Table 6). Crude protein content decreased from April to August for both species although the dicotyledon content increased during this period. A sharp increase took place from August, when the first rain occurred, to September from where it decreased slightly. Figure 15 shows a significant (r = 0,63 t = 3,035 df = 14; p < 0,01) positive correlation between the monocotyledon proportion and the crude protein content in the rumen when data of impala and nyala are pooled. The correlation between monocotyledon proportion and crude protein in the rumens of impala alone is significant (r = 0,82 t = 3,79 df = 7; p < 0,01) but not for nyala alone (r = 0,68 t = 2,07 df = 5; p > 0,05).

Table 6. The percentage crude protein in unwashed and washed rumen contents of impala collected during Autumn, Winter and Summer 1987, in the Mkuzi Game Reserve.

Rumen cont.	Unwashed	Washed	Difference	Significance
Autumn	18,656	12,903	5,754	***
Winter	12,402	8,677	3,725	***
Summer	20,631	15,917	4,714	***
			4,730	

t-Test P<0,005 ***

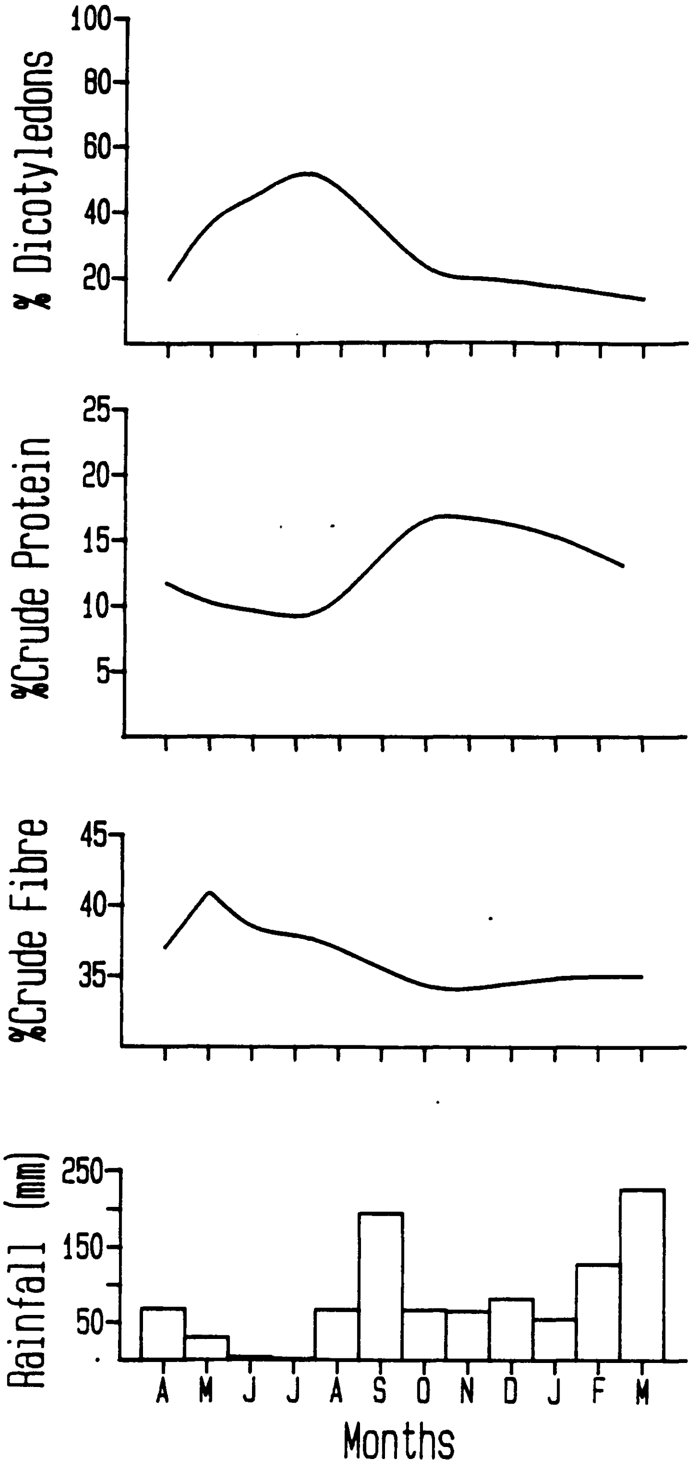


Figure 13. The diet of impala in Mkuzi Game Reserve during 1987/8. The monthly %dicotyledons, %crude rumen protein and %crude fibre in the diet as well as the monthly rainfall in Mkuzi Game Reserve.

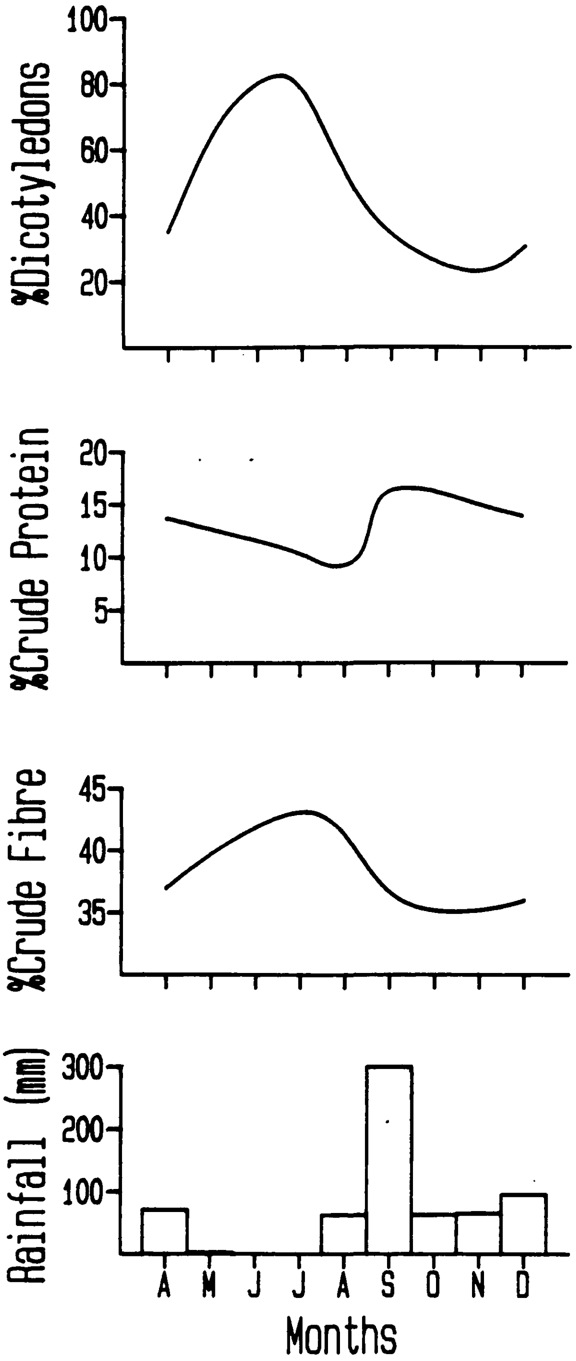


Figure 14. The diet of nyala in the Ndumu Game Reserve during 1988. The monthly %dicotyledons, %crude rumen protein and %crude fibre in the diet as well as the monthly rainfall in Ndumu Game Reserve.

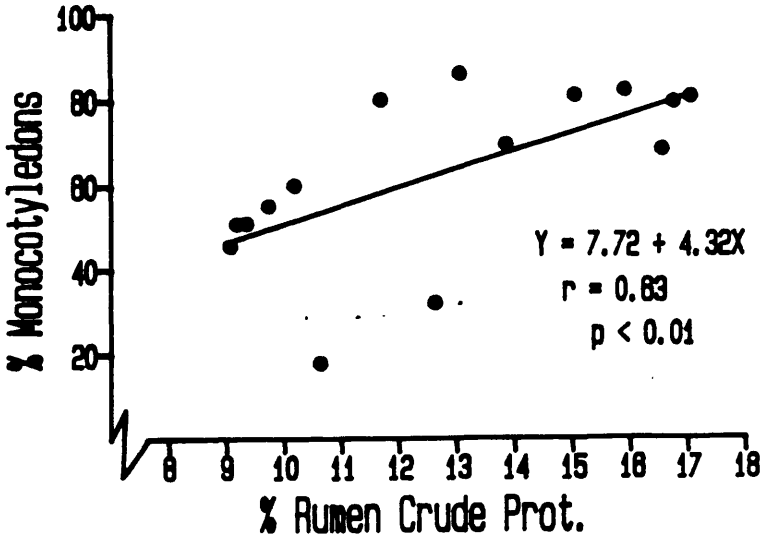


Figure 15. The % monocotyledons of both impala and nyala plotted against the % rumen crude protein. A positive relationship exists between these variables.

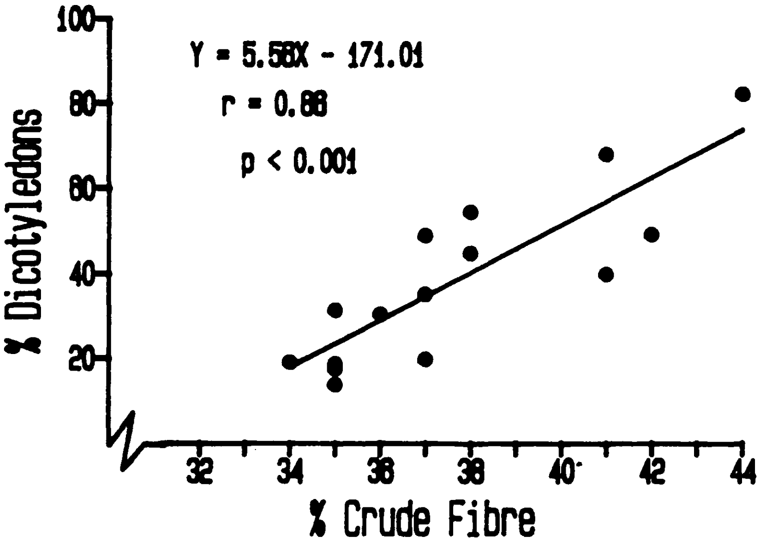


Figure 16. The % dicotyledons of both impala and nyala plotted against the % crude fibre. A positive relationship exists between these variables.

Crude fibre in the diet of both species follows the same trend as that of the dicotyledon content, being high in winter and declining sharply after the first rains when monocotyledon content increases. Crude fibre correlates well with dicotyledon content in the rumen of both species and when data are pooled the relatioship is highly significant ($r = 0{,}86$ $t = 6{,}31$ df = 14; $p < 0{,}001$) (Figure 16).

Discussion

The importance of ruminants lie in the fact that they can convert apparently indigestible carbohydrates and chemically trapped proteins into products useful to mankind. Of the 150 extant ruminant species the majority of research being done today consentrates on two domestic species; sheep and cattle (Hofmann 1989). Nevertheless wild ruminants play an increasingly important role in modern game farming. A sound knowledge of the ruminant's diet in his natural environment as well as the factors affecting it are thus crucial in the understanding of ungulate ecology and management.

The purpose of this chapter was to define the diet of impala and nyala in Zululand and to describe it in relation to the monocotyledon:dicotyledon ratio of plant material ingested and the quality of the diet, measured by the protein and fibre content.

The technique used to determine the monocotyledon:dicotyledon ratios is described and discussed in Chapter 5.

When analysing rumen contents for protein, the inclusion of rumen microorganisms will influence the results. Therefore both washed and unwashed samples were analysed in order to test for possible differences. It was assumed that "all" microorganisms were "eliminated" from the sample when the sample was rinsed under running water. As all samples were collected adjacent to the oesophagus within an hour post mortem it was further assumed that no digestion had taken place. Significantly less nitrogen was contained in washed samples (Table 6). Accordingly the difference in protein content can be attributed to a) the contribution of the microorganisms present in the rumen, b) the recycled urea from the blood and saliva and c) endogenous N from abraded epithelial cells in the rumen (Ørskov 1982).

Dunham (1980) did not wash rumen contents after preservation in formaldehyde, and rumen crude protein percentages are comparable with the unwashed samples in the present study (see Table 6). Skinner et al. (1984) did not wash rumen contents before N determination and attributed high crude protein values obtained to the presence of rumen micro biota and recycled urea. Values between 15,9% and 28,6% crude protein were found, 6% higher than the handpicked simulated diet of impala during the same months. Unwashed rumen contents in the present study were on average 4,73% higher in crude protein than washed rumen contents. Therefore the use of unwashed rumen contents may result in an over-estimation of crude protein in the rumen of ungulates, however the basic trends are not greatly influenced. Although it is possible that some micro-organisms may remain in the sample, most of the recycled urea is lost by washing and crude protein estimation is thus more accurate.

The diet of impala and nyala concur with what would be predicted for intermediate feeders (Hofmann 1988), although Anderson (1979) classified nyala as intermediate feeders he did not present any evidence for this conclusion. Such ungulates are characterised by their ability to change their diet over a short period of time and are highly variable and flexible with regard to diet selected even in a single year or vegetation cycle (Hofmann & Stewart 1972). From Figure 12 it can be deduced that nyala are flexible when selecting food items and do select a diet that varies according to seasons as influenced by rainfall. Moreover, as in the case of impala, nyala show considerable variation in dicotyledon content in their diet, from 18,7% in November to 81,9% in July.

Although the same trend in dietary dicotyledon content is evident in both species these variations in the diet of impala in Mkuzi Game Reserve are not as dramatic as those of nyala in Ndumu Game Reserve. Impala prefer a monocotyledonous diet [being preferrential grazers (Hofmann & Stewart 1972)]. The high rainfall during 1987 in Mkuzi Game Reserve may have made this possible. Nevertheless, Dunham (1980) in reporting even greater seasonal variations in monocotyledon consumption from 94% in summer to 18% in winter is in full agreement. Nyala, on the other hand can be defined as intermediate feeders preferring browse.

In order to explain seasonal dietary changes the quality of monocotyledons and dicotyledons must be taken into account. Novellie (1983) found the crude protein content of dicotyledon leaves (utilised by kudu) to be between 20% and 25% during the early growing season when new leaves appear. These initial high values declined to between 13% and 16% during the dry season when leaves were mature (mature leaves are higher in structural carbohydrates and lignin).

Sauer, Skinner & Neitz (1982) determined the nutritional value of various common tree species utilised by giraffe (Giraffa camelopardalis. They found a positive relationship between moisture content and protein content, and a negative relationship between crude fibre and moisture. The crude fibre will thus increase and crude protein decrease during the dry winter. Dicotyledons will thus have their lowest nutritional value at the end of winter, with low protein and moisture and high fibre contents. The same trends were also described by Bonsma (1942), Joubert & Eloff (1971) and Novellie (1983).

Melton (1978) determined the nutrient content of T. triandra and P. coloratum in the Umfolozi Game Reserve, Natal. He found crude protein and water content to be highest during summer. Crude protein content of T. triandra and P. coloratum varied between two and six percent and increased to between ten and twelve percent during the wet season. Crude fibre did not vary greatly, as expected for stuctural material. It is however known that with age, grass lignifies and digestibility declines. Both graze and browse will thus reach their lowest nutritional value towards the end of the dry season.

These general trends concur with those found by Buys (1987) who compared the nutritional quality of graze to browse for eland (Taurotragus oryx) in the western Transvaal Highveld. He found the nutritional quality of browse superior to that of grass being higher in protein and lower in fibre throughout the year.

From these data the observed diet of impala and nyala can be explained.

The dicotyledon proportion in the rumens of both species increased from April to July as grass became drier with the consequent decline in protein content. More dicotyledons are eaten during winter because of their superior protein content. The protein content of the diet decreased during this period, not because of the higher dicotyledon intake, but as a result of the fact that the protein content in dicotyledons (and monocotyledons) itself decreases during late summer and winter.

Grass leaves although more digestible than dicotyledons are digested more slowly and are more digestible than dicotyledons, thus yielding more protein, but grass takes much longer to digest (Owen-Smith 1982). Moreover with the higher dicotyledon intake the crude fibre content in the diet increased. This correlation may be fortuitous as the fibre content of dicotyledons has been found to be lower than that of monocotyledons (Buys 1987). If this is the case it can be explained by the fact that dicotyledons only predominate in the diet during the dry months when fibre content of dicotyledons is at its highest and monocotyledons are eaten during the rainy season when their fibre content is at its lowest.

Dicotyledon proportion peaked at 54,4% for impala and 81,9% for nyala during July.

Directly after the first rains during August, when succulent grass (high in protein and moisture and low in fibre and lignin) sprouts, the dicotyledon intake decreased dramatically. Together with this decrease in dicotyledons the crude protein content in the diet increased to reach a maximum of 17,1% in October for impala and 16,6% for nyala in

September. The positive correlation between the monocotyledon intake and the protein content of the diet can be explained in the same way as the crude fibre content of the diet. The monocotyledonous material predominates in the diet when crude protein is highest and when this declines during winter both ungulate species switch to browse whose protein content is higher. Dunham (1980) also found a good correlation between monocotyledons in the rumen contents and crude protein.

The positive relationship between protein and monocotyledon content, and the fibre and dicotyledon content in the diet of these animals seems anomalous. Dicotyledons are superior to monocotyledons, being lower in fibre and higher in crude protein throughout the year (Buys 1987). However these positive relationships do not indicate a higher protein content in the diet because of a higher monocotyledon proportion or higher fibre content with a higher dicotyledon proportion. This means that these ungulates are forced to eat dicotyledons when fibre is high and protein is lower because of an even lower protein content in the dry grass and the unacceptability of lignified grass during winter.

The positive relationship between monocotyledon proportion and protein content suggests that sprouting monocotyledons are preferred after the rains when their protein content is relatively high and fibre is low. Sprouting dicotyledons show a similar trend after the first rains but are not preferred because of their higher tannin content. In addition, as preferential grazers (Hofmann & Stewart 1972) impala may be less well adapted to overcome this higher tannin content of browse than nyala. Although in small quantities both species still include dicotyledons after the first rain, which may explain the very high protein proportion in the diet.

Both nyala and impala select an available diet that will best suit their nutritional demands. Grass becomes coarse, high in lignin and less abundant during winter. The monocotyledon intake thus declines during winter. The diet is then supplemented with dicotyledons which are available either as dead fallen leaves or from deciduous trees. These leaves are however lower in protein and high in fibre during the dry season.

Nutrition is important to any animal as it determines the amount of energy and nutrients available for growth and reproduction. Climate, especially rainfall, is the most important factor influencing the quality and quantity of food available to herbivores (White 1978). In areas where rainfall is seasonal, food quality is high during the rainy season and declines during winter. Both impala and nyala changed their diet during the course of the study period in a responce to the quality of food which was influenced by rainfall.

Hofmann (1973) described morpho-physiological changes in the digestive tract of various ruminants in responce to changes in diet. Intermediate feeders in particular have this ability to switch from a browse diet to a graze diet over a short period of time and facilitate digestion and absorption of nutrients with the morpho-physiological changes described by Hofmann (1973). It is probably this reason that makes intermediate feeders like the impala such a successful species, occurring in large numbers in appropriate habitats.

CHAPTER 7

The crude protein requirements of impala for maintenance, pregnancy and lactation.

Introduction.

Digested carbohydrates and fat are merely considered a source of metabolizable energy, and are frequently referred to in terms of kilojoules. Protein on the other hand can serve as a source of energy but it is primarily important as a source of amino acids from which an organism can build its own structural and functional proteins (Lloyd, McDonald & Crampton 1978).

Protein is required for the maintenance of normal basic life processes such as the synthesis of enzymes, replacement of catabolized body tissue and replacement of tissue abraded from internal surfaces of the digestive tract and the skin. More protein is needed for growth, and in the female for pregnancy and lactation.

Ruminants can utilise both protein and non-protein nitrogenous substances because microorganisms in the rumen use both sources of nitrogen to synthesize their own protein used for growth and reproduction. The amino acids of the microbial protein then become available to the host animal by the normal processes of digestion. The use of crude protein in calculation of protein requirements is thus justified in this context.

The protein requirements of domestic ruminants have been studied in detail, but information on African wild ruminants is limited. North American deer protein requirements have been documented (Robbins, Prior, Moen & Visek 1974, Smith, Holter, Hayes & Silver 1975, Kopf, Brown & Drawe 1984, Meyer, Brown & Graham 1984, Schwartz, Regelin & Franzmann 1987). Novellie (1983) followed Moen's (1973) scheme to determine the protein requirements of kudu. The same procedure will be followed in the present chapter to determine the protein requirements of impala.

Materials and Methods

Nitrogen makes up about 16% of the molecular weight of protein. The Kjeldahl technique determines the amount of nitrogen in a sample and is then multilplied by 6,25 to obtain an estimate of 'crude protein'. This however causes a bias in the estimate of protein as non-protein nitrogen is included in the calculation. This non-protein nitrogen is however successfully used by the microorganisms in the rumen and then by the herbivore itself.

Nitrogen requirements are calculated from the protein requirements by dividing the latter by 6,25.

Protein requirements for maintenance.

Even if an animal is fed a completely nitrogen free diet some nitrogen appears in the faeces and urine. This nitrogen is thus of endogenous rather than dietary origin. Endogenous urinary nitrogen (EUN) is derived from the catabolism of body tissue and is related to the metabolic weight of the animal (Crampton & Harris 1969). EUN can be calculated using the following equation (Moen 1973):

$$Q_{eun} = 2 * 70(W^{0,75}) / 1\ 000$$

Where Q_{eun} = endogenous urinary nitrogen in g / day
2 = The N ratio in mg to kcal in the equation for basal metabolism.
W = animal mass in kg.

The endogenous N in the faeces, known as Metabolic Faecal Nitrogen (MFN) is from microbial cells, tissue abraded from the digestive tract and spent enzymes. MFN is related to quantity of food eaten. The faeces of cattle and sheep contain approximately 5g of N/day/kg dry matter taken in. The MFN is however markedly increased in case of browsers where phenolics in the plant material are ingested and form irreversible complexes with digestive enzymes which are then lost (Mould & Robbins 1981). Since impala are mixed feeders and not pure grazers like sheep and cattle the MFN value used by Robbins et al. (1974) was used in the present study for impala (7,55 g N/kg dry matter intake).

The loss of EUN and MFN must be replaced by nitrogen from the diet. Protein requirements for maintenance can thus be calculated as 6,25(EUN) + 6,25(MFN).

Protein requirements for gestation.

The foetus, placenta, uterus and the fluid surrounding the foetus increase in weight as pregnancy progresses. The amount of N retained increases in a logarithmic manner during pregnancy. The equation derived by Moen (1973) to calculate protein requirements in wild ruminants is as follows:

$$Q_{pp} = \{e^{-3,1206 + 0,0298(t/c)}\} / W_1 * W_2$$

where Qpp = Quantity of protein required for pregnancy (g/day/kg foetus weight at birth)

c = conversion factor for the gestation period for impala 196/280 = 0,7 (Impala gestation period 196 days, (Fairall 1969)

W_1 = The weight of the average domestic calf at 45Kg

W_2 = weight of impala at birth i.e. 5kg (Fairall 1969)

Protein requirements for lactation.

Lactation is the most demanding stage of reproduction and must therefore be considered when calculating the protein requirements of any animal. To determine the requirements of the female it is necessary to know the protein supplied to the offspring and how this demand declines as the offspring becomes more independant until it is weaned. Moen (1973) proposed that 100% of the offspring's requirements are met by the female's milk at birth and that this declines to zero at weaning. He assumed that the protein content of the female's milk is sufficient to meet the protein 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 female to produce this amount of milk can then be determined from data available on domestic ruminants.

The following data are required to calculate the protein requirements of the lactating female:

a) the growth rate of the offspring

b) the protein requirement of the offspring per unit body weight

c) the developement of the rumen in the growing offspring (this gives an indication of the percentage of protein requirements that are derived from the milk)

d) the protein content of the milk

Some information on impala is lacking but information on other animals with similar requirements can be used. The growth rate of impala before weaning is known (Eloff, Dafel, Ludemann & Lademann 1973, Hirst 1975, Howells & Hanks 1975, Fairall & Braack 1976, Monro 1979). The protein requirement of the growing offspring (Q_{pf}) can be assumed to be of the same order as that of whitetailed deer fawns (3,3g crude protein per kg per day) which weighs 3kg at birth and 25kg when weaned (Moen 1973). Impala weigh 5kg at birth (Fairall 1969) and should weigh 15,3kg at four months (in April) when weaned if a growth rate of 2,575kg/month is followed.

Moen (1973) derived a linear regression from rumen development of the growing whitetailed deer relating the percentage of nutrients met by the milk to the weight of the fawn. A linear regression relating milk dependance to weight for impala is then:

$$MD = 148,54 - 9.7W$$

where MD = the percentage of nutrients met by the milk

W = the weight of the lamb in kg.

Moen's (1973) equation to calculate the milk production to meet the protein requirements of the lamb is:

$$Q_{mp} = (W)(MD)(Q_{pf}/6,25) \ / \ (0,01728)(0,85)$$

where Qmp = grams milk produced per day

W = weight of the lamb in kg

MD = fraction of the offspring's protein requirements met by the milk

Q_{pf} = the protein required by the offspring

0,01728 = N proportion of impala milk. The protein content of impala milk is 10,8% (Smith 1970).

0,85 = net protein coefficient for milk

6,25 = protein : nitrogen ratio for tissue

The total amount of nitrogen metabolized by the body each day can be expressed by the equation:

$$Q_n = Q_{eun} + Q_{mfn} + Q_{np} + Q_{nl}$$

where Q_{eun} = the sum of endogenous urinary nitrogen,

Q_{mfn} = metabolic fecal nitrogen,

Q_{np} = nitrogen for gestation,

Q_{nl} = nitrogen for milk production.

$= Q_{mp} * N * 6.25$

Nitrogen used for body growth is not considered in the present study, as it has been assumed that all animals are adults, and no body growth is taking place. Nitrogen used for hair growth and replacement of abraded skin is ignored as it comprises only small fraction of the total nitrogen need.

The total crude protein required for male and female impala is given in Appendix 2 from January to December. Peak mating takes place on 18 May, the lambs are born at the end of November after a gestation period of 196 days after which the lambs suckle for four months and are weaned when they weigh 15,3kg.

The calculated crude protein requirements for impala can be compared with the crude protein intake discussed in Chapter 6. Not all dietary nitrogen is used by the ruminant and a certain amount is lost. This is undigested protein, and is thus a factor of the digestibility of the protein. The true digestibility of protein is generally between 90% and 100%. Robbins et al. (1974) reported true digestibility of white-tailed deer diet to be 93,7%. Thus 6,3% of all dietary nitrogen is not used. The percentage nitrogen absorbed from the digestive tract which is retained by the ruminant (i.e. not excreted via the urine) is defined by McDonald, Edwards & Greenhalgh (1973) as the biological value. The biological value varies according to the crude protein proportion in the diet, ranging from 54,8% to 87,3% when dietary crude protein proportion varied from 26% to 5% (Robbins et al. 1974). The biological value of impala crude protein percentage in the diet can be determined from the equation determined by Robbins et al. (1974) for white-tailed deer:

$$\mathrm{Log}_e Y = 4{,}9825 - 0{,}3096\mathrm{Log}_e X$$

Where Y = Biological value

X = Dietary crude protein.

The proportion of the crude protein in the diet available to the animal for maintenance, growth, gestation and lactation can be determined by multiplying the dietary protein concentration by the true digestibility and biological value, the latter two expressed as fractions.

Results

From the data in Appendix 1 the protein requirements for maintenance, pregnancy and lactation for female impala and maintenance requirements for males were calculated and are presented in Appendix 2.

EUN is a factor of metabolic body size and remains constant during the year for both males and females. Males, because of their larger body size, need more protein to replace EUN. MFN is a factor of the quantity and type of food eaten and it is assumed that male and female impala consume the same amount of food (the male digestive tract is larger than that of the female), the MFN is the same for both male and female impala. The MFN increases with an increase in food consumed to reach a maximum during December and January. The total protein requirements of male impala are thus the sum of the EUN and MFN.

On the other hand, females need more protein to satisfy the demands of reproduction. Protein requirements during the first four months of pregnancy are very small (less than 5g/day extra is needed) (see Figure 17). During the last two months of pregnancy there is a drastic increase in the protein requirements. The protein requirements during lactation increase at first and then decline once the lamb starts feeding, to zero when the lamb is weaned.

In Figure 18a & b the required and observed protein requirements of male and female impala are illustrated. For most of the year female impala are in a negative protein balance, only after the first rains in August does the protein intake exceed the requirement. Male impala are in a negative protein balance during the rut and winter when food consumption is low together with a low protein content of forage.

Discussion.

The calculation of the protein requirements of an adult ruminant is based on the assumption that all protein used per day must be replaced. Thus the requirements for maintenance are just the replacement of EUN and MFN. It is clear from Figure 15 that late pregnancy and early lactation is the most demanding period of reproduction for the female impala. Protein requirements increase dramaticaly during this time.

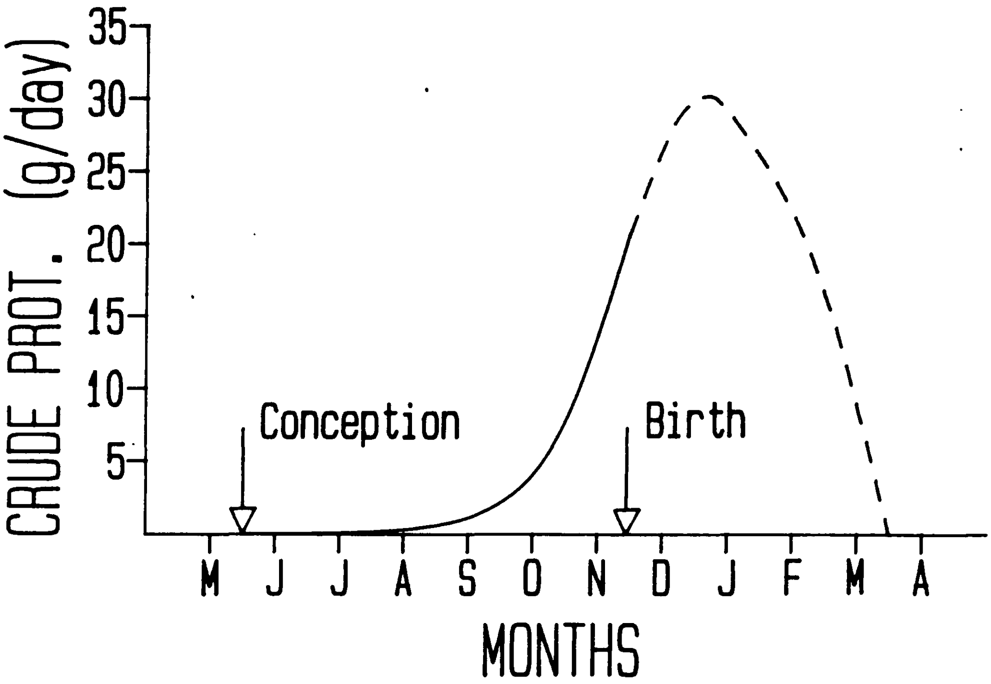


Figure 17. The crude protein requirements of impala females during pregnancy and lactation. Females conceive on average on 18 May and lambs are born at the end of November. Lactation lasts until the end of May.

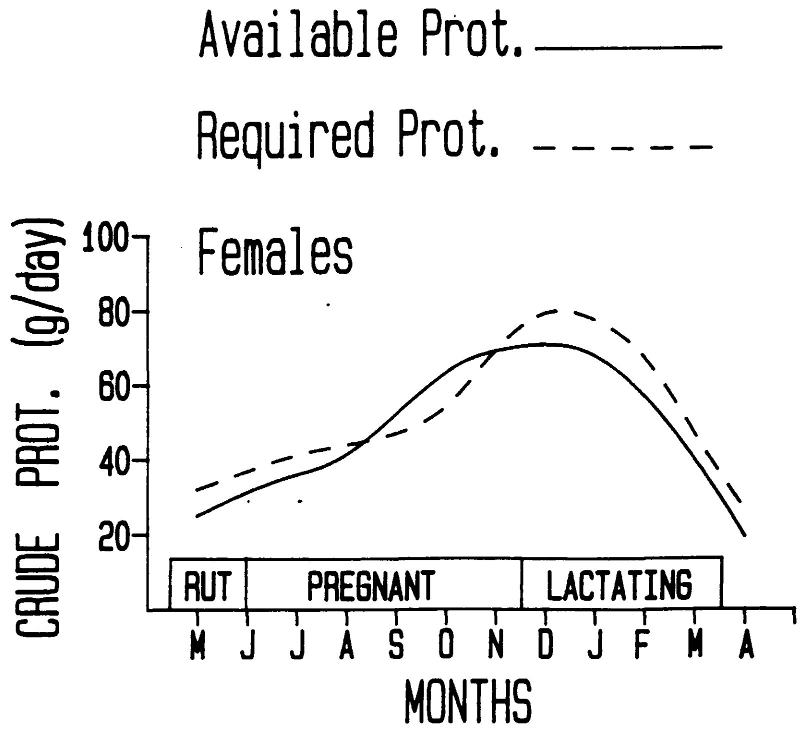


Figure 18a. The crude protein requirements of impala females for maintenance, pregnancy and lactation compared to the available protein as observed in the diet of impala during 1987/8.

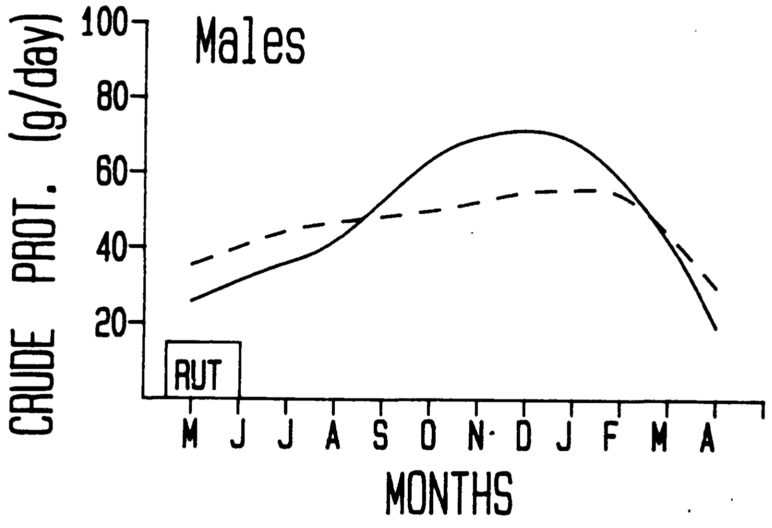


Figure 18b. The crude protein requirements of impala males for maintenance compared to the available protein as observed in the diet of impala during 1987/8.

After the first rains protein intake exceeds requirements resulting in a positive protein balance during late pregnancy. During January when protein requirements are at their highest (peak lactation) protein intake again falls short of requirements.

When calculating the protein requirements the same data on daily feed intake were used for males and females. These data were however based on food intake of one male impala (Monro 1979). Lactating red deer females on the Isle of Rhum, spent two more hours per day grazing than non-lactating females, and did so in areas where food quality was high (Clutton-Brock, Iason, Albon & Guinness 1982). It is known that the monogastric albino rats Rattus norvegicus increased their food intake by up to 60% during pregnancy and by up to 250% during lactation (Cripps & Williams 1975). Two other changes also occurred in the albino rat; the alimentary canal increased in weight and size, and higher absorption rates for certain nutrients were evident. Female impala may thus 1) increase food intake to ensure higher protein intake, 2) change the absorption rate of the alimentary canal to absorb more nutrients, and 3) select a diet that is higher in protein (Dunham 1980).

During the present study no attempt was made to determine food intake or changes in the alimentary canal. There was however no significant difference in the protein proportion in the diets of male and female stomach contents during all months studied, but females consumed more monocotyledons during April than either territorial or bachelor males. As a positive correlation exists between fibre and dicotyledons the diet of females may have contained less fibre than that of males. This may then have the effect that the digestibility of the female diet may be higher than that of the males.

During the later stages of pregnancy impala females cannot increase food intake as the foetus reduces the capacity of the rumen to expand to its full potential (R.R. Hofmann pers comm.). Following parturition, capacity for intake may be stimulated due to removal of competition for space. This increased capacity for food intake during lactation may be an important means of increasing nutrient intake, and this together with the possible morpho-physiological changes in the alimentary canal during pregnancy and lactation requires further elucidation.

Male impala are in a positive protein balance during the period August to March which allows them to build up body reserves, primarily in the form of protein. Protein intake declines from January onwards and protein requirements exceeds intake at the start of the rut, during which territorial male impala spend less time feeding (Jarman & Jarman 1973). Territorial males spent only 25% of the time between 07H00 and 11H00 feeding when accompanied by females and less than 20%

when alone during the rut compared to 50% outside the rut. Females outside the rut spent almost 80% of this time feeding (Murray 1982). The influence of reduced food intake on papillary growth or recession is unknown. The rut occurs however during a period of relatively high dicotyledon intake. Moreover, Hofmann (1973) described a digestive tract surface enlargement factor of impala that were almost exclusively browsing of 18x. Whether this is the case for territorial rams during the rut is uncertain.

Nevertheless, the decreased food intake and subsequent protein shortage, together with increased activity of territorial males (Murray 1982) leads to a dramatic loss of condition during the rut (van Rooyen 1986) when males presumably rely on stored protein.

It is thus evident that periods of protein shortages are interrupted by periods during which protein intake exceeds requirements. Presumably it is during these times (after first rains) that excess protein is stored for later use during winter. As ruminanats can utilise both protein and non-protein nitrigenous substances to synthesize their own protein used for growth and reproduction, knowledge of crude protein availability (in the habitat) and the efficiency to which it can be utilised by ruminants will lead to a better understanding of the ruminant's interaction with its environment.

CHAPTER 8

The body condition of impala and nyala as determined by the Kidney Fat Index.

Introduction

"The assessment of body condition in an animal is important as it can serve to link growth and reproduction rates with the nutritional level of individuals and populations in different seasons and under a variety of environmental conditions" (Brooks, Hanks and Ludbrook 1977 p.61). Body condition is also considered important not only to assist in management but also to provide information for potential meat production (Monro & Skinner 1979). In order to measure and quantify the condition of an animal Riney (1955) developed the Kidney Fat Index (KFI).

Physiological condition is determined by the amount of fat around the kidney expressed as a percentage of the kidney weight. This method is widely used by biologists to determine body condition in ungulates.

The KFI is influenced by various factors other than nutrition alone. Rainfall and habitat will influence body condition as both these factors have an affect on nutrition. This is clear in a study on two gazelle species by Stelfox & Hudson (1986), where it was concluded that the condition of males was affected proximately by forage quality, indirectly by animal distribution (habitat) and ultimately by rainfall patterns. The body condition of males and females can also be influenced by the sexual cycle; territorial male impala lose condition during the rut as a consequence of increased activity and decreased food intake (Murray 1982, van Rooyen 1986). Likewise, pregnant females of most species studied to date have a KFI higher than non-pregnant females during the same time of the year. For example, himalayan thar Hemitragus jemlahicus (Caughley 1970) and Grant's gazelle Gazella granti (Spinage 1985) respond in this manner. Body condition of ungulates is thus influenced both directly and indirectly by an array of factors, and is not only a responce to nutritional status.

Material and methods

Impala and nyala were culled in the Mkuzi and Ndumu Game Reserves during 1987/8 in order to control these populations. Kidneys together with capsula adiposa were removed at death, separated and weighed to the nearest gramme. These weights were then used to calculate the KFI as follows:

$$KFI = \frac{\text{Weight of capsula adiposa}}{\text{Weight of both kidneys}} * 100$$

Results

The monthly KFI of nyala males and females is tabulated in Table 7. Due to great variation between individuals together with small sample sizes it is not feasible to present the data in a flow graph. Nyala males do not show any seasonal trend in KFI which remains fairly constant throughout the year. The monthly KFI of pregnant nyala females is consistantly higher than that of non-pregnant females (Table 7). The KFI of all pregnant females is significantly higher than that of all non-pregnant females, irrespective of season (t = 8,012; p < 0,005).

The monthly KFI if impala males and females is tabulated in Table 8. Small sample sizes again preclude detailed analyses of the data, but certain trends do emerge. The KFI of territorial impala males (KFI = 207,2) before (April) the rut was significantly higher than that of bachelors (KFI = 184,9)(t = 7,191 p < 0,005). Territorial males however lose a significant (t = 25,46 p < 0,005) amount of fat during the rut, to have a KFI of 123,5 after the rut, which is significantly lower (t = 3,707 p < 0,01) than that for bachelors during the same period (KFI = 169,0). Although the KFI of bachelors after the rut (KFI = 169,0) was lower than before the rut (KFI = 184,9), this change is not significant (t = 0,987; p > 0,05).

Table 7. The monthly KFI of nyala collected in the Ndumu and Mkuzi Game Reserves during 1987.

	ALL MALES			FEMALES					
				Pregnant			Non-Pregnant		
MONTH	X	n	SE	X	n	SE	X	n	SE
4	30,82	4	8,92	33,90	7	5,96			
5	22,36	4	4,16	35,70	1		19,64	3	7,96
6									
7	24,56	5	2,29	118,44	1				
8	24,30	3	4,59	17,91	4	7,23	13,30	4	0,49
9	18,36	6	2,33	141,52	2	27,63	49,94	2	8,17
10									
11	14,04	3	1,51	76,37	1		15,05	1	
12	14,56	13	1,66	76,18	7	15,57	17,40	4	7,88
12*	13,52	13	1,42	31,49	8	8,52	7,99	2	0,69

*Nyala collected in The Mkuzi Game Reserve.

Table 8. The monthly KFI of territorial male impala, bachelors and females in the Mkuzi Game Reserve during 1987.

		MALES		FEMALES	
MONTHS		Bachelors	Territorial	Non-Preganant	Pregnant
4	$\bar{x}$:	184,9	207,2	144,0	
	n:	10	10	11	
	s:	50,3	45,7	13,9	
5	$\bar{x}$:	169,0	123,5		
	n:	4	5		
	s:	32,9	13,8		
6+7	$\bar{x}$:	127,6	121,3		
	n:	3	8		
	s:	14,3	11,0		
8	$\bar{x}$:			135,7	208,4
	n:			2	5
	s:				46,0

Small sample sizes prevented the statistical comparison of pregnant ewes with non-pregnant ewes. However when comparing the KFI of all ewes collected during April 1987 with all pregnant ewes collected during August, there is a significant ($t = 8,09$ $p < 0,005$) increase in the KFI. (KFI in April, when no animals can be pregnant was 144,0 while KFI of pregnant females in August was 208,4. Only two non-pregnant females were collected during August; their mean KFI was 135,7).

Discussion

The validity of this index has been questioned by Dauphine (1975), who found that significant seasonal changes took place in the kidney weight of male caribou Rangifer taurundus. Batcheler & Clarke (1970) and Suttie (1983) also reported seasonal weight changes in the kidneys of red deer Cervus elephas. This tendency has not been found in impala kidneys (Brooks 1978) or nyala kidneys (Anderson 1985). Moreover a significant correlation between the total body fat and KFI for impala was found by Smith (1970).

Although major changes in nutritional quality of food consumed by nyala males occurred during the study no significant changes in their body condition were evident. The KFI stayed fairly low during the study period, similar to Anderson's (1980) results from the same study area.

The body condition of territorial male impala declined from

April to July. The dramatic loss in condition of territorial rams can be attributed to reduced food intake and increased activity associated with territorial tenure (Murray 1982). This does not occur in bachelors as they are prevented from taking an active part in the rut (Leuthold 1970).

The loss in condition after the rut when the territorial system disintegrates can be attributed to deterioration of food quality and quantity supply. Protein content declines and fibre content increases during winter and all male impala are in a negative protein balance (see Chapter 5 & 6). Body condition will increase soon after the rains stimulate high protein, low fibre grass to grow.

No apparent trend in female nyala KFI could be found, although Anderson (1980) grouped pregnant females at thirty day intervals of gestation and by season, and still found no trend. On the other hand when all pregnant females collected during the study period are compared with all non-pregnant females the pregnant females had significantly more perinephric fat than non-pregnant animals. The condition of pregnant impala females increased during the first three months of pregnancy to August. The same trends were found by Dunham & Murray (1982) for yearling, adult and old pregnant impala ewes. The kidney fat index increased from after the rut to June and then declined to reach a nadir in January and February when milk production and therefore energy requirements were at a maximum.

This increase in perinephric fat after the rut cannot be ascribed to nutrition as food quality declined during this period and is rather a consequence of hormonal action such as progesterone influencing fat deposition. It is known that in women and animals there is an increase in weight of fat and lean tissue during pregnancy (Dugdale & Eaton-Evens 1989).

This stored energy is used later in the reproductive cycle, during late pregnancy and lactation which is the period of reproduction demanding most energy consumption (Sadlier 1969, Moen 1973). The question is however where this energy comes from. Quality of food ingested declines during the gestation period (see Chapter 6). Increased hormonal levels may induce fat deposition, but energy is required for this and can only be obtained if the female either increases the amount of food ingested [as in red deer, Clutton-Brock _et el._ (1982)], takes in a higher quality diet [as in red deer Staines, Crisp & Parish (1982), white tailed deer _Odocoileus virginianus_, Beier (1987) and impala Dunham 1980, van Rooyen & Skinner (1989)] or increases the absorptive capacity of the digestive tract [as in the albino rat (Cripps & Williams 1975)].

It is known that impala exhibit interchangeable stomach linings (Hofmann 1973) to accommodate their catholic diet. It is thus not inconceivable that pregnant females, can change the digestive tract to enhance absorption of nutrients that could lead to the higher retention of energy. This energy can be stored for later usage when energy and protein requirements increase because of higher reproductive demands at the end of pregnancy and early lactation.

Body condition as expressed by the KFI is an accurate indication of the fat stored in the body, although it is not valid when decling below 40 (Brooks et al. 1977). The KFI reveals differences between animals of different sexes and social status and seasonal changes in condition are clear as fat is mobilized from around the kidney before any other region. Contrary to the original idea, body condition as determined by indices of fat does not always reveal the true physiological state of the animal as determined by food quality alone. Use of condition indices to assess habitat suitability as done by Shackleton & Granger (1989), where social status, sex and reproductive state were not considered, should thus be done with care.

When condition indices such as the KFI are used to evaluate quality of habitat it is suggested that sex and social status be accounted for, or that a sector of the population which is not affected by the influence of reproduction be used. Bachelor males (in the case of seasonal breeders such as impala) are not affected by the rut and their body condition is thus not influenced by factors other than food quality and age. They are however excluded from optimal habitat by territorial males, and this should be considered.

CHAPTER 9

Intermediate feeders coexisting in a seasonal habitat.

The majority of researchers dealing with ruminants concentrate their attention on only two domestic ruminant species while the remaining 150 extant species are to a large extent ignored (Hofmann 1989). Furthermore, wild African ruminants play an increasing role as potential meat producers, in an environment in which they evolved, each in his own niche thus reducing inter- as well as intraspecific competition. Moreover, insight into the factors influencing the diet of ungulates in areas where resources are seasonally limited, and there adaptations to overcome these periods of nutritional stress, which will lead to a better understanding of ruminant ecology, is sparse.

Both impala and nyala are intermediate feeders, with the difference that impala are preferential grazers (Hofmann & Stewart 1972) and nyala appear to be preferrential browsers (present study). Both species make use of high quality grass during the wet season whith browse intake increasing during the dry season. Protein intake of the two species during the year is similar, decreasing during winter with a sharp increase after the first rains.

Chemical compounds in dicotyledons have been described as an adaptive defence system to counter consumption by herbivorous insects (Cooper & Owen-Smith 1985). Chemical repellants in the form of phenolics are largely absent from monocotyledons which evolved later during the miocene. Such phenolics affect the fibre splitting key enzyme cellulase negatively, thus reducing the digestibility of forage. As a counter adaptation, proteins in the saliva of concentrate selectors and intermediate feeders (Hofmann 1989) form insoluble complexes with the phenolic compounds of dicotyledonous plants. Later these indigestible tannin-protein complexes are dissolved in the more acidic abomasum (Hofmann 1989). On the other hand, monocotyledonous food sources present the problem of high fibre low protein ratios during the dry season.

Both these intermediate feeders' diets changed gradually at the end of the wet season, slowly including more and more browse, as the grass lignified, to reach a maximum dicotyledon intake just before the first rains. Hofmann (1989) noted that gazelles and impala with better developed salivary glands (compared to grass and roughage feeders) would rather eat bitter acacia leaves than sundried lignified grass which they are unable to digest. Little is known about nyala but they may be more efficient in neutralising the effect of secondary compounds than impala enabling them to include more browse in their diet.

Ruminants being anaerobic forestomach fermenters, are restricted by protein and not energy (Hungate 1985). Upon examining Figures 13 and 14 it is apparent that protein intake during winter is very low for both species. Requirements exceed protein intake for male impala during the rut (when food intake is very low) and the winter following directly after the rut (Figure 18b). Females on the other hand are in a negative protein balance during the last trimester of pregnancy, while lactating and during the winter (Figure 18a). They conceive at a time when body condition reaches a nadir (van Rooyen 1986). Nevertheless, this does not seem to affect them adversaly, as a conception rate of more than 90% is generally achieved (Fairall 1983).

Seasonal breeding in ungulates evolved to ensure that young are born when conditions are optimal for the survival of both the mother and the young (Baker 1938). Most seasonally breeding ungulates in southern Africa produce their young after a period af active vegetation growth commences. Plants are high in protein and low in fibre during this time. Furthermore 'predator swamping' (through synchronised births) is said to be a secondary adaptation aimed at increasing the survival of the young (Skinner & van Jaarsveld 1987).

The proximate factor initiating seasonal breeding in impala is photoperiod (Skinner, van Zyl & Oates 1974), while the ultimate factor is survival of the lambs resulting in the pattern having become genetically fixed. The ultimate factor in impala is thus an adequate supply of green grass for optimal milk production (Skinner 1989). Impala's reproductive cycle is thus geared to produce young during optimal conditions when the female's nutritional demands are at their highest (during late pregnancy and early lactation).

Although Skinner & van Jaarsveld suggested that 'predator swamping' must have been preceded by seasonal breeding it is realistic to argue that if synchronisation of births to reduce predation is adaptive it would be optimal to do so when resources are abundant, as in impala.

When predation pressure is such that predator swamping will be ineffective, synchronisation of births would have no advantage apart from births being synchronised with a flush of new plant growth. Predation pressure on impala and nyala is different. The basic social group of the nyala is the family unit which consists of an adult female and her offspring while males are usually solitary (Anderson 1980). Unlike impala, nyala calves do not aggregate in groups, and together with their secretive behaviour in thick vegetation probably makes them less susceptible to predation. Synchronisation of births would thus have little effect on predation.

It has been argued that the extent to which intermediate feeders (which react to two breeding cues: increasing and decreasing daylength) will display a bimodal reproductive pattern will depend on their ability to adapt to seasonal changes in food supply (Anderson 1979).

In other words if a lactating female and her offspring can survive at any time of the year, births throughout the year would be possible although selection would still favour births occurring during spring. Nyala have two breeding peaks (one during April and May and the other during October) with a gestation period of seven months and a post-partum oestrus (Anderson 1979). The breeding season during April/May results in births during late spring, with subsequent advantages to the lactating female. Furthermore, it is possible for a female which has conceived during the spring conception peak to give birth and conceive again during the following autumn conception peak. The inverse is impossible as the female would still be pregnant during the following spring conception peak (Anderson 1979). This has the advantage that a part of the female population can breed three times in two years.

Evolution is an ongoing process, and nyala's breeding pattern may not be 'stable in time' and it is possible that nyala are evolving a strictly seasonal breeding regime such as that of impala. This would be the case if natural selection favours lambs being born in summer, resulting in the pattern becoming genetically fixed. Aepyceros evolved more than 3,0 Myr ago while Tragelaphus species evolved 2,0 Myr ago (Vrba 1985). It is thus possible that nyala are still evolving into seasonal breeders.

On the other hand, female nyala may be able to cope with the high nutritional demands during the last trimester of pregnancy and early lactation when this occurs during a period of low food quality. As protein is probably the limiting factor, and not energy, knowledge about mechanisms of protein storage in African ungulates will lead to insight into the role of nutrition in seasonal breeding. When the peak protein requirements of the female occurs during winter (when protein intake is low) protein reserves in muscle fibres may play an important role. In the case of nyala, this may be possible as they are not only larger than impala ewes but in addition do not rely on flight to escape predators, relying rather on hiding in thickets and freezing when alarmed.

Furthermore, it is not only the quality of the diet that changes but, in response to this, the amount ingested and the digestibility and retention times change as well as absorption rates. Hofmann (1989) described a reduced food intake of Alpine chamois Rupicapra rupicapra (an intermediate feeder) from the rut in late fall which continued through to winter. A dramatic loss in surface area of the rumen (by regression of pappilae) together with an increase in ruminoreticular capacity (up to 300% - with subsequent longer retention times) enabled chamois to become highly efficient roughage eaters. On the other hand, during summer the rumen mucosa surface enlarged 20 - 30 times (with consequent higher absorption of nutrients).

Hofmann (1973) also described similar surface enlargements for impala (4 - 5x), induced by the response to consuming sprouting green grass, which allows more nutrients to be absorbed. Similar changes can be expected to occur in nyala. It may thus be that such similar morpho-physiological changes in the digestive tract of nyala in conjunction with their superior diet and stored protein allow them to overcome periods of low quality food intake when nutritional requirements are high, enabling them to reproduce when conditions are not optimal.

The quality of the diet of ungulates is influenced primarily by rainfall. Factors such as reproductive status and the quality of the diet will determine the amount of food ingested and the proportion of the ingested food to be digested and absorbed. All in order to fulfill the nutritional requirements of reproduction.

Habitat is the key to ruminant ecology as it provides food water, cover against the elements and predators and space to exert social activities. Rainfall changes the habitat through the quality of food and the distribution of surface water. The amount of high qality food in a given habitat will limit the number of individuals that can forage together in that area. Variations in habitat suitability for impala can be determined by monitoring changes in group size, while accounting for changes in group size due to the social system.

Due to the different feeding types amongst ungulates, they will select habitats that suit their nutritional requirements best. The total number of different vegetation types within an area will consequently determine the number of different species represented in the area. Differential habitat selection of species whose diet is comparable make it possible for them to occur in the same reserve without the detrimental affects of competition. High densities of one or more of these species will negate this, with consequent over utilisation of resources.

The ability of ungulates to adapt to seasonal changes in food quality will determine their survival rate. These adaptations include changes in diet, morpho-physiological changes of the digestive tract and the storage of protein and energy for times when requirements exceed intake. Synchronisation of births during periodes when high quality food is available add to the survival of the species.

Impala and nyala occur in large numbers in the Zululand game reserves. Although the diets of these ungulate are comparable, possible competition is to a large extent minimised by differential habitat selection. The pleistocene sands in the centre of Mkuzi Game Reserve were found to be the area of geatest overlap. Despite the fact that food resources in this land unit may not be limited, the availability of the artificial water holes has a considerable influence on the distribution of ungulates during the dry season. The impact of the concentration of these water dependant species in the pleistocene sands during the dry season is unknown. As 'system conservation' should be the aim, rather than conservation at the species level, it is suggested that provision of water during the dry season in Msinga and Bube pans be discontinued and the effect on ungulate distribution monitored. Furthermore, that these water holes should be moved to the Mkuzi river which will result in a more natural distribution of surface water without the loss of viewing hides as a tourist attraction.

SUMMARY

Habitat selection, diet and body condition of impala (Aepyceros melampus) and nyala (Tragelaphus angasi) were investigated in Mkuzi and Ndumu Game Reserves, Zululand, South Africa.

Because it is the habitat of ungulates which provides their food, water and shelter, the feeding styles of each species will be of primary importance in determining their preferred habitat. Although both impala and nyala are considered to be intermediate feeders they separated into different habitats within the study area: Impala density was highest in the Lebombo rhyolite land unit, followed by the Pleistocene sands, Early Cretaceous (Cr_3), Late Cretaceous (Cr_2) and Alluvial floodplain (Al). In addition the relative biomass was higher in those areas of highest population density, whilst impala group size was also positively correlated to habitat preference, being largest in the Lebombo rhyolite land unit.

In contrast the density of nyala decreased from east to west within the reserve, which resulted in a high degree of habitat separation between the two species. An overlap in habitat preference existed within the centre of the reserve (the Pleistocene land unit) which contained two water sources, Msinga and Bube pans. These may have attracted impala and nyala, particularly during the dry winter months, even though food may not have been limiting elsewhere.

The diets of impala and nyala were affected by rainfall. During the dry season dicotyledon intake increased to reach a maximum during the month prior to the first rains. Both species subsequently switched to a diet comprising almost solely grass at this time.

Although dicotyledons are less fibrous and contain more protein than monocotyledons at any set time of the year, both these plants exhibit seasonal changes in fibre and protein content, being less fibrous and richer in protein during the wet season. Thus, although the protein content in the diet of both impala and nyala correlated well with monocotyledon content, which might suggest that the acquisition of grass during the wet season is of primary importance to the protein balance of both species, this finding refers to the relative increase in protein acquisition which occurred at that time of the year in which impala and nyala predominantly ate grass. During winter, when dicotyledons comprised most of the diet of impala and nyala, and exhibited their highest fibre content, there was a significant, positive correlation between fibre and dietary dicotyledon content.

Analysis of the protein intake of impala of both sexes revealed that protein requirements exceeded intake during the dry season. However, in summer, male impala exhibited a positive protein balance whilst this was also displayed by breeding females during the early stages of gestation. However, even with an increase in protein intake by breeding females towards the end of gestation and during early lactation their protein requirements exceeded intake. For this reason parturition amongst impala ewes is synchronised during that time of the year in which active growth of vegetation took place, providing the high quality diet required to meet their elevated nutritional demands. In contrast, nyala exhibit two breeding peaks, one in autumn at the end of the growing season, the other in spring as the vegetation recovered from the dry winter. Nyala's ability to extend their breeding season outside the wet season may result from the higher protein content of the dicotyledons which comprised much of their diet. However, it is not clear from the present study whether they might also be able to store fat and protein in greater quantities than impala throughout the year and thus retain an inherent capacity to reproduce even when the quality of available food is poor.

Whilst the kidney fat index (KFI) might provide an indication of habitat quality, with respect to ungulate condition, territorial male impala lost condition during the rut due to a reduction in food intake and displayed a lower KFI than bachelors. In addition, pregnant females of both impala and nyala had higher KFIs than non-pregnant individuals, which suggests that fat deposition by pregnant animals was enhanced, even when food quality was low. Therefore, the KFI of bachelor males or non-pregnant females should provide a more accurate indication of habitat quality when compared to that of rutting males or pregnant females.

The present study indicates that the habitat preference of impala and nyala is primarily determined by a difference in their diet. Although both species are believed to be intermediate feeders, nyala consume more browse than impala, and graze to a large extent only during the initial period of sprouting following the onset of the summer rains. Whether this difference in diet is a result of specific physiological adaptations, such as an ability by nyala to neutralise the tannins ingested along with browse, is worthy of investigation. However, it is probable that the superior quality of the nyala diet enables them to extend their breeding season compared to that of impala, whose diet comprises a greater proportion of graze with its variable nutritional content.

OPSOMMING

Die habitatvoorkeur, dieet en liggaamskondisie van rooibokke Aepyceros melampus en nyalas Tragelaphus angasi is in die Mkuzi en Ndumu Wildtuine, Zululand bestudeer.

Habitat verleen aan die herbivoor 'n bron van voedsel, water en skuiling, dit is dus die voedingstyl wat die bepalende rol speel in habitatvoorkeur. Alhoewel beide nyalas en rooibokke as intermediere voeders beskou word, was daar 'n duidelike skeiding in verkose habitat in die Mkuzi Wildtuin. Rooibok getalle per oppervlakeenheid was die hoogste in die weste (Lebombo-rhyoliet grondtipe; Jr), gevolg deur die Pleistoseen-sand grondtipe, Jong Cretaceous (Cr_3), ouer Cretaceous (Cr_2) en Alluviale vloedvlakte (Al). Tesame hiermee, het die relatiewe biomassa per oppervlakeenheid dieselfde tendens getoon. Gemiddelde tropgrootte was die grootste in die verkose habitat (Jr) en het afgeneem in dieselfde volgorde as die habitatvoorkeur.

Nyalas, in teenstelling met rooibokke, se laagste digthede was in die weste (Jr) waargeneem en het toegeneem na die ooste. Hierdie verspreiding van die twee herbivore het dus gelei tot 'n groot mate van habitat verdeling. Die Pleistoseen-sand grondtipe in die middel van die wildtuin was die enigste gebied waar beide spesies in groot hoeveelhede saam voorgekom het. Die teenwoordigheid van die twee waterbronne; Msinga en

Bube panne het waarskynlik 'n groot invloed op die verspreiding van die twee waterbenodigende spesies gehad, veral tydens die droe seisoen.

Die dieet van beide spesies was hoofsaaklik deur die reënval bepaal. Tydens die droe seisoen het nyalas en rooibokke 'n groot hoeveelheid dikotiele plante gevreet terwyl grasse gedurende die nat seisoen die oorwegende voedseltipe was. Dikotiele plante het meer ru-proteien en 'n laer veselinhoud as monokotiele. Seisoenale veranderinge in die vesel en proteieninhoude kom egter voor na gelang van die reënval. Proteien neem toe in die reënseisoen terwyl veselinhoud afneem tydens nuwe groei. Die waargenome positiewe korrelasie tussen die monokotielinhoud van die dieet en die proteien gehalte daarvan was dus indirek, omdat monokotiele gevreet was wanneer hul relatiewe proteieninhoud hoog was, en dikotiele gevreet was wanneer hul proteieninhoud relatief laag was. 'n Soortgelyke indirekte korrelasie is gevind tussen die vesel- en dikitielinhoud van die dieet.

Die proteienvereistes van rooibokke het die vasgestelde proteienvereistes gedurende die winter oorskry. Met die verhoogde proteieninname na die reënseisoen is rooibok ramme in 'n positiewe proteienbalans. Dragtige ooie is egter slegs vir 'n kort periode in 'n positiewe proteienbalans. Proteienbenodigdhede gedurende die laaste gedeelte van dragtigheid en laktering vermeerder drasties en nieteenstaande verhoogde proteieninname, oorskry vereistes steeds die proteieninname.

Rooiboklamming vind plaas gedurende die periode wanneer hoë gehalte voedsel beskikbaar is. Rooibokooie maak dus van die verhoogde voedselkwaliteit gebruik om aan hoër benodigdhede te voldoen. Nyalas beskik egter oor twee teelseisoene wat waarskynlik moontlik gemaak word deur hul hoër kwaliteit dieet. Dit is egter nie duidelik of nyalas a.g.v. groter liggaamsmassa oor 'n hoër potensiaal beskik om voedingstowwe te stoor vir latere gebruik nie.

Die niervetindeks kan gebruik word om die invloed van veldkwaliteit te bepaal. Die liggaamskondisie van territoriale rooibokramme word egter tot 'n groot mate deur die teelseisoen beinvloed, terwyl die liggaamskondisie van bachelors nie daardeur geraak word nie. Verder vind daar 'n beduidende toename in die niervetindeks van dragtige ooie plaas, alhoewel die voedselkwaliteit afneem gedurede dié periode. Dit word waarskynlik moontlik gemaak deur 'n verhoogde opname van voedingstowwe wanneer ooie dragtig is.

Die studie dui aan dat die moontlike rede vir die verdeling in habitat van die twee intermediere voeders in hul dieet le. Beide die herbivore vreet 'n groot hoeveelheid gras na die reënseisoen wanneer dit hoog in proteien is en oor 'n lae veselinhoud beskik. Nyalas vreet egter die res van die jaar meer dikotiele. Die verskil in dieet kan moontlik toegeskryf word aan fisiologiese aanpassings van nyalas om tanniene, teenwoordig in 'n dikotiel dieet, te neutraliseer. Dit is verder moontlik dat die hoe kwaliteit dieet van nyalas hul in staat stel om voort te plant wanneer veldtoestande nie optimaal is nie, terwyl rooibokke moontlik deur hul meer varieerbare dieet verhinder word.

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Appendix 1.

Information used to determine protein requirements of impala for maintanance, pregnancy and lactation.

Body weight: males; 54,5kg
females; 40,9kg (Smithers 1983).

Oestrus 18 May (Skinner 1971).
Gestation 196 days (Skinner 1971).
Weight at birth 5kg (Fairall 1969).

Growth rate during the first four months:

2,66kg/month	(Monro 1979).
2,13kg/m	(Hirst 1975).
2,31kg/m	(Howells & Hanks 1975).
3,20kg/m	(Fairall & Braack 1976).

x = 2,575kg/m
e.i. 0,08583kg/day

The weight when weaned at four months is then 15,3kg

The crude protein of impala milk is 10,8% (i.e. 0,01728N) (Smith 1970).

Appendix 2.

The crude protein requirements of impala females for maintanance pregnancy and lactation from May (conception) to the end of lactation. The percentage protein in the rumen is converted to available protein (see text) to compare protein requirements to observed protein intake.

	MAINTANANCE		PREGNANCY		LACTATION		Tot. Prot.	Food	% Prot	Abs. Prot.	Biol.	Avail
Months	EUN	MFP	Days	Prot.	Days	Prot.	required	(g)	in diet	intake	value	Prot.
M	14,15	17,93	14	0,009			32,01	380	10,19	38,72	71,07	25,78
J	14,15	22,65	44	0,032			36,83	480	9,74	46,75	72,08	31,57
J	14,15	27,36	75	0,119			41,63	580	9,08	52,66	73,66	36,35
A	14,15	29,25	106	0,447			43,85	620	9,36	58,03	72,97	39,68
S	14,15	30,67	136	1,603			46,42	650				
O	14,15	31,61	167	5,999			51,76	670	17,08	114,44	60,58	64,96
N	14,15	34,45	Part,	20,618			69,22	730	16,79	122,57	60,90	69,91
D	14,15	37,75			31	29,80	81,70	800				
J	14,15	37,75			62	26,18	78,08	800	15,94	127,52	61,88	73,97
F	14,15	38,69			90	16,79	69,63	820				
M	14,15	26,89			121	0	41,04	570	13,08	74,56	65,79	45,96
A	14,15	12,27					26,42	260	11,67	30,34	68,16	19,38

Appendix 2. (cont.)
The crude protein rquirements of impala males for maintanance and the available protein to compare the requirements to observed protein intake.

	MAINTANANCE		Tot. Prot.	Food	% Prot	Abs. Prot.	Biol.	Avail.
Months	EUN	MFP	required	(g)	in diet	intake	value	Prot.
M	17,55	17,93	35,48	380	10,19	38,72	71,07	25,78
J	17,55	22,65	40,20	480	9,74	46,75	72,08	31,57
J	17,55	27,36	44,91	580	9,08	52,66	73,66	36,35
A	17,55	29,25	46,80	620	9,36	58,03	72,97	39,68
S	17,55	30,67	48,22	650				
O	17,55	31,61	49,61	670	17,08	114,44	60,58	64,96
N	17,55	34,45	52,00	730	16,79	122,57	60,90	69,91
D	17,55	37,75	55,30	800				
J	17,55	37,75	55,30	800	15,94	127,52	61,88	73,97
F	17,55	38,69	56,24	820				
M	17,55	26,89	44,44	570	13,08	74,56	65,79	45,96
A	17,55	12,27	29,82	260	11,67	30,34	68,16	19,38