ECOLOGY OF WATERBUCK *KOBUS ELLIPSIPRYMNUS* (OGILBY, 1833) IN THE UMFOLOZI GAME RESERVE

by

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ABSTRACT

Between 1970 and 1975 Natal Parks Board helicopter counts of waterbuck (*Kobus ellipsiprymnus*) in the Umfolozi Game Reserve (UGR) declined from 1 098 to 494. The purpose of this project was to study the ecology of waterbuck with an emphasis on population regulating mechanisms, so that the reality and significance of this decline could be assessed.

Density estimates for 1976-1977 were over twice the 1976 helicopter count of 319, but the population was confirmed to be declining. The ecological density of waterbuck represented 11,9 per cent of the metabolic biomass of grazers, which compared well with data from other areas. However, the other species' proportionate contributions to biomass were far from optimal, with an excess of short grass feeders.

High juvenile mortality (80,7 per cent), attributable mainly to severe tick (*Rhipicephalus appendiculatus*) infestations, was the principal cause of the present decline. These severe infestations

were probably symptomatic of poor condition of the whole waterbuck population, which meant that the ultimate cause of juvenile mortality lay elsewhere.

The hypothesis that the waterbuck population was in a stressed condition was supported by their habitat utilization patterns, their feeding ecology and aspects of their behaviour. The dynamics of interspecific associations suggested that the primary habitat of waterbuck was that now occupied by nyala (*Tragelaphus angasi*) and what had been recorded were the results of competition pushing waterbuck into an unfavourable habitat. Feeding studies indicated that nutritious food for herbivores represented a limited resource in UGR during winter, for which waterbuck may be largely outcompeted and that nyala and impala (*Aepyceros melampus*) were the main competitors.

Interspecific competition was the probable ultimate cause of the decline of waterbuck in UGR. It was recommended that the numbers of nyala and impala be reduced and that this action be integrated into a more precise management plan for UGR than exists at present.

ACKNOWLEDGEMENTS

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CHAPTER 1

INTRODUCTION

WILDLIFE RESEARCH - A BROAD PERSPECTIVE

Before giving details of this study it is worth considering the overall role of research in wildlife conservation, with particular reference to Africa. Although a few game reserves were created before the end of the 19th century, most reserves and national parks were not set aside until after World War II. Originally many of these areas were surrounded by undeveloped land, but now this is becoming the exception rather than the rule. With agricultural land contiguous with conservation areas there is no room for animals to disperse in response to habitat alteration, predator concentrations, or seasonally to obtain sufficient water or enough good quality food. This situation makes it vital to understand how the grazing and browsing species interact with their habitat and with each other and likewise how predators interact with each other and with their prey species. Only with this knowledge can a reserve be successfully managed, enabling a diverse assemblage of endemic species to coexist without drastically harming vegetation through overabundance, but at the same time without losing species through competition or depredation.

Unfortunately the long-term success of research and management activities in protected areas lies with processes occurring outside these areas. The appearance of these processes is varied, ranging from overgrazing by livestock and the subsequent loss of topsoil, to the creation of reservoirs that flood wildlife areas; however, the underlying problem is always the same, the exponential increase of the human population. Many workers have used the increasingly true analogy between conservation areas and islands and have emphasised the need to reappraise conservation in the broader ecological context of the development of whole countries of groups of countries, with full attention being given to land use planning, resource utilization and the limitation of human population growth (Allen 1959, Huxley 1961, Black 1968, Dasmann 1976, Hanks 1976). This then is the long-term context within which all conservation action must be viewed, but in the short-term research in protected areas remains vital to maintaining these "island ecosystems".

OBJECTIVES OF THE STUDY

Between 1970 and 1975 Natal Parks Board (NPB) helicopter counts of waterbuck (*Kobus ellipsiprymnus*) in the Umfolozi Game Reserve (UGR) declined from 1098 to 494 (see Chapter 3). The purpose of this project is to study the ecology of waterbuck in UGR with an emphasis on population regulating mechanisms, so that the reality and significance of this decline can be assessed and the need for management action evaluated. Work is therefore centred around a main theme of current ecological research and at the same time has direct importance in the management of the species in UGR and in other areas. The study began in January 1976 and most fieldwork was terminated in December 1977.

Much ecological research in Africa has centred on problems which take the form of "too many of a species" or "too few of a species". Although it is often necessary to concentrate on immediate problems this is far from an ideal way of organising wildlife research, especially if adequate background knowledge is lacking on the functioning of the whole ecosystem in question. This was largely the case in UGR where although a number of projects had been, and are being, carried out, little is known of the interactions between animals and their environment and between species themselves. Because of this lack of information the present study was allowed a broad base and due consideration was given to the other main grazers in UGR in those areas which have importance in defining the ecology of waterbuck in the reserve. Thus the abundance, habitat utilization patterns and feeding ecology of all main grazers in UGR were examined. The need for a broad base in ecological studies, even when the focus is on one species, cannot be overemphasised. Ecology is well defined as the scientific study of the interactions that determine the distribution and abundance of organisms (Krebs 1972), where it is the environment, abiotic and biotic including animals of the same and different species that produce observed patterns of distribution and density (Andrewartha and Birch 1954).

The abundance of waterbuck was specifically studied so that the reality of the believed decline could be investigated (Chapter 3). The absolute abundance figures for waterbuck and other species also allow the present density of waterbuck to be assessed in the most useful way of percentage contribution to the biomass of all grazers. In Chapter 5 the demography of the waterbuck population is described so that age-specific reasons for any change in density can be investigated; this necessitated providing age determination methods for skulls and for live animals observed in the field (Chapter 4). The proximate reasons for mortality of waterbuck in UGR are given in Chapter 6, along with an account of the physiological condition of animals. The possibility that behavioural attributes of waterbuck could help to explain their ecology is explored in Chapter 7. Habitat utilization by waterbuck and the other main grazers in UGR is quantified in Chapter 8, which allows competition between waterbuck and other species to be defined in terms of area utilization. The feeding ecology of waterbuck and other herbivores is presented in Chapter 9, which allows competition to be defined in terms of the food eaten. Finally overall conclusions are drawn as to the present status of waterbuck in UGR and the need for any management action (Chapter 10).

THE TAXONOMY AND DISTRIBUTION OF WATERBUCK

The following taxonomy of the common waterbuck is as given by Meester and Setzer (1971):

Order .... Artiodactyla
Family .... Bovidae
Sub-family .... Reduncinae
Genus .... *Kobus*
Species .... *Kobus ellipsiprymnus*

The common waterbuck and the defassa waterbuck (*K. defassa*) are now considered to be conspecific. They overlap in their distributions in north-eastern Tanzania and Kenya, where they interbreed and the resulting hybrids show many variations on the pure *K. ellipsiprymnus* ring type rump patch and the pure *K. defassa* solid white patch (Backhaus 1958, Kiley-Worthington 1965). Other species of the genus *Kobus* are *K. megaceros* the nile lechwe, *K. leche* the lechwe, *K. kob* the kob and *K. vardoni* the puku; the last two comprise a superspecies.

The present distribution of waterbuck has been described by Heyden (1969), Dorst and Dandelot (1970) and Meester and Setzer (1971). Waterbuck occur throughout much of Africa south of the Sahara; in the west they range from Senegal to southern Angola and in the east from Somalia to northern Natal. Du Plessis (1969) has reviewed the past and present distribution of waterbuck in southern Africa. Its present range in South Africa comprises northern Natal and eastern and northern Transvaal, which is only a slight contraction over its past distribution in the 19th century. A number of early travellers reported seeing waterbuck in northern Natal during the 1800's, including observations in what is now UGR. The main present population in Natal is in UGR, but a few animals have been translocated from there to St. Lucia Game Reserve to the east and to Itala Game Reserve to the north.

CHAPTER 2

THE STUDY AREA

INTRODUCTION

Umfolozi Game Reserve is a triangle of land lying primarily between the Black Umfolozi and White Umfolozi Rivers in northern Natal (Figs. 1 and 2). It is one of the oldest conservation areas in Africa having been established along with the nearby Hluhluwe Game Reserve (HGR) in 1897. The two reserves are still joined by a corridor of State Land, the whole confluent wildlife area being known as the UGR-Corridor-HGR Complex. Since 1897 UGR has been deproclaimed and reproclaimed three times and its boundaries variously altered (Vincent 1970). At the present time the reserve covers 493 km^2 and is fenced except where it abuts the Corridor.

Outbreaks of nagana amongst the domestic stock of European farmers were the main reason for the several deproclaimations. The principal method used to combat trypanosomiasis was to attempt to eradicate or severely reduce the main carriers of the disease, the indigenous large mammals of the reserve and surrounding areas. Two main organised eradication campaigns were undertaken during the period 1929 to 1950, which accounted for the death of some 25 000 animals in UGR and many more outside the reserve (Mentis 1970). Insecticides were used finally to wipe out the tsetse fly (*Glossina* spp.) and in 1952 the reserve was handed back to be administered by the Natal Parks Game and Fish Preservation Board. Since that time the only shooting or removal of wildlife has been during control operations which became necessary after animal populations increased in the 1960's.

CLIMATE

The climate of UGR is divisible into two main seasons, a moist hot summer which extends from October to March inclusive and a dry cooler winter from April to September. The mean annual rainfall recorded at Mpila, the reserve headquarters, was 686 mm for the period 1959 to 1973, while 870 mm and 919 mm were measured during 1976 and 1977 respectively. The reserve is in the summer rainfall region of southern Africa, where winter equates with a dry season and summer a wet season. The monthly distribution of rainfall during the study period is shown in Fig. 3, as are the mean monthly figures for 1959

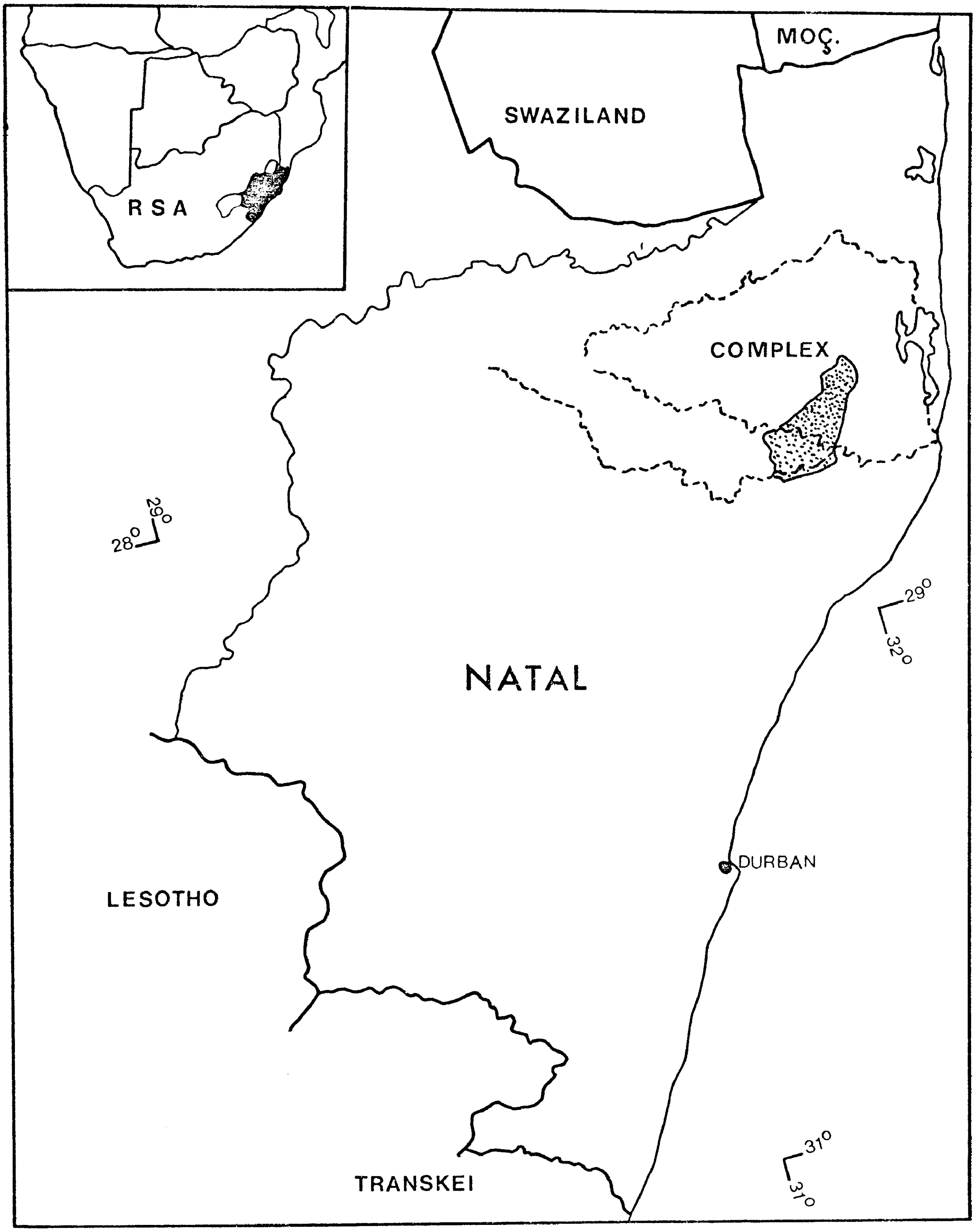


Figure 1. The position of the Umfolozi Game Reserve-Corridor-Hluhluwe Game Reserve Complex in southern Africa.

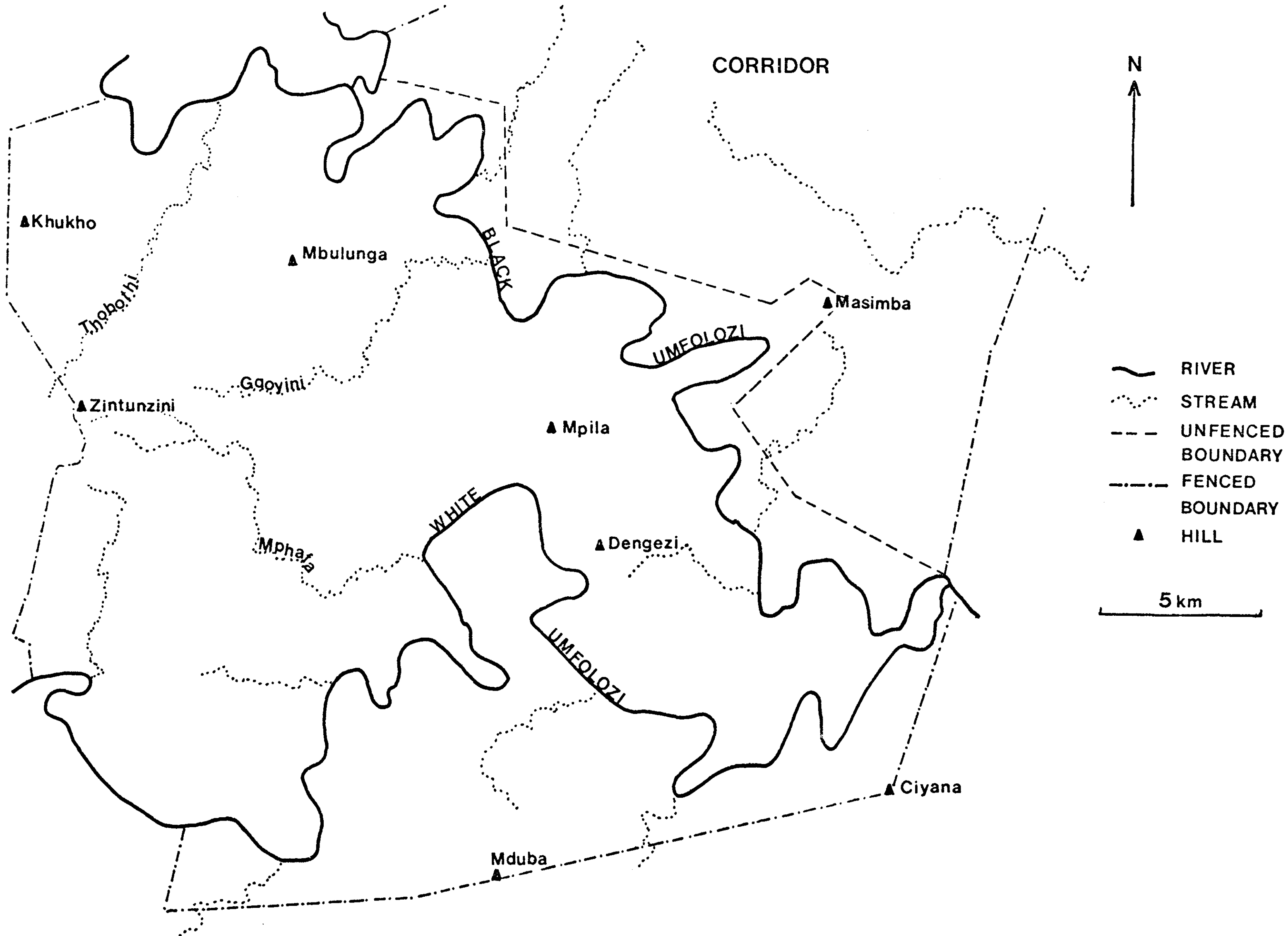


Figure 2. The Umfolozi Game Reserve.

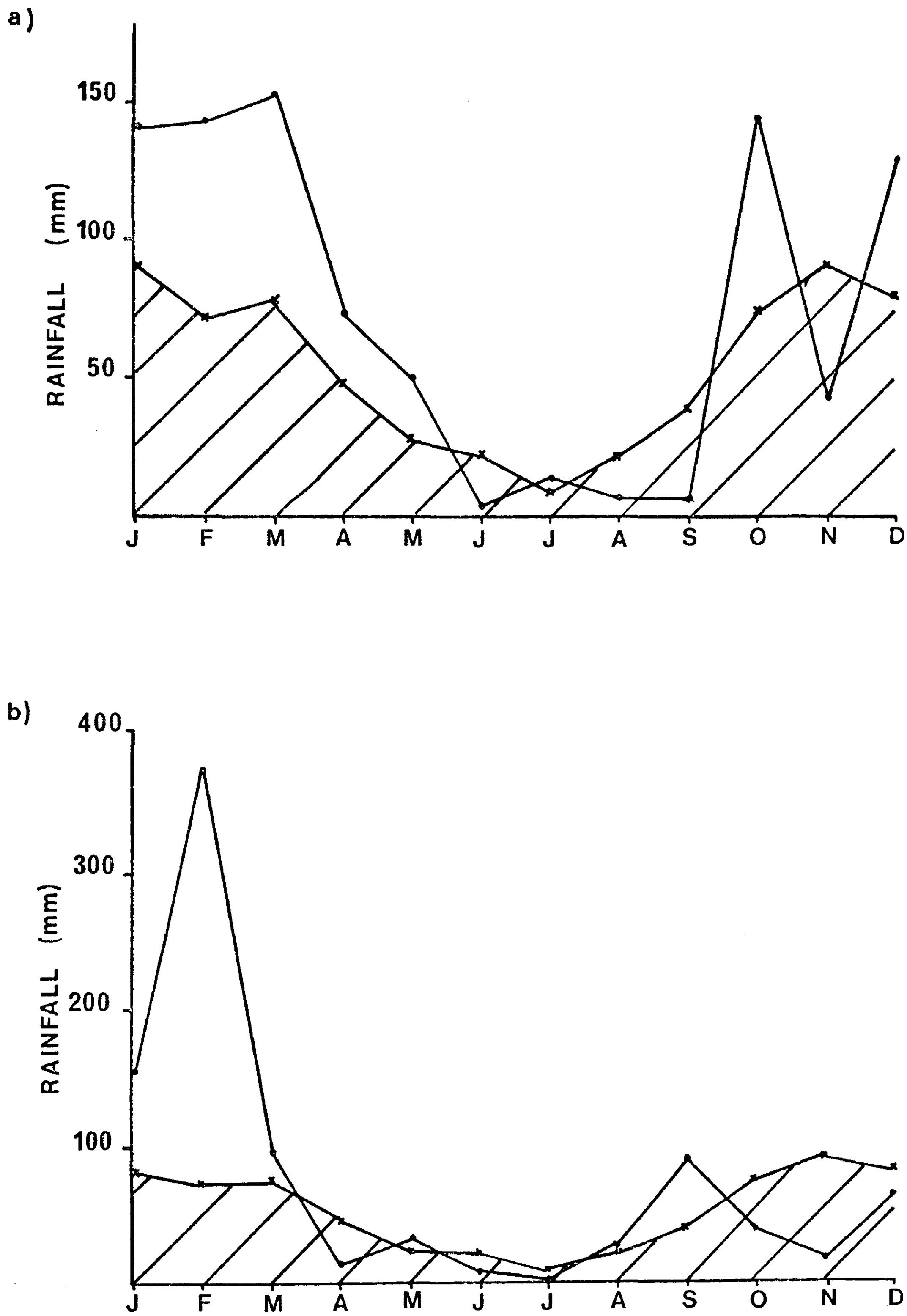


Figure 3. The monthly distribution of rainfall measured at Mpila during a) 1976 and b) 1977, along with mean figures over a 14 year period (shaded).

to 1973. During the rainy season surface water occurs in numerous pans, drainage lines and streams throughout the reserve, but during winter water is confined mainly to the Black and White Umfolozi Rivers. Both of these main rivers are subject to flash floods and the difference in water level at these times compared to the reduced winter flow is considerable. This is demonstrated by photographs of the Black Umfolozi River taken near Sontuli during February 1977 and June 1977 (Fig. 4).

Mean monthly maximum and minimum temperatures calculated from daily readings taken at Mpila over 1976 and 1977 are shown in Fig. 5. Mean monthly maxima did not fall below 27 °C in summer nor 23 °C in winter and mean monthly minima did not fall below 9 °C in winter nor 17 °C in summer. Mpila at an altitude of 290 m.a.s.l. represents a hill location; at lower altitudes greater temperature extremes have been recorded (Downing 1972). At Mpila daily maximum temperatures in excess of 40 °C are only occasionally measured during summer. In general low lying areas experience the lowest minimum temperatures since temperature inversions at night cause cold air to flow into valley bottoms and even frost occurs on rare occasions (Vincent 1970). This aspect of temperature was quantified for the present study by placing one maximum-minimum thermometer on Mbhuzana Hill (altitude 213 m.a.s.l.) and one in a depression (altitude 122 m.a.s.l.) 500 m away. The thermometers were shaded by wooden awnings and read for seven consecutive days during most months between August 1976 and July 1977 (Fig. 6). There was little difference between the maximum temperatures in these locations, although a perspiring animal would no doubt benefit from cooling breezes on hilltops. Minimum temperatures, however, were consistantly lower in the depression, particularly in winter when the difference reached six centigrade degrees and near freezing temperatures were recorded.

TOPOGRAPHY

The reserve is in part two large valleys produced by the Black and White Umfolozi Rivers which enter in the north-west and south-west corners respectively and leave at their confluence in the east (Fig. 2). The wedge shaped watershed that comprises the central part of the reserve has its highest point at Zintunzini (579 m.a.s.l.) on the western boundary and falls in altitude through a series of ridges until it meets the confluence, which is the lowest point (45 m.a.s.l.).

Three land surfaces are present in UGR representative of the Miocene, Pliocene and Quaternary Periods (Downing 1972). The oldest a

b

Figure 4. The Black Umfolozi River near Sontuli; a) in flood during February 1977 and b) during June 1977.

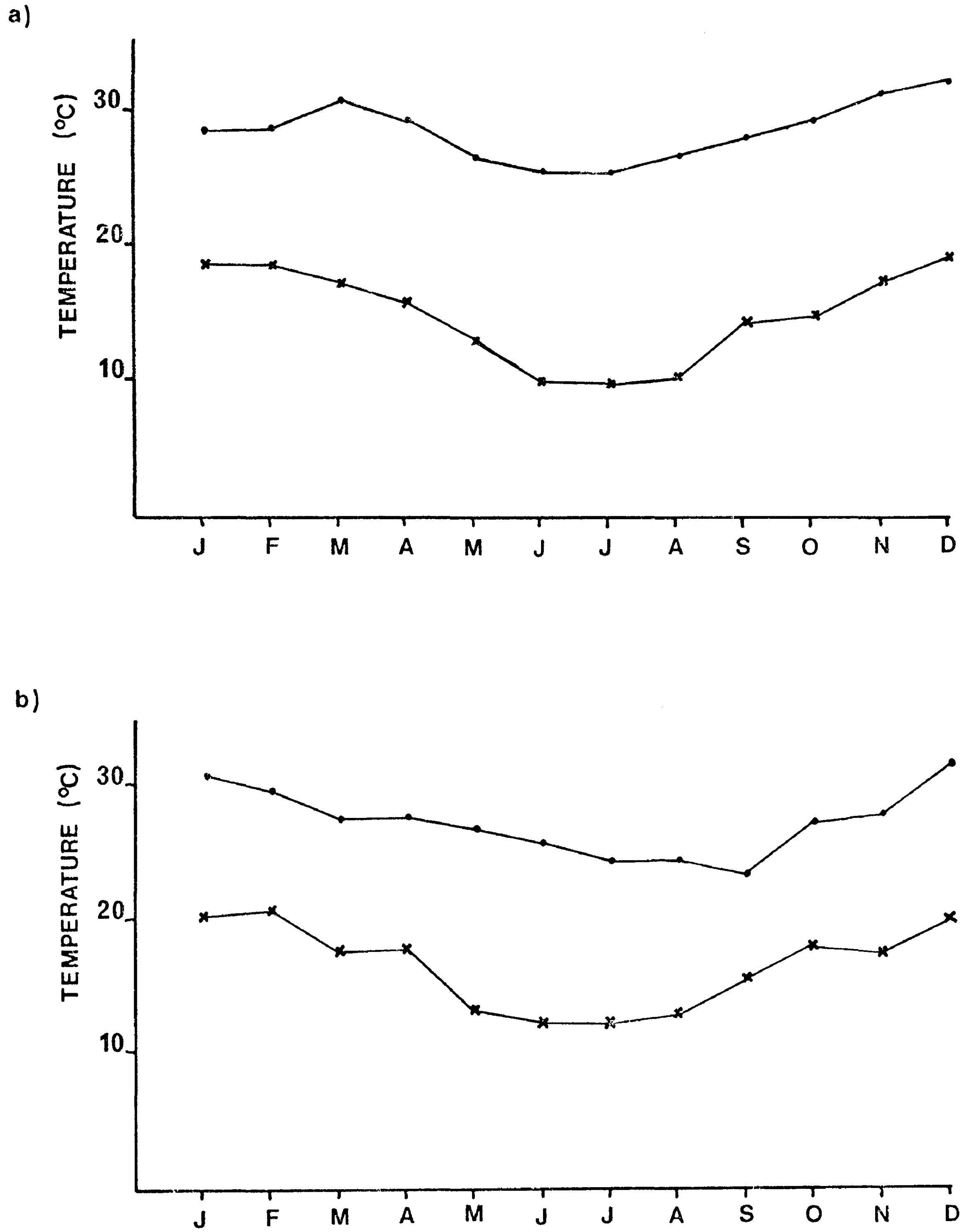


Figure 5. Mean maximum (—•—) and mean minimum (—x—) temperatures recorded at Mpila during a) 1976 and b) 1977.

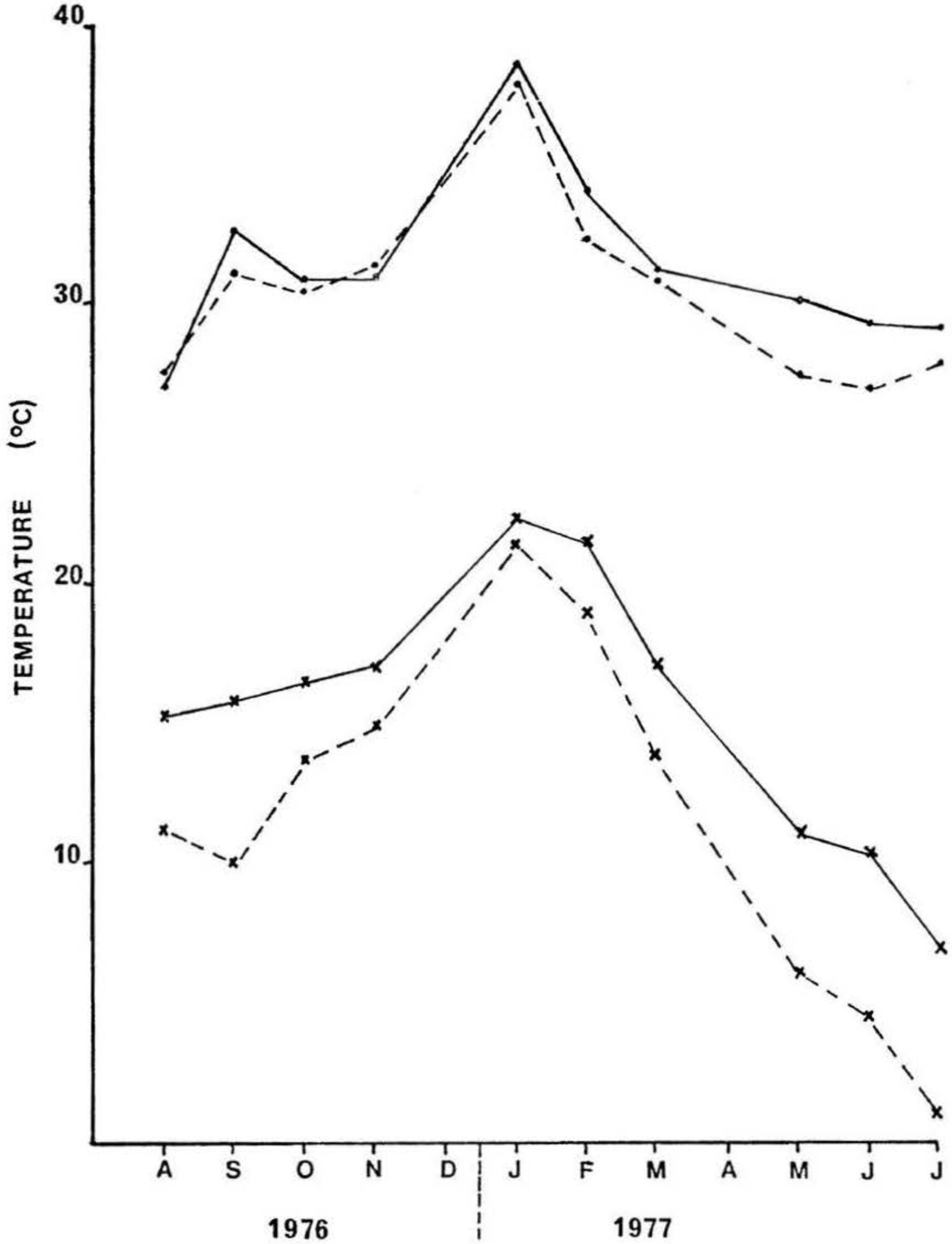


Figure 6. Mean maximum (•) and minimum (×) temperatures measured at a hill location (—) and in a depression (--) in the Umfolozi Game Reserve.

Miocene surface is represented only on and near the summits of the main hills. River incision and erosion of the Miocene surface has produced large areas of undulating country which are a main feature of the reserve and constitute the Pliocene surface. The greater extent of the Quaternary surface consists of fairly level alluvial terraces.

SOILS

Downing (1972) classified soils in UGR into one of three major associations, upland, bottomland or riverine, according to their topographic position. Upland soils are developed *in situ* and bear a close resemblance to the underlying parent rock. They are stony, shallow and leached and have a low moisture content. Bottomland soils are present in localities where water run-off drains away slowly or tends to accumulate, as in valley bottoms or alluvial terraces. They are up to several metres deep and are considered highly fertile from an agricultural standpoint. The riverine soil association consists of unconsolidated alluvia often over 5 m deep. They are mainly confined to the beds and banks of the two main rivers and provide water for plant growth near these rivers throughout the year.

VEGETATION

The reserve lies mainly within the low altitude form of the Zululand Thornveld of the Coastal Tropical Forest type defined by Acocks (1953). Downing (1972), using the basic terminology of Phillips (1971), identified the following physiognomic types: grassland, open woodland, closed woodland, thicket, open-closed woodland and riverine woodland, Woodland vegetation was split into three main associations, the *Acacia-Combretum* open woodland association, the *Acacia-Spirostachys* closed woodland association and the *Acacia-Ficus* riverine association. Open woodland occurs mainly on higher ground with *Themeda triandra* usually the dominant grass. Closed woodland is confined mainly to the lowest lying bottomland areas where *Panicum coloratum*, *Urochloa mossambicensis* and *Panicum maximum* are common grasses. It is these low-lying areas near to the main rivers that are most heavily utilized by large herbivores.

Controlled burning has been carried out in UGR since 1959 with three main aims (Porter 1975): first, to remove excess moribund plant material and so stimulate grass growth; second, to attract grazers away from over-utilized areas and third, to control bush encroachment which has been increasing since that time. These criteria have resulted in upland areas being more often burnt than the more heavily utilized bottomland areas. The frequency of burning has varied between two and six years and generally takes place after the first spring rains in September or somewhat earlier.

LARGE MAMMALS

Ungulates

Bourquin, Vincent and Hitchins (1971) list 21 species of ungulate as occurring in UGR. Nineteen of these are listed in Table 1 as being present during the study period. Omitted are blesbok (*Damaliscus dorcas*) which were escapees from a nearby farm and eland (*Taurotragus oryx*) which became extinct in 1973 following reintroduction in 1964 and 1965. Of these 19 species eight can be classified as the main grazers in UGR because of their feeding habits and higher densities. They are, in no particular order, waterbuck, white rhino (*Ceratotherium simum*), zebra (*Equus burchelli*), warthog (*Phacochoerus aethiopicus*), impala (*Aepyceros melampus*), wildebeest (*Connochaetes taurinus*), nyala (*Tragelaphus angasi*) and bùffalo (*Syncerus caffer*). The history of these species in UGR will be discussed briefly as they comprise waterbuck and the potential competitors of waterbuck; their densities will be examined in detail in the next chapter.

About 100 waterbuck were believed to have been present when UGR was handed back to NPB in 1952 (Foster 1955, *In:* Vincent 1970). Since that time they have not been shot or captured to any extent, but their numbers have declined in HGR since about 1955 and in UGR over the past eight years.

Umfolozi Game Reserve has always been considered a particular sanctuary of the white rhino. This species was removed from the IUCN's list of endangered species as a result of conservation measures in UGR and subsequent translocation to many areas (Player 1967). Approximately 500 individuals were reported present in UGR in 1952 (Foster *op. cit.*).

Zebra was the most common species in UGR prior to 1930, but was virtually eliminated from the Umfolozi area during the nagana shooting (Mentis (1970). Numbers have increased since 1952.

Some 13 000 warthog were destroyed in the Umfolozi area during

Table 1. Nineteen species of ungulate present in the Umfolozi Game Reserve during the study period.

Order Perissodactyla	
Family Rhinocerotidae	
Diceros bicornis	Black rhinoceros
Ceratotherium simum	White rhinoceros
Family Equidae	
Equus burchelli	Burchell's zebra
Order Artiodactyla	
Family Suidae	
Potamochoerus porcus	Bushpig
Phacochoerus aethiopicus	Warthog
Family Giraffidae	
Giraffa camelopardalis	Giraffe
Family Bovidae	
Cephalophus natalensis	Red duiker
Sylvicapra grimmia	Grey duiker
Raphicerus campestris	Steenbok
Oreotragus oreotragus	Klipspringer
Redunca arundinum	Reedbuck
Redunca fulvorufula	Mountain reedbuck
Kobus ellipsiprymnus	Waterbuck
Aepyceros melampus	Impala
Connochaetes taurinus	Wildebeest
Tragelaphus scriptus	Bushbuck
Tragelaphus angasi	Nyala
Tragelaphus strepsiceros	Kudu
Syncerus caffer	Buffalo

the nagana campaign of 1942 to 1950 (Mentis 1970). However, as early as 1960 their density in UGR was believed too high and they have been shot or removed in high numbers ever since.

There is no evidence that impala occurred in the Complex prior to 1935, but several authors have suggested that they probably did because of known populations nearby (Bourquin *et al.* 1971, Hitchens and Vincent 1972). No impala were recorded shot during the 1929 to 1930 nagana campaign and only a few were accounted for during that of 1942 to 1950 (Mentis 1970). Between 1936 and 1938 over 100 individuals were introduced into HGR and since then they have dispersed and become established in UGR (Hitchens and Vincent 1972).

Wildebeest, like zebra, were virtually eliminated during the nagana shooting campaigns (Foster *op. cit.*). Their numbers have increased since then and they were extensively shot or removed from UGR in the late 1960's and early 1970's because of their believed role in overgrazing.

There are no records for nyala in UGR prior to the 1940's, but Baldwin (1894) gives a sighting for Hluhluwe. No nyala were shot in the Umfolozi area during the 1929 to 1930 campaign and only 39 were accounted for between 1942 and 1950 (Mentis 1970). A small number were reintroduced into HGR in 1936 and since then the population has expanded to cover the whole Complex.

Buffalo were common in UGR prior to the nagana campaign, but their numbers dropped before shooting commenced and only 157 were reported shot in the Umfolozi area (Mentis 1970). Herds are believed to have returned from the north after cessation of shooting in 1950 and since then the population has steadily increased.

Predators

The larger predators that occur in UGR are lion (*Panthera leo*), leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), hyaena (*Crocuta crocuta*), black-backed jackal (*Canis mesomelas*) and serval (*Felis serval*) (Bourquin *et al.*1971). Lion were probably common throughout Zululand at the beginning of this century but were extinct in UGR by 1938. Immigration and reintroduction of a few animals in the 1950's and 1950's re-established the population which is now believed to number about 60 individuals (Anderson[1] pers. comm.). Lion, particularly

1. J.L. Anderson, Natal Parks Board.

young males, have begun recently to journey outside the reserve to kill cattle, which has prompted regular selective culling.

Cheetah were extinct in northern Natal by the 1920's, but since 1965 64 individuals have been released in the Complex and they now occur throughout UGR. They appear to be breeding well although no density estimate can be given. Hyaena, leopard and jackal are also widespread in UGR and again are of unknown density. Only a few observations of serval have ever been made in the reserve.

THE MAIN STUDY AREA

All intensive studies on waterbuck were carried out in a 36 km^2 main study area located in the north-west of UGR (Fig. 7), which was chosen to include all main aspects of environmental variation found in the reserve.

A computer drawn perspective block diagram illustrates the topography of the area as viewed from the north-west (Fig. 8). The grid lines are 250 m apart and represent a subdivision of the 500 m x 500 m block system which was used for most location purposes and which is marked at the edges of Fig. 9. The main study area is bordered in the north by the winding Black Umfolozi River and in the south by Mbulunga Hill (338 m.a.s.l.) and the Gqoyini Stream. Altitude falls from both south to north and from west to east, with the Black Umfolozi River staying close to the 125 m.a.s.l. contour line. Like much of UGR the area is mainly one of undulating hills with temporary streams in the depressions.

The top of Mbulunga Hill represents the only Miocene landsurface in the area, while ground between approximately the 225 m.a.s.l. and 300 m.a.s.l. contour lines comprises the Pliocene surface. Lower lying land nearer to the Black Umfolozi River is the Quaternary surface. Volcanic dolerite rock has intruded through the sedimentary strata of all the Miocene and Pliocene surface and some of the Quaternary surface in the west. This has also occurred in other parts of UGR and results in red tinted soil of potentially high mineral content (Downing 1972).

Figure 10 shows the vegetation of the main study area as mapped by Downing (1972). *Acacia nigrescens* open woodland is the most common woody community with the associated grasses *Themeda triandra* and *Panicum coloratum*. Closed woodland occurs along drainage lines and on level ground near the Black Umfolozi River. The vegetation of the main study

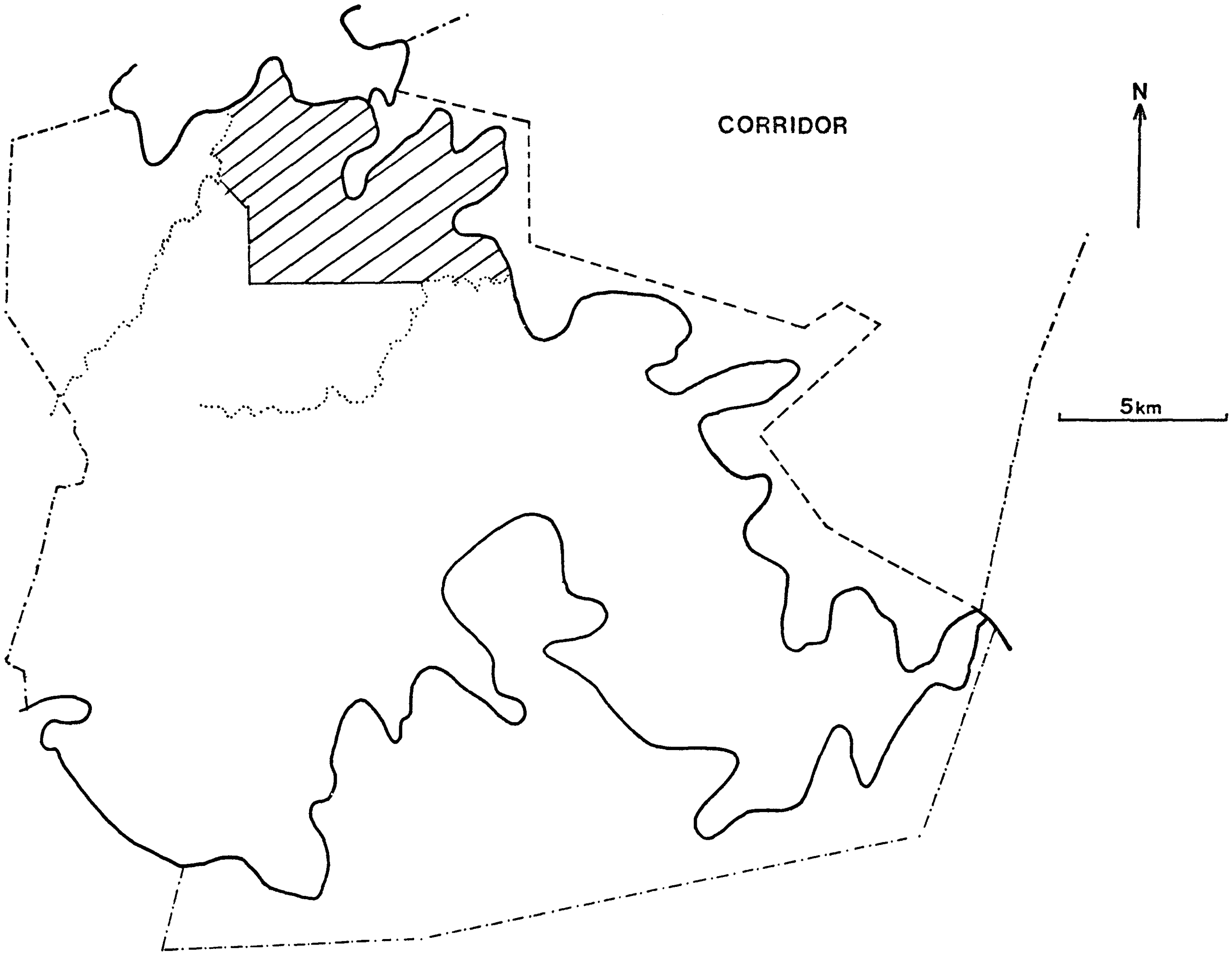


Figure 7. Location of the main study area (shaded) in the Umfolozi Game Reserve; key as in Fig. 2.

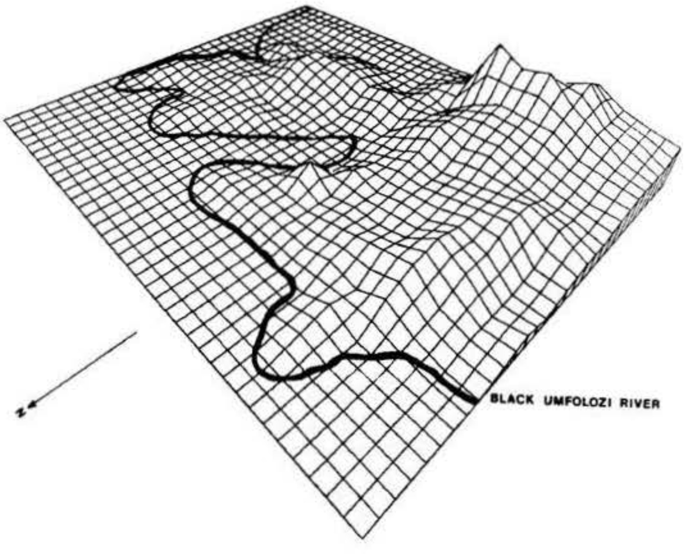


Figure 8. A computer drawn perspective block diagram of the main study area which illustrates the topography as viewed from the north-west. The grid lines are 250 m apart.

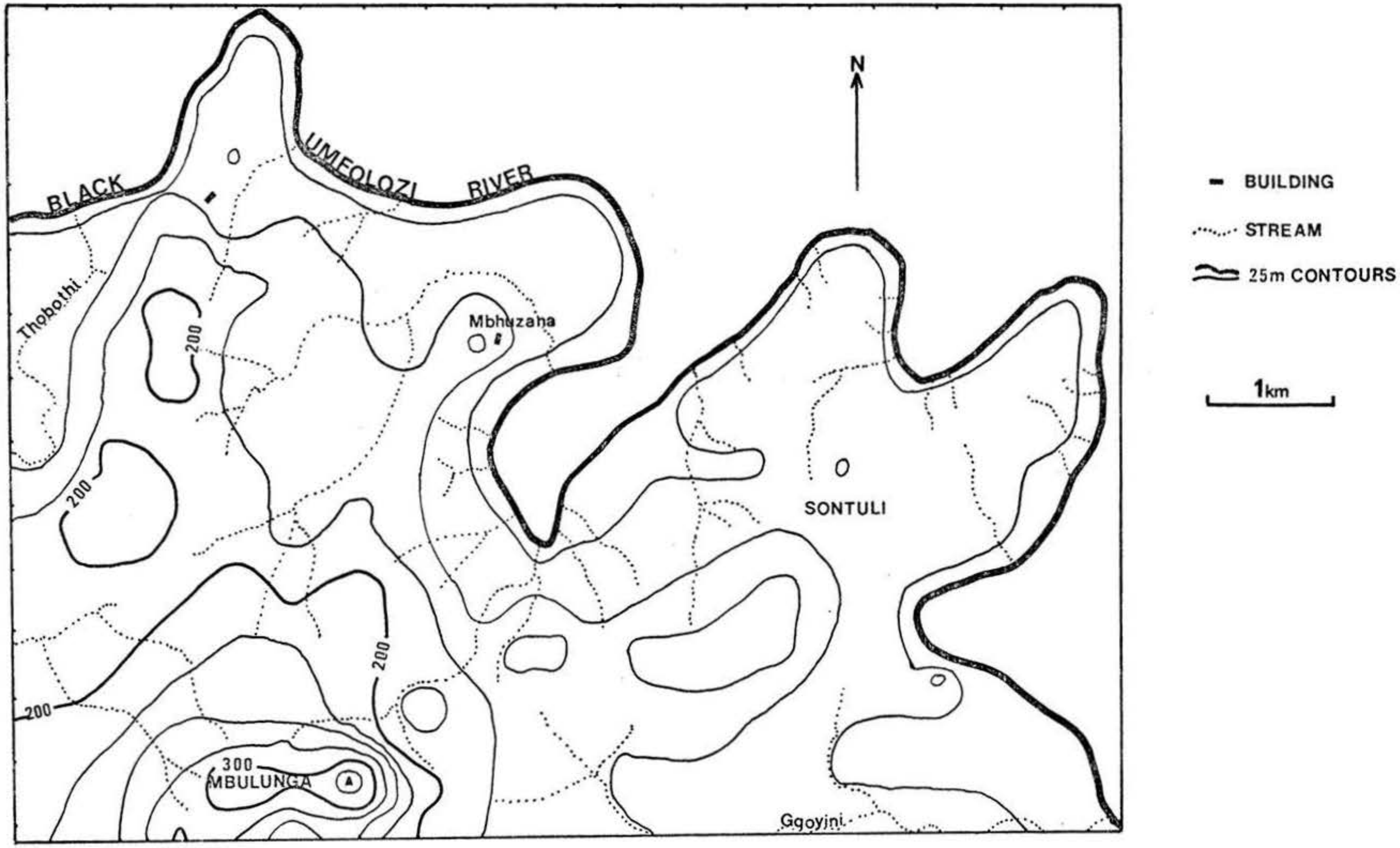


Figure 9. A topographic map of the main study area.

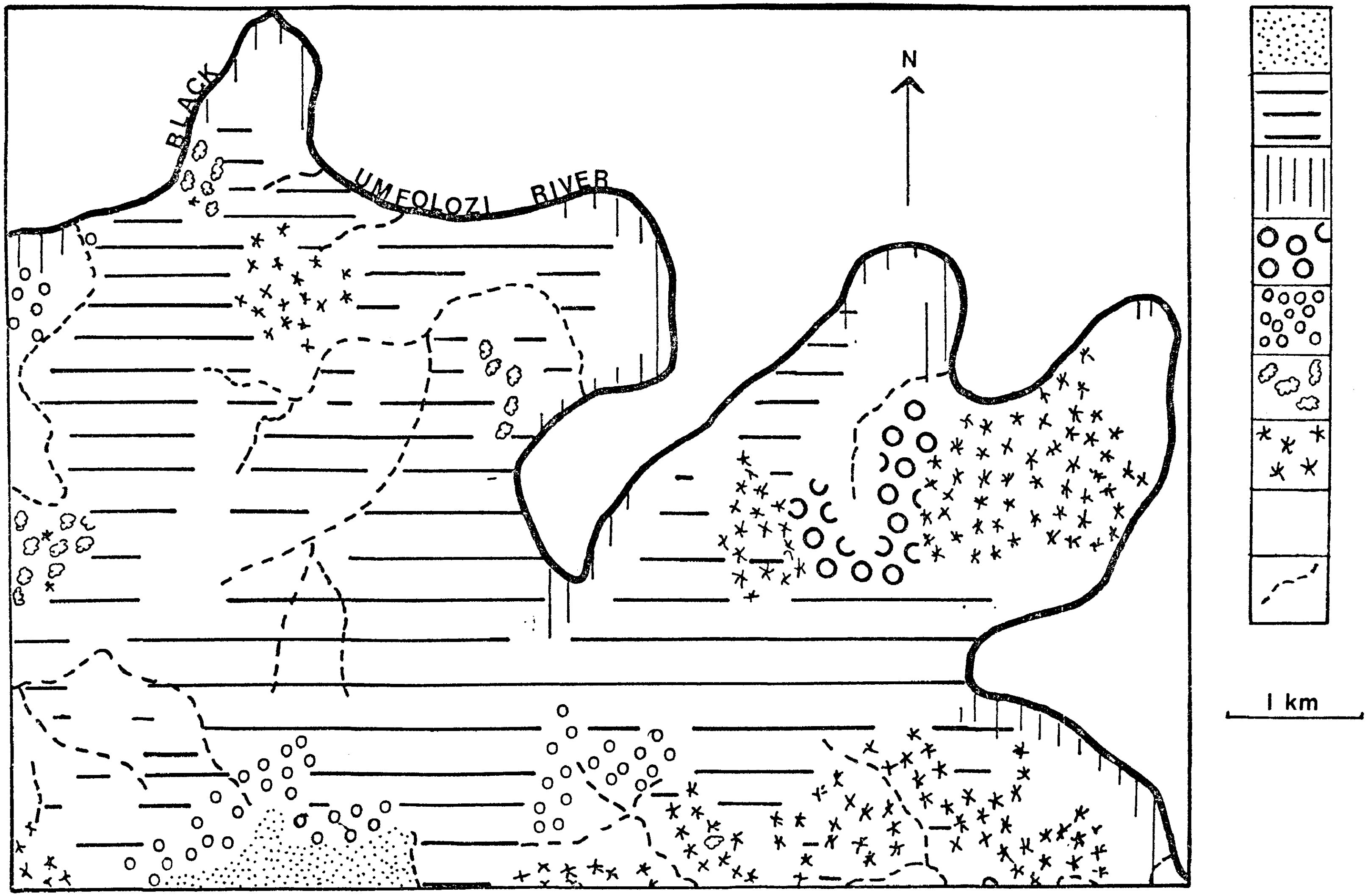


Figure 10. A map of the woody vegetation communities in the main study area (after Downing 1972). 1 - *Acacia caffra* open woodland; 2 - *Acacia nigrescens* open woodland; 3 - *Acacia robusta-Phoenix reclinata* closed woodland; 4 - *Acacia burkei* open woodland; 5 - *Acacia tortilis* open woodland; 6 - *Combretum apiculatum* open and closed woodland; 7 - *Acacia nilotica* open and closed woodland; 8 - *Acacia grandicornuta* closed woodland; 9 - *Spirostachys africana* closed woodland.

area was quantified for this study along with other environmental features, in order to examine herbivore-habitat relationships (see Chapter 8). Details of parameters measured will not be given here apart from mentioning the main grasses present during the study period as quantified by the per cent contribution to biomass method of Mannetje and Haydock (1963). The five dominant species were *Themeda triandra* (26,6 per cent), *Urochloa mossambicensis* (13,5 per cent), *Panicum maximum* (12,8 per cent), *Panicum coloratum* (12,6 per cent) and *Eragrostis superba* (5,0 per cent).

All parts of the main study area were burnt twice between 1970 and 1977. Figure 11 shows the extent of the 1976 and 1977 burns, which together covered the whole area. In 1976 *Themeda* dominated grassland of the southern upland area was burnt, while in 1977 the area nearer to the Black Umfolozi River was burnt.

The main study area is also representative of the faunal community of UGR. All predators apart from serval were sighted as were all ungulates listed in Table 1; all those ungulates which were common in UGR were seen frequently apart from giraffe (*Giraffa camelopardalis*).

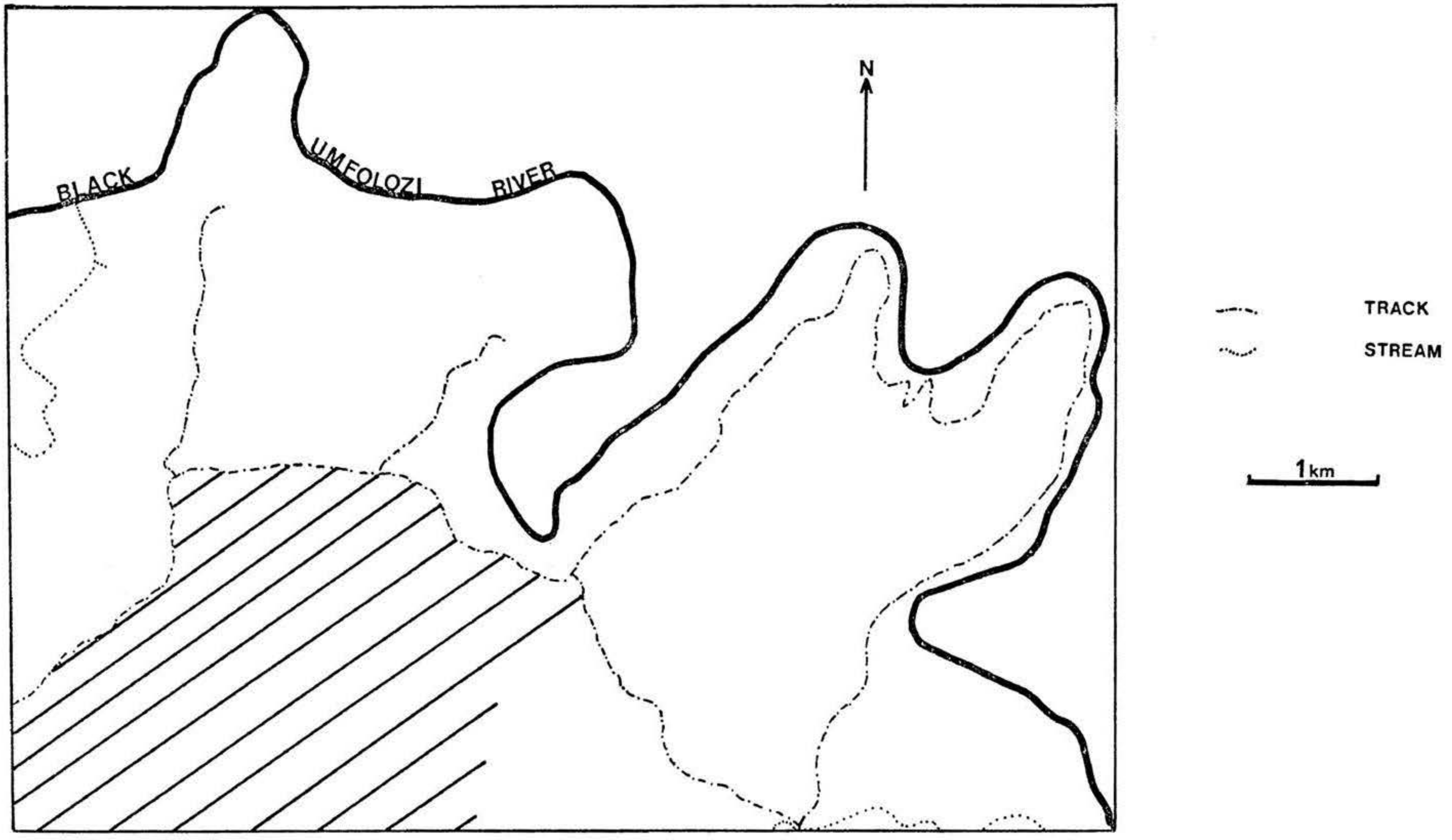


Figure 11. A map of the main study area showing the parts burnt in 1976 (shaded) and the remainder which was burnt in 1977.

CHAPTER 3

ABUNDANCE OF WATERBUCK AND OTHER HERBIVORES

INTRODUCTION

As stated by Caughley (1977) estimates of abundance have no intrinsic value and should not be considered ends in themselves. The analysis of waterbuck density carried out here is made first to provide absolute abundance estimates so that the UGR population can be compared with populations elsewhere. Numerical comparisons along with a knowledge of types and amounts of habitats available can be used to gauge the status of the UGR population. Such examinations are more meaningful when made in terms of per cent contribution to the biomass of all herbivores or better still energy expenditure (Macfadyen 1963). Thus it is necessary to estimate the densities of other species as well. The total biomass of herbivores present is also an important parameter within which to view the per cent contributions of individual species, since its "optimal" value in an area is empirically related to primary production and rainfall (Phillipson 1975, Coe, Cumming and Phillipson 1976).

The second use of the density estimates is to examine trends in population size. For this study trend analyses are important for waterbuck and for species competing with waterbuck.

A number of ground and aerial methods are used and comparisons made to identify biases in methods and suggest those that produce the most accurate absolute estimates and the best indices of trend.

METHODS

Four ground methods were employed to estimate the density of waterbuck in the study area; two of these were also used for other large herbivores. Fixed wing aerial censuses were made of waterbuck over all UGR and an experiment was carried out with helicopter counting in order to assess undercounting bias of the regular NPB helicopter counts of UGR.

Ground census

This method consists of an intensive foot coverage of the study area over a twelve day period. The area was split into twelve counting units that each took between three and five hours to cover. The numbers of all species seen were recorded and their positions noted with reference to a 1:25 000 map with a 500 m grid overlay. Counting was confined to mornings, as early as possible. In this way all grid squares (blocks) were searched each month to give uniform indices of density which could be used for trend analyses and, with calibration, as absolute density estimates. Monthly ground censuses were carried out from July 1976 to December 1977, apart from February and August 1977. An additional census of waterbuck was made in May 1976.

King's census

King's census is a sample count method using an unbounded transect (Leopold 1933, Robinette, Loveless and Jones 1974). The width of census strip is calculated for each species by doubling the mean sighting distance from the observer to the animal at first sighting. This sighting distance is that at which all individuals of a species are being seen under prevailing conditions of visibility. Inasmuch as the observer should, on average, be able to see the same distance in all directions, including those perpendicular to the census line, the distance is doubled for the effective width of the census strip.

The formula for the population estimate is:

$$P = \frac{AN}{2SL}$$

where P = population of area being sampled,
A = total area (using same units as used for sighting distances and length of the census line),
N = number of animals seen (each species analysed separately),
S = mean sighting distance (by species), and
L = length of the census line.

The census was carried out from a Landrover using two observers over 23 km of track within the study area (Fig. 12). All species seen were recorded, and so that data could be analysed on a stratified basis observations were logged as to distance along the census route. Sighting distances were initially paced on foot, but with experience they were estimated by eye for distances less than 100 m. The route was travelled twice during the morning and twice during the late afternoon for each month, so allowing the importance of time

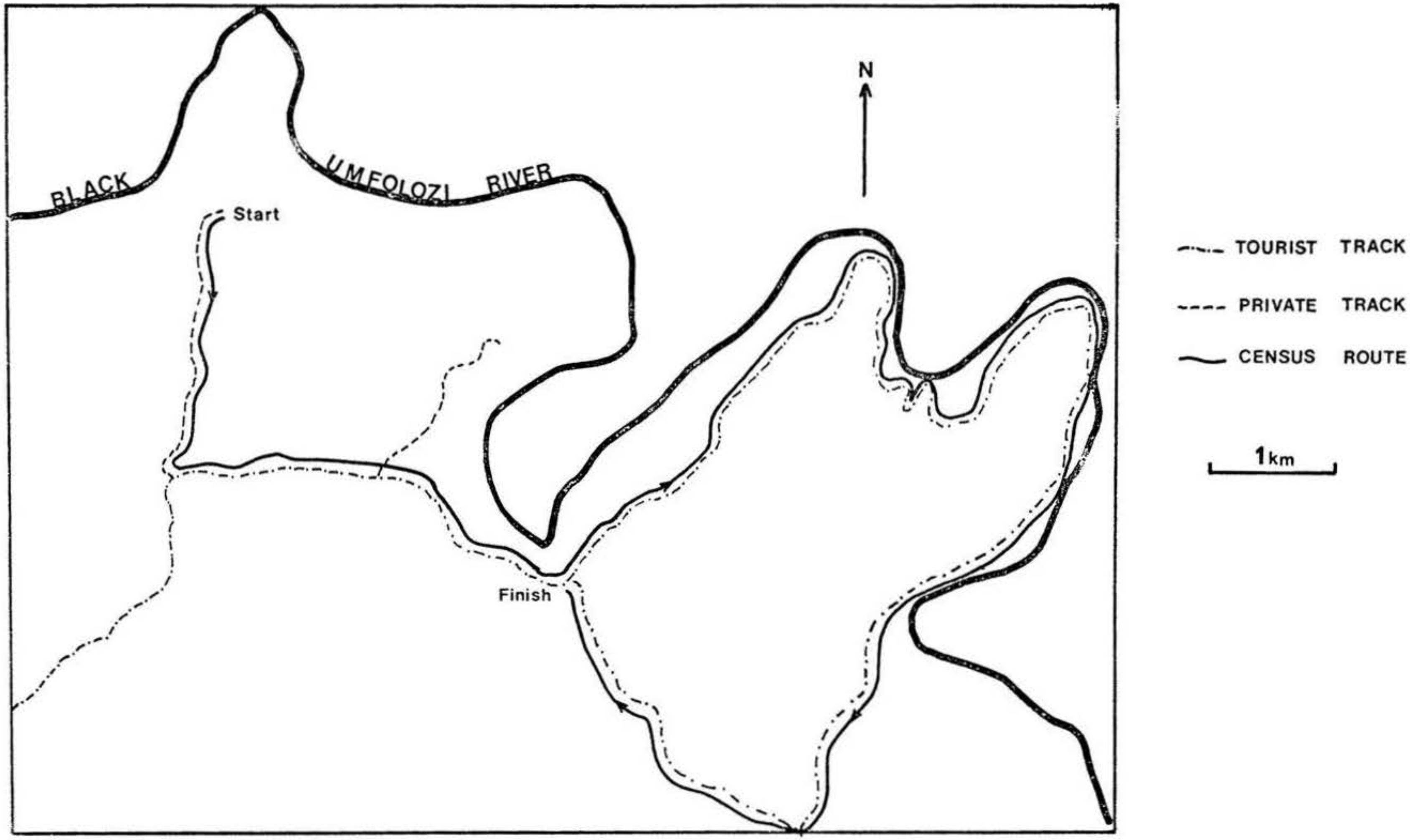


Figure 12. A map of the main study area showing the King's census route.

of sampling to be investigated. On average the mean number of a species seen per census stabilised after the second sampling. Thus four samples a month were considered sufficient to reduce error owing to sample size. No formal examination was made with regard to increasing the sample size further as the intensity used represented the highest possible because of time and cost.

King's censuses were made from July 1976 to December 1977 with an additional census for waterbuck in May 1976.

Maximum number seen estimate

This method was used to produce absolute density estimates for waterbuck in the study area. The method involved a detailed knowledge of the sex and age composition of herds and their movements during any one month. Marked animals (see Chapter 7) helped define the monthly areas used by herds and within those areas the maximum numbers of each sex and age class were added to give herd totals. Herd totals were then summed to produce a maximum number seen estimate for the whole study area. Monthly estimates were made from May 1976 to December 1977, apart from June 1976, February 1977 and August 1977.

Peterson estimate

This method was used for waterbuck within the study area and involved resightings of animals marked near the beginning of the study period (see Chapter 7). The Peterson estimate, often called the Lincoln Index, is the simplest mark-recapture estimate of numbers, involving marking animals on one occasion and recording their presence in a sample on a second occasion (Peterson 1896, Caughley 1977). The formula for the population estimate is:

$$P = \frac{Mn}{m}$$

where P = population of area being studied,
M = number of marked animals in population,
n = number of animals sampled, and
m = number of marked animals in sample.

All sightings of waterbuck in the study area were used to calculate this estimate. The value of M varied because of known deaths and known emigration from the study area. Because of this, each month could be treated as a separate mark-recapture operation. The relatively small proportion of the population marked and the restriction of marking to essentially one period preclude the use of a more sophisticated data analysis.

The estimate was calculated from August 1976 to July 1977. The method was terminated just before collars began to show significant signs of wear and so became difficult to observe.

Fixed wing aerial censuses

Two fixed wing aerial censuses of waterbuck were made over UGR in 1976 and three in 1977. The 106 km route was the same in each case (Fig. 13). It was not a random one but was designed to cover the main habitat types in the reserve, with an emphasis on areas near permanent water, since previous habitat analyses showed that waterbuck often occur at higher densities near water (Lamprey 1963, Herbert 1972). Within these constraints the route was chosen for convenience of landmarks to enable easy repetition. The plane used was a Cessna C177, with a pilot, a navigator who also positioned sightings onto a 1:50 000 map of the reserve, and two observers.

The plane was flown at an altitude of approximately 125 m and a speed of approximately 110 kph. The lack of struts precluded the attachment of streamers to delineate the census strip. The effective width was calculated by flying over a set of markers (telephone poles) in the reserve and noting the cut-off point used by observers for observing game. Measurement on the ground gave this distance to be approximately 250 m on either side of the plane. The estimation of this value is not at all critical because of the way undercounting bias corrections are made. Eighteen kilometres of the route were over the study area. Using the strip width of 500 m allows a mean density figure for the study area to be calculated from a 9 km^2 sample. This value was compared to the best estimate from the study area for that month and a conversion factor produced. The factor was applied to all raw data before analysis on a stratified basis was carried out. For calculations the route was split into 26 2 km^2 contiguous sample units, which were stratified with respect to distance to permanent water. Calculations and theory are as given by Snedecor and Cochran (1967).

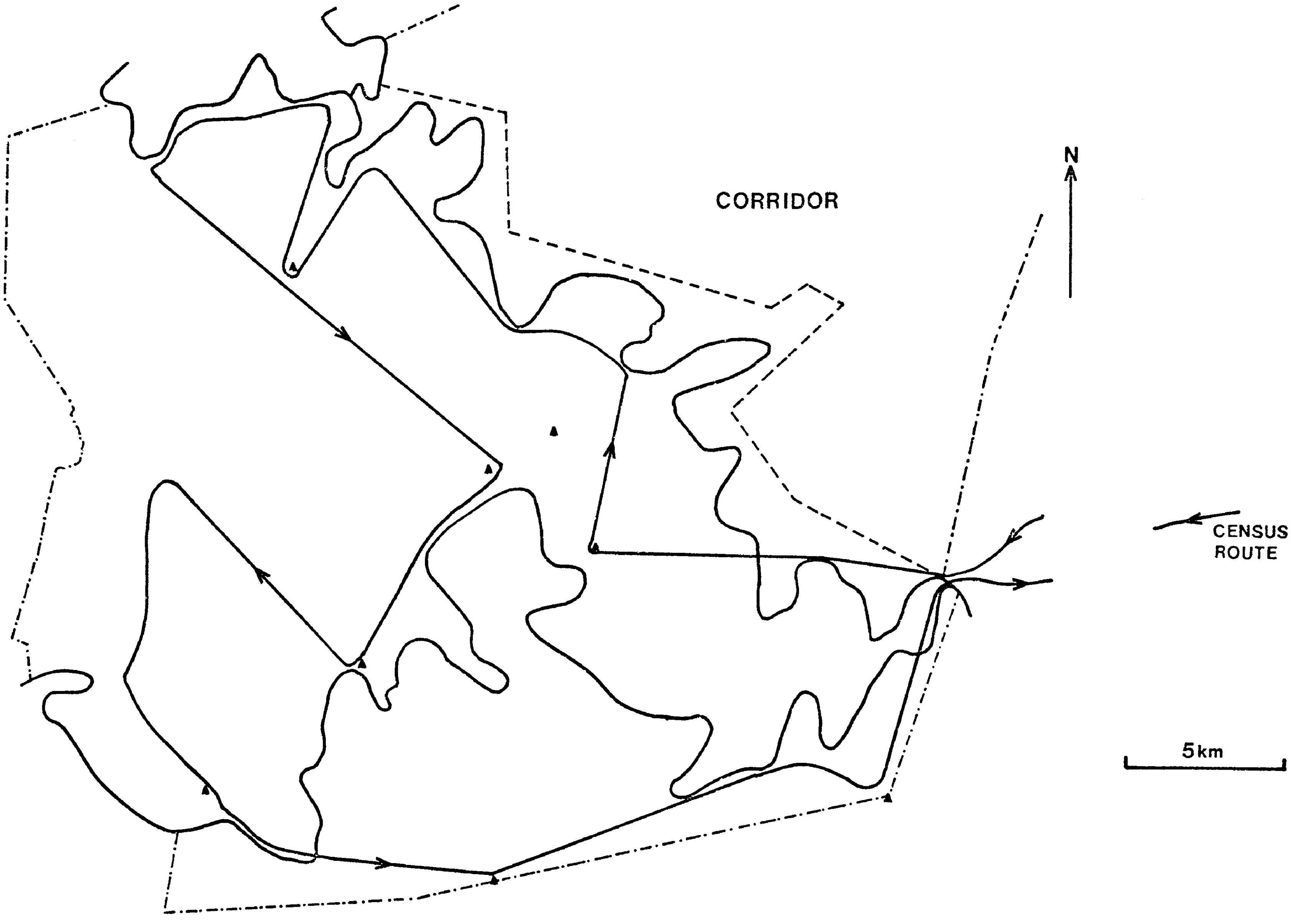


Figure 13. A map of the Umfolozi Game Reserve showing the 106 km fixed wing aerial census route.

Helicopter censuses

Since 1970 annual helicopter game censuses have been made of the HGR-Corridor-UGR Complex (Whateley, Goodman, Brooks, Forrest and Densham 1976). For each census the area is split into counting blocks delineated by conspicuous landmarks, such as the boundary fence, roads and rivers. Each block is covered once and all animals seen recorded. Block totals for each species are summed to give reserve and Complex total count estimates. This single sample method produces results that may be valid as indices of trend in numbers but not absolute density estimates. As it is generally accepted that most aerial censuses of game animals return underestimates (Caughley 1974) an evaluation of the undercounting bias of helicopter censuses in UGR was carried out.

In July 1976 a part of the study area (Sontuli) represented a complete counting block in the annual helicopter census of the Complex. There was no complete census in 1977, but to examine undercounting bias the Sontuli area was again counted for all species in July, as was the rest of the study area (Thobothi). An additional slow helicopter count was made of the Sontuli area, which took almost twice the normal flying time (Table 2).

RESULTS AND DISCUSSION

Density estimates in the main study area

The monthly density estimates of waterbuck using four methods are shown in Fig. 14. Stratified King's census results are given in Table 3 with the details of stratification in Table 4; the habitat variables stratified are two of those showing importance in separating species throughout the study period (see Chapter 8).

The pattern of variation in numbers is similar in all methods but the absolute values vary considerably. The ground census and the maximum number seen estimate are the most similar having means of 74,3 and 91,8 respectively. The unstratified and stratified King's censuses give higher results with total period means of 210,3 and 165,0 respectively; the Peterson estimate also has a higher mean of 141,8, but this value is not strictly comparable with the others as the sampling period was shorter. The ground census is expected to represent a constant underestimate, but what of the other methods? The use of data from helicopter counts suggest that the maximum number seen estimate

Table 2. Details of helicopter counts in the main study area used to analyse aerial undercounting bias.

	July 1976	July 1977		
Location	Sontuli	Sontuli	Sontuli	Thobothi
Area (km^2)	13,5	13,5	13,5	22,5
Time taken (min)	45	40	70	52
Helicopter	Hughes 300c	Hiller ultra air	Hiller ultra air	Hiller ultra air

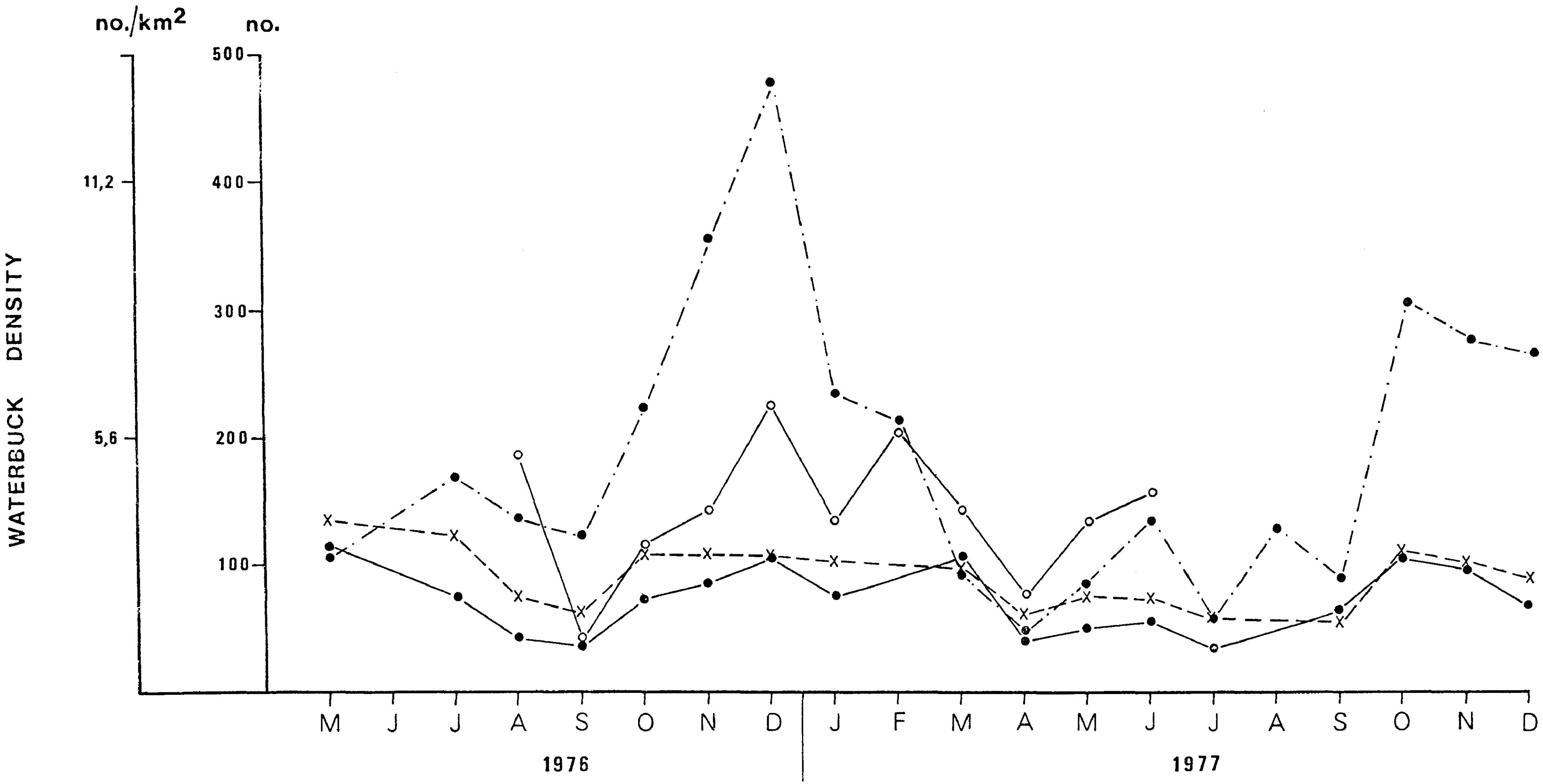


Figure 14. Monthly density estimates for waterbuck in the main study area from four census methods; ground census (—•—), maximum number seen estimate (–x–), King's census (-·•-·) and the Peterson estimate (—o—).

Table 3. Stratified King's census results for waterbuck in the main study area.

Month	Stratum 1		Stratum 2		Stratum 3		Stratum 4		Total	
	no	no/km^2	no	no/km^2	no	no/km^2	no	no/km^2	no	no/km^2
1976										
May	26	3,3	71	5,9	0	0	21	1,5	118	3,4
Jul	20	2,5	91	7,6	0	0	64	4,6	175	5,0
Aug	50	6,3	31	2,6	0	0	0	0	81	2,3
Sep	43	5,3	25	2,1	0	0	0	0	68	1,9
Oct	34	4,3	160	13,3	0	0	0	0	194	5,5
Nov	37	4,6	238	19,8	0	0	0	0	275	7,9
Dec	81	10,1	244	20,3	0	0	138	9,9	463	13,2
1977										
Jan	47	5,9	92	7,7	0	0	118	8,4	257	7,3
Feb	55	6,9	90	7,5	0	0	61	4,4	206	5,9
Mar	9	1,1	77	6,4	0	0	0	0	86	2,5
Apr	9	1,1	29	2,4	0	0	0	0	38	1,1
May	19	2,4	38	3,2	0	0	0	0	57	1,1
Jun	26	3,3	95	7,9	0	0	0	0	121	3,5
Jul	7	0,9	30	2,5	0	0	21	1,5	58	1,7
Aug	10	1,3	67	5,6	0	0	0	0	77	2,2
Sep	4	0,5	75	6,3	0	0	0	0	79	2,3
Oct	58	7,3	185	15,4	0	0	7	0,5	250	7,1
Nov	76	9,5	117	9,8	2	2,0	103	7,4	298	8,5
Dec	25	3,1	164	13,7	18	18,0	19	1,4	226	6,5

Table 4. Stratification of the main study area used for King's census data analysis.

	Distance to Black Umfolozi River (km)	Density of trees (no/0,05 ha)	Habitat description	Area (km^2)	Per cent of study area
Stratum 1	< 1	> 12	Closed woodland near river	8	22,9
Stratum 2	< 1	< 12	Open woodland near river	12	34,3
Stratum 3	> 1	> 12	Closed woodland away from river	1	2,9
Stratum 4	> 1	< 12	Open woodland away from river	14	40,0

is the most accurate. Because there was no increase in the number of white rhino counted by flying more slowly, it is concluded that probably all white rhino are counted during normal helicopter censuses (Table 17). This means that white rhino densities could be used to compute corrected waterbuck densities from ground census results using the ratio count method. Thus in July 1976 there were 22 white rhino in the Sontuli area, of which 15 were counted during the ground census, giving a conversion ratio of 1,47:1. This gives a corrected waterbuck count of 41,1, whilst the maximum number seen estimate was 48. A similar analysis for the whole study area in July 1977 gives a corrected ground census of 58,1 waterbuck with a maximum number seen estimate of 59. A final way a near 100 per cent waterbuck count can be produced with which to compare other estimates comes from a slow helicopter count of the Sontuli area in July 1977. This census produced a total of 37 waterbuck, compared to seven counted during a normal count. It is likely that this figure represents virtually all waterbuck in the area. The maximum number seen estimate was 36.

If the maximum number seen estimate is the best then the ground census is the next best as it significantly ($P<0,01$) linearly correlates with it, with a mean of 80 per cent of its value (1,25:1 conversion factor). The relationships of all three methods to the maximum number seen estimate are shown in Figs. 15 to 17. The highest linear correlation and lowest y intercept are given by the ground census. The other two sample methods appear to overestimate waterbuck numbers, particularly at higher densities. The very high peaks shown by the King's census are somewhat reduced by stratification. It is not possible to advocate the maximum number seen estimate as that which should be used to compute absolute animal densities by reserve biologists in their regular monitoring of game, because of the time involved. It therefore seems that an intensive coverage method would be preferable to a sample method, the reason being that the complexities of species habitat associations as described in Chapter 8 make it very difficult to apply meaningful stratification.

It is suggested that the mean maximum number seen estimate of 2,6 waterbuck/km^2 is nearer to an ecological density than a crude one (Odum 1959), as the whole area was utilized by the species. Density estimates for waterbuck in 12 other areas of Africa are included in Table 26. This figure is not far below the average ecological density of 6,5 per km^2 calculated for these areas. If the high density of

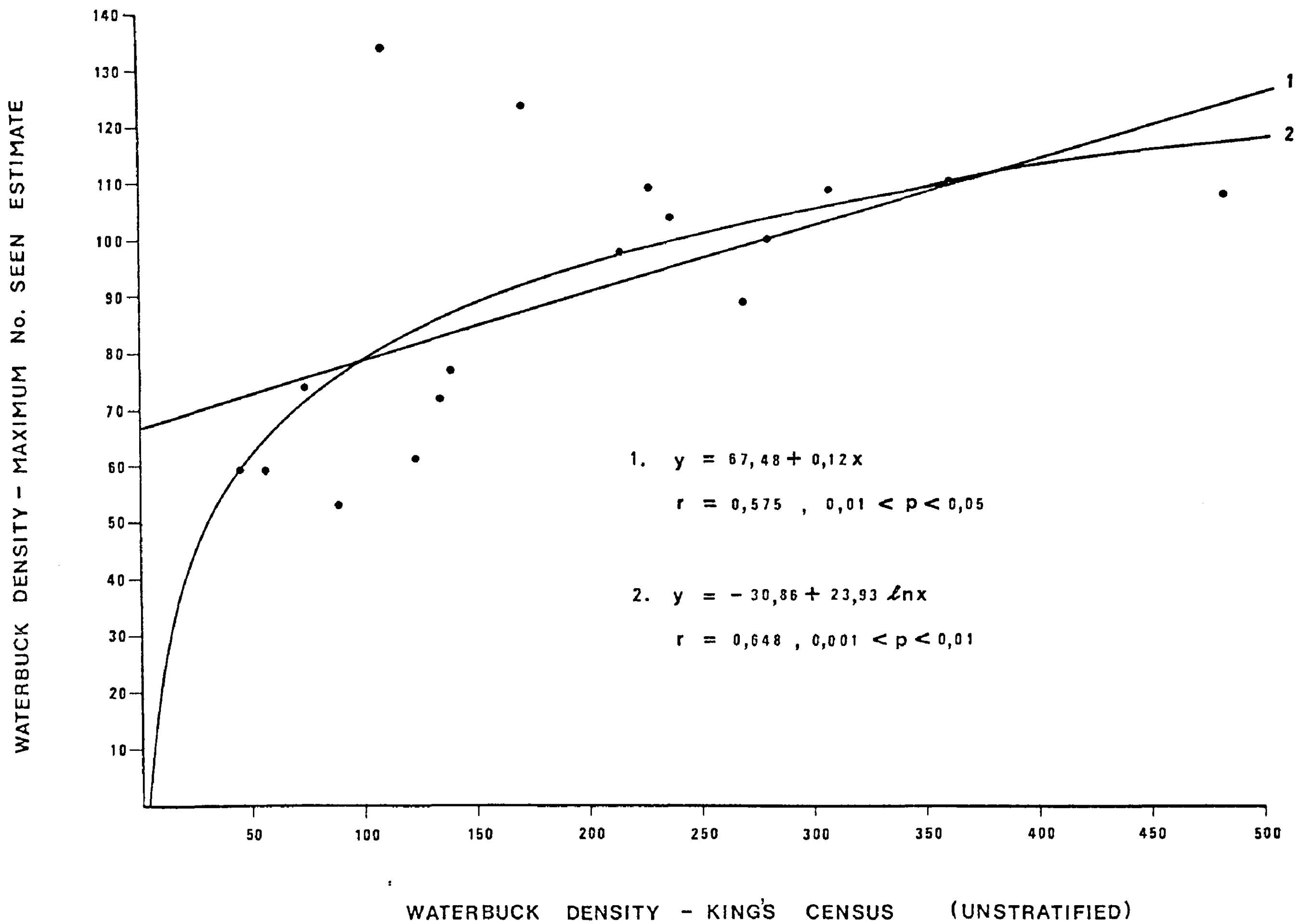


Figure 15. Comparison of waterbuck density estimates in the main study area given by the King's census method with those given by the maximum number seen estimate.

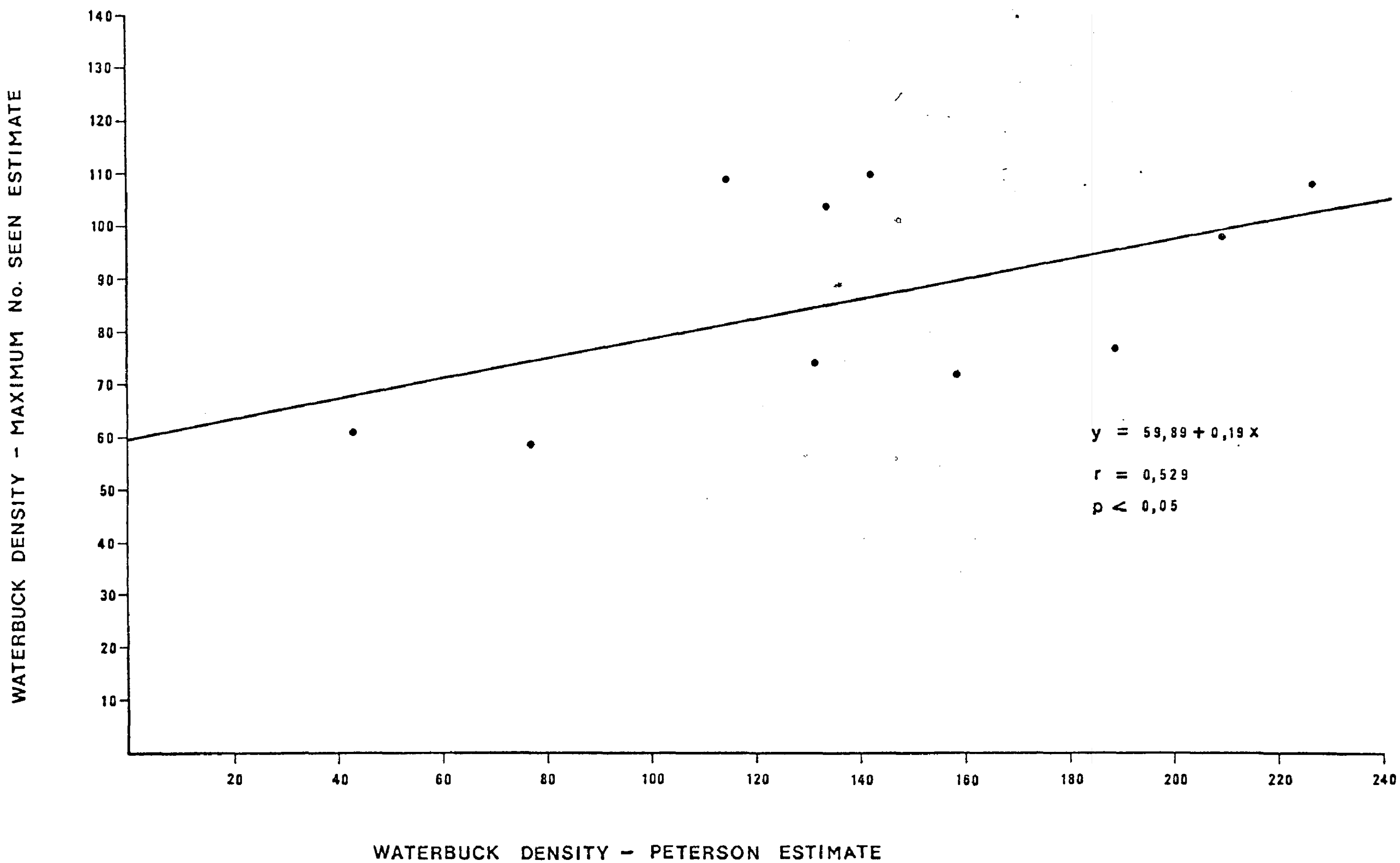


Figure 16. Comparison of waterbuck density estimates in the main study area given by the Peterson estimate with those given by the maximum number seen estimate.

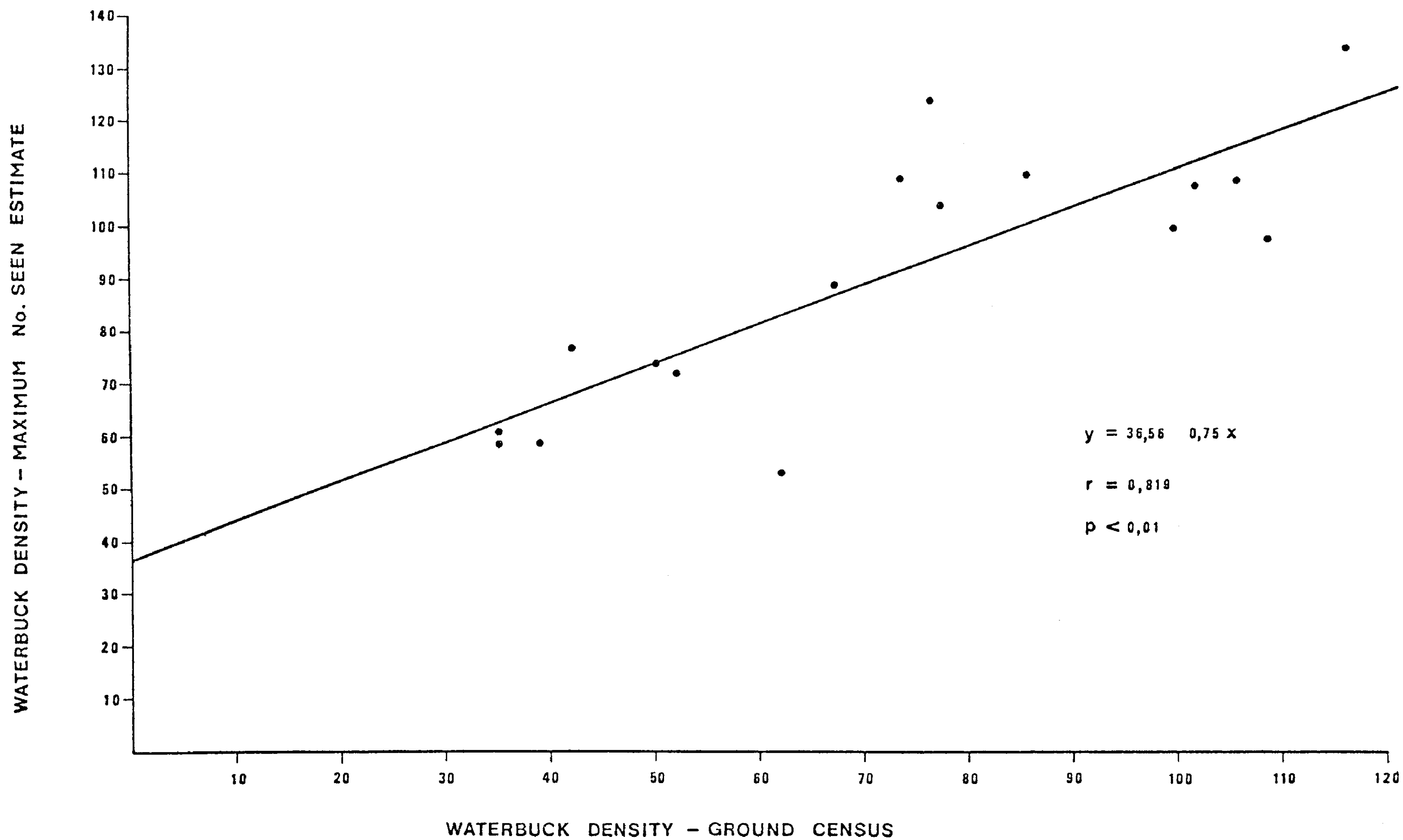


Figure 17. Comparison of waterbuck density estimates in the main study area given by the ground census with those given by the maximum number seen estimate.

31,1 per km^2 recorded at Lake Nakuru (Kutilek 1974) is omitted the mean density elsewhere falls to 3,7 per km^2. The highest local density recorded for waterbuck is 82,4 animals per km^2 in a 1,7 km^2 part of a newly enclosed 55 km^2 area in Kenya (Elliott 1977); the density over the whole area was 3,6 per km^2. A more detailed discussion of relative abundance will be made later using units of metabolic biomass.

Density estimates of the other seven main grazing species and waterbuck using the ground census and King's census are graphed in Figs. 18 to 21. Monthly ground census results for the less common grazers, for browsers and for predators are given in Table 5.

The largest variation in numbers including near zero values is shown by buffalo and zebra, indicative of their non-resident status in the study area, which has been confirmed by marking studies (Brooks[1] pers. comm.). Mean densities of species in the study area during 1976-1977 are included in Table 21. They were calculated by assuming all species were undercounted equivalently during the ground census and by using the 1,25:1 waterbuck conversion factor. It is suggested that this assumption is valid for the main grazers bearing in mind the intensive nature of the ground census. The numerically commonest species is impala, with 320 individuals, then nyala with 150 and then warthog with 130. Porter (1975) presented monthly census results for a 2,7 km^2 portion of the main study area over a 16 month period during 1972-1973. A comparison of his results with those of the present ground census is given in Table 6. The numerically predominating species were also impala and nyala during the earlier time, but in reverse order. In general all his values were higher than those presented here which is likely because he used three observers to cover the area. This is not necessarily so, but the differences in method mean that a direct numerical comparison cannot be made. A more meaningful comparison using per cent contribution to biomass is presented later.

Variation of estimates with time of day and season

Because there was not a complete year's sampling in 1976 these study area density data must be tested for homogeneity with respect to season before they can be analysed for trend. This analysis and one investigating variation in counts with the time of day have been carried out using the raw data of the King's census as indices of

1. Dr P.M. Brooks, Regional Scientist HGR.

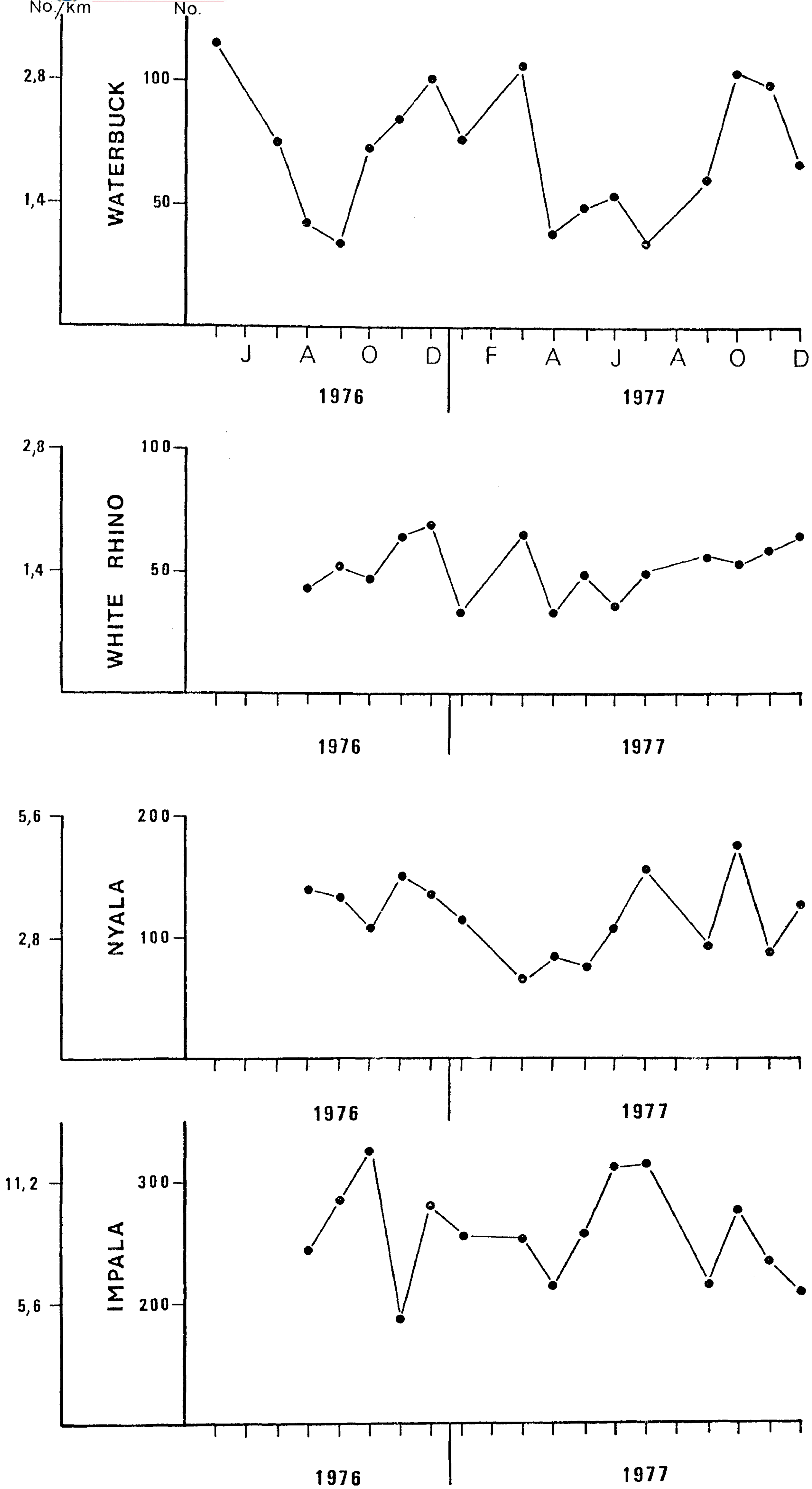


Figure 18. Ground census estimates of waterbuck, white rhino, nyala and impala in the main study area.

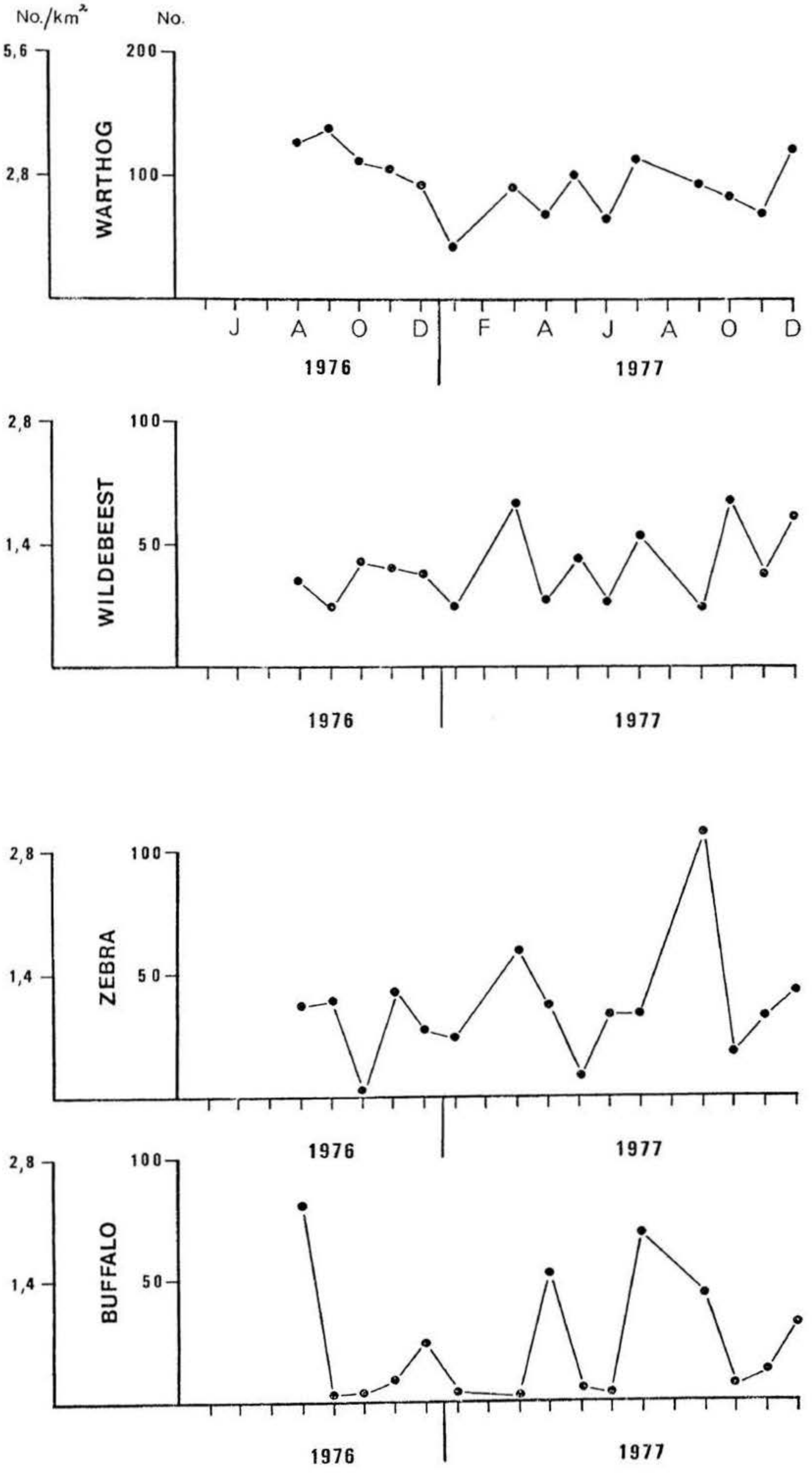


Figure 19. Ground census estimates of warthog, wildebeest, zebra and buffalo in the main study area.

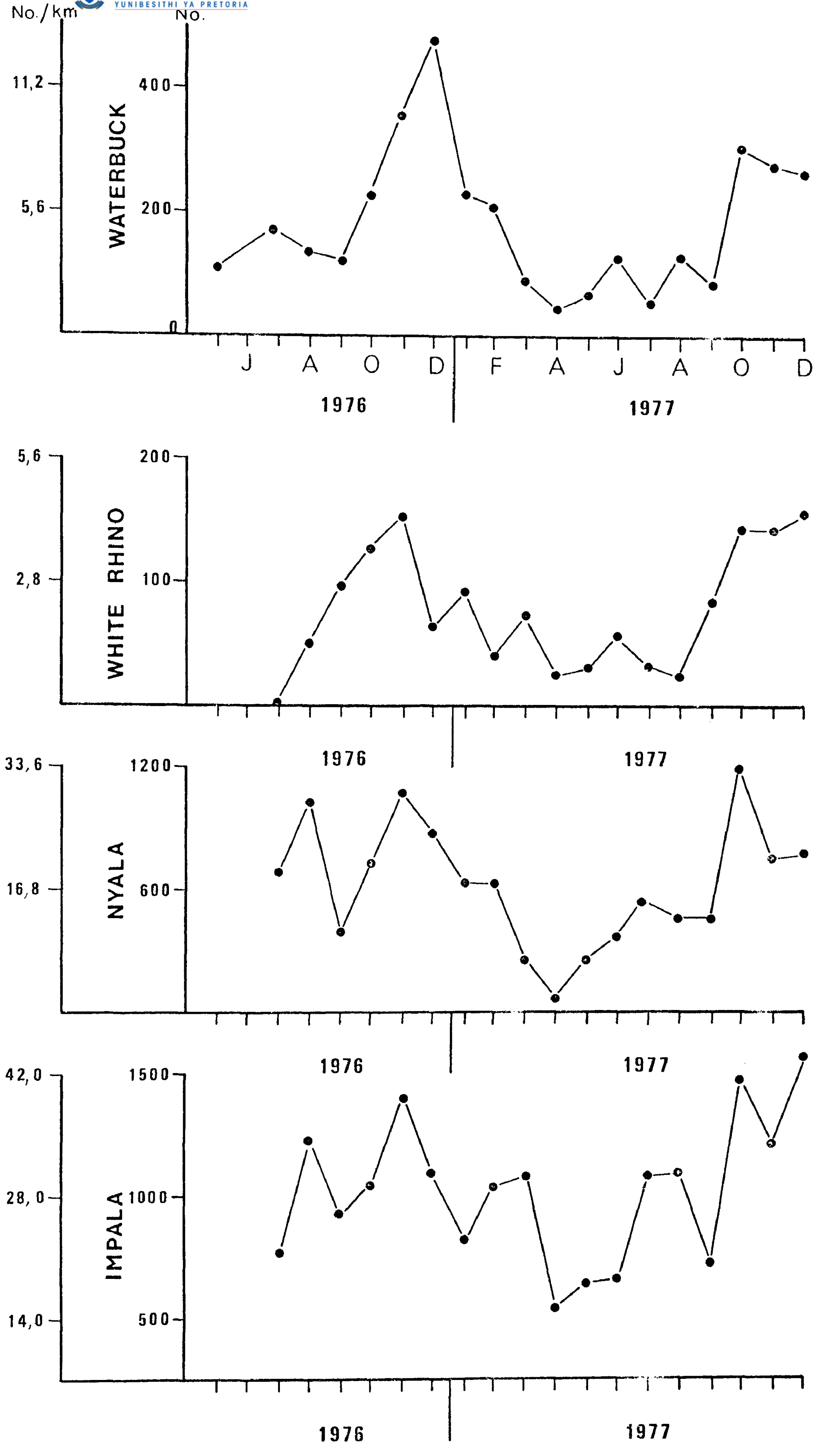


Figure 20. Unstratified King's census estimates of waterbuck, white rhino, nyala and impala in the main study area.

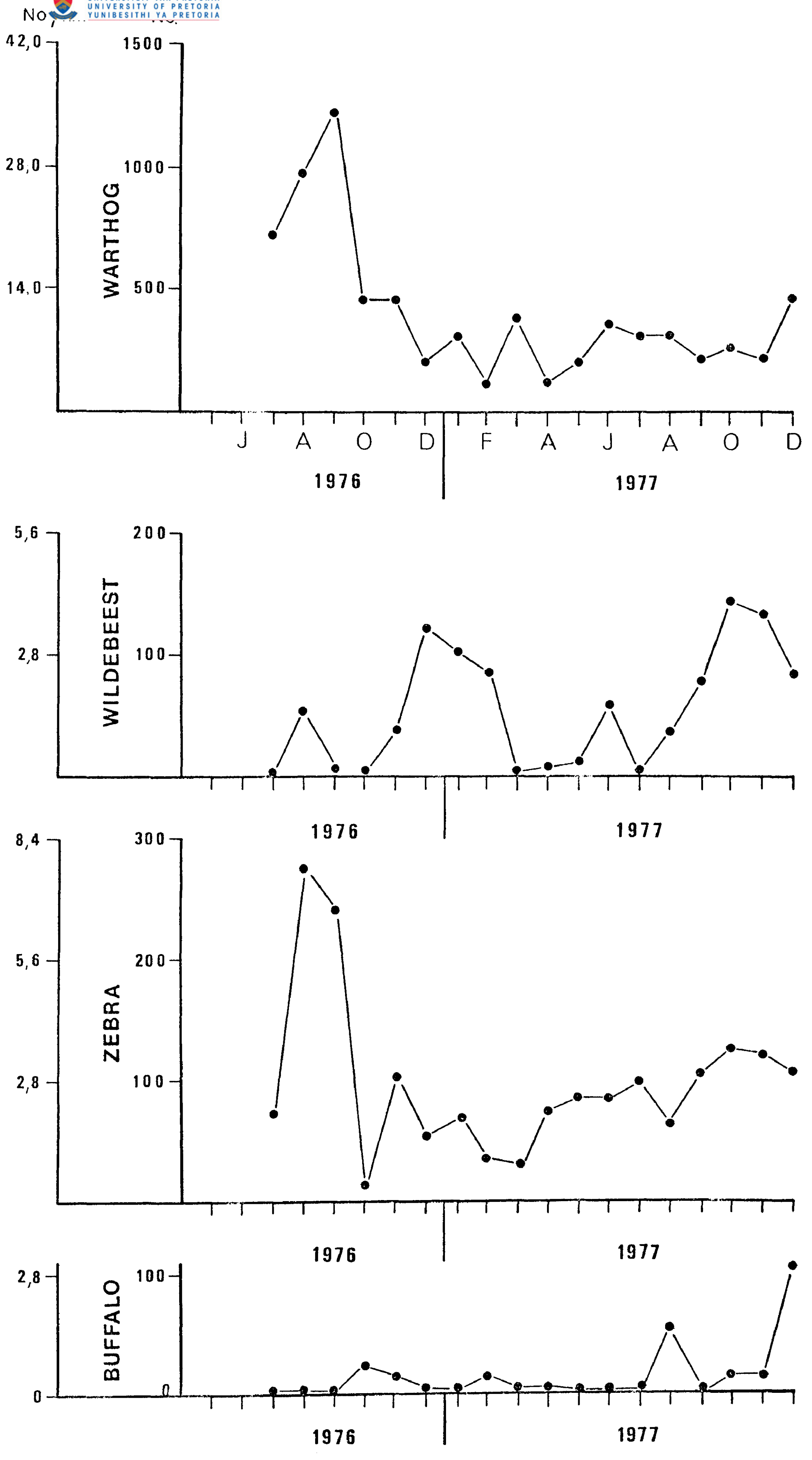


Figure 21. Unstratified King's census estimates of warthog, wildebeest, zebra and buffalo in the main study area.

Table 5. Monthly ground census estimates for the less common grazers, browsers, baboons, lion and cheetah in the main study area.

Month	Common reedbuck	Mountain reedbuck	Steenbok	Kudu	Black rhino	Grey duiker	Giraffe	Baboon (troops)	Lion	Cheetah
1976										
Aug	1	1	1	43	1	5	0	2	2	2
Sep	0	0	1	17	1	3	0	6	0	0
Oct	0	4	4	25	3	1	0	6	5	0
Nov	0	0	3	53	1	3	0	4	0	2
Dec	1	5	2	27	4	3	0	7	0	0
1977										
Jan	0	0	4	10	0	4	0	3	0	0
Mar	0	0	3	25	1	1	1	1	0	0
Apr	1	0	0	20	1	0	0	3	0	0
May	0	0	0	8	2	1	0	1	3	0
Jun	0	0	0	29	0	0	0	3	0	0
Jul	0	0	1	26	3	3	0	1	0	0
Sep	0	0	3	23	0	3	0	5	5	0
Oct	0	0	3	46	2	1	0	6	0	0
Nov	1	0	3	29	1	3	1	3	0	1
Dec	0	0	1	17	2	2	0	4	0	0

Table 6. Comparison of the 1972-1973 ground census results in part of the main study area with the 1976-1977 ground census results presented here.

Species	Mean estimates 1972-1973 ground census* (no/km^2)	Mean estimates 1976-1977 ground census (no/km^2)
White rhino	4,5	1,5
Buffalo	0,06	0,7
Zebra	5,6	1,0
Waterbuck	8,9	2,0
Wildebeest	4,6	1,1
Warthog	3,8	2,8
Impala	12,3	7,2
Nyala	13,2	3,7
Steenbok	0,7	0,06
Grey duiker	0,5	0,07
Black rhino	0,04	0,04
Kudu	2,7	0,9

* Data reanalysed from Porter (1975)

density (Tables 7 and 8). The only two species affected by the time of day were warthog and nyala. Significantly ($P < 0{,}05$) more warthog were seen during the morning in the dry months and significantly ($P < 0{,}05$) more nyala during the afternoons of wet months.

More species varied with respect to season. Significantly more waterbuck ($P < 0{,}001$), wildebeest ($P < 0{,}01$), nyala ($P < 0{,}05$), impala ($P < 0{,}001$) and white rhino ($P < 0{,}001$) were counted during the wet months. This trend can be seen in many of the census estimates (Figs. 18 to 21), particularly for waterbuck. This may be related to more animals utilizing the shorter low-lying grasslands in the wet months (see Chapter 8); certainly some waterbuck leave the area during dry periods as shown by collar resightings (see Chapter 7).

Trend analyses

An analysis of trends in density between 1976 and 1977 was made for all eight main grazers, taking into account seasonal and temporal variability. Table 9 shows the comparison for waterbuck using only paired months. All three census methods for which this was possible indicate a decline in numbers, which is almost significant for the maximum number seen estimate ($0{,}05 < P < 0{,}1$). The observed exponential rates of increase ($\bar{r}$, Caughley 1977) from these three methods range between -0,14 and -0,29, suggesting a finite loss rate (λ) of between 13 and 25 per cent per year (Table 9). Little reliance can be placed on these figures owing to the relatively short period over which the study was made and the unknown contribution of dispersal. It is probable though that the population is declining at present. The removal of waterbuck from UGR over the study period was only 17 and need not be taken into account in trend analyses (Table 10).

Results of using King's census raw data to indicate trend for all eight main grazers are given in Table 11. Again waterbuck show a decline, this time significantly so comparing the dry months ($P < 0{,}05$). The only other significant trend is for a decline in warthog as judged from morning censuses only ($P < 0{,}05$).

A by month comparison of 1976 with 1977 ground census estimates for all species shows no significant differences (Table 12).

Density estimates in Umfolozi Game Reserve

Table 7. Comparison of morning and afternoon censuses in both wet and dry months for the eight main grazing species using King's census raw data counts in the main study area.

	Mean morning count		Mean afternoon count		Significance of morning-afternoon differences	
	Dry months	Wet months	Dry months	Wet months		
Species	Apr-Sep[1]	Oct-Mar[2]	Apr-Sep	Oct-Mar	Dry	Wet
Waterbuck	8,05	19,58	4,90	21,0	NS*	NS
Buffalo	0,94	1,89	0	1,33	NS	NS
Zebra	7,40	7,79	7,80	4,95	NS	NS
Wildebeest	3,15	7,43	1,70	7,81	NS	NS
Warthog	25,45	18,93	12,10	19,19	$t=2{,}72$ $P<0{,}05$	NS
Nyala	19,00	27,36	28,40	53,29	NS	$t=2{,}6$ $P<0{,}05$
Impala	50,90	83,93	60,10	94,90	NS	NS
White rhino	3,40	7,71	3,00	10,24	NS	NS

1. n=20
2. n=14
* $P>0{,}1$

Table 8. Comparison of dry and wet season censuses taking into account significance of morning-afternoon variability, for the eight main grazing species using King's census raw data counts in the main study area.

Species	Mean count in dry months Apr-Sep		Mean count in wet months Oct-Mar		Significance of seasonal differences	
Waterbuck	7,00		20,43		t=-6,37, df=63 P$<$0,001	
Buffalo	0,63		1,55		NS*	
Zebra	7,53		6,09		NS	
Wildebeest	2,67		7,66		t=-2,86, df=61 0,001$<$P$<$0,01	
Impala	53,97		90,51		t=-3,45, df=61 P=0,001	
White rhino	3,27		9,23		t=-4,37, df=61 P$<$0,001	
	Morning	Afternoon	Morning	Afternoon	Morning	Afternoon
Warthog	24,45	12,10	18,93	19,19	NS	NS
Nyala	19,00	28,40	27,36	53,29	NS	t=-2,26 df=29 0,01$<$P$<$0,05

* P$>$0,1

Table 9. Comparison of the 1976 and 1977 waterbuck census estimates in the main study area, using the Student's t test for paired (by month) variates.*

Census method	1976 mean	1977 mean	λ	$\text{Log}_e\lambda = \bar{r}$	Significance of trend
Maximum number seen estimate	107,7	80,7	0,75	-0,29	t=2,35, df=5 0,05<P<0,1
Ground census	80,8	69,7	0,86	-0,15	NS**
King's census (unstratified)	228,9	199,5	0,87	-0,14	NS

* See text for explanation of terms.

** P>0,1

Table 10. Numbers of game removed (shot or captured) from the Umfolozi Game Reserve between 1959 and 1977.

		1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977
Warthog	S*	302	680	801	1798	2081	3051	1512	861	523	543	677	595	399	837	314	475	364	176	39
	C**	-	-	-	-	-	-	-	-	-	4	3	-	-	-	263	71	172	122	304
Wildebeest	S	19	32	30	-	76	90	387	176	69	78	159	91	183	454	127	50	-	-	-
	C	-	-	-	-	-	-	-	-	-	106	-	433	1030	-	164	341	20	40	-
Impala	S	1	31	16	19	30	30	40	32	7	21	83	67	167	523	104	48	110	72	75
	C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	317	565	228	168	179
Nyala	S	-	-	-	-	6	1	21	21	-	-	-	-	-	3	-	10	60	36	20
	C	-	-	-	-	-	-	-	-	-	2	-	3	-	-	217	115	198	-	-
Zebra	S	15	41	5	-	-	2	84	11	-	-	3	-	86	-	-	-	-	-	-
	C	-	-	-	-	-	-	-	-	-	-	-	-	-	102	61	-	-	30	2
Waterbuck	S	-	-	-	-	-	-	31	3	-	-	-	-	-	-	-	-	-	-	-
	C	-	-	-	-	-	-	-	-	-	7	5	23	-	21	-	-	17	11	6
Bushbuck	S	2	16	15	4	20	4	1	3	-	-	-	-	-	-	-	-	-	-	-
	C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Buffalo	S	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	50	84	22	2
	C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	22
Kudu	S	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	26	15
W. rhino	C	-	-	10	46	46	214	-	-	17	68	54	179	148	448	289	263	91	37	14
B. rhino	C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2

* shot

** captured

Table 11. Comparison of 1976 King's census raw data counts with those of 1977, using the Student's t test, taking into account significant differences between morning and afternoon counts.

	Dry Months			Wet months		
Species	1976	1977	Significance	1976	1977	Significance
Waterbuck	11,0	5,8	t=2,1, df=28 $P<0,05$	23,9	17,6	$P>0,1$
Wildebeest	1,4	3,2	$P>0,1$	4,6	9,0	$P>0,1$
Impala	59,8	57,4	$P>0,1$	74,5	93,7	$P>0,1$
White rhino	2,4	3,7	$P>0,1$	7,9	9,8	$P>0,1$
Buffalo*	Wet + dry 1976 = 0,72;	wet + dry 1977 = 1,4				$P>0,1$
Zebra*	Wet + dry 1976 = 4,8;	wet + dry 1977 = 7,0				$P>0,1$
	Morning 1976	Morning 1977		Afternoon 1976	Afternoon 1977	
Warthog*1	39,5	19,9	t=2,5 df=30 $P<0,05$	16,3	17,2	$P>0,1$
				Afternoon wet 1976	Afternoon dry 1976	
Nyala[2]	27,8	22,9	$P>0,1$	52,8	54,3	$P>0,1$
	Afternoon dry 1976	Afternoon dry 1977				
	17,0	35,7	$P>0,1$			

* Seasonal differences not significant (Table 8) therefore data combined.

1. Significant differences between morning and afternoon counts. Therefore data compared separately.

2. Significant differences between morning and afternoon counts and between seasons during afternoon counts.

Table 12. Comparison of the 1976 study area ground census estimates with those of seasonally equivalent months in 1977 for the eight main grazers.

Species	Mean 1976 estimate	Mean 1977 estimate	Significance of trend
Waterbuck	80,8	69,7	NS*
Buffalo	23,8	32,6	NS
Zebra	29,0	46,8	NS
Wildebeest	36,0	48,6	NS
Warthog	115,6	98,6	NS
Nyala	133,0	126,8	NS
Impala	263,7	248,4	NS
White rhino	54,8	56,4	NS

* $P > 0,1$

Stratified fixed wing censuses

The results of the 1976 fixed wing census of waterbuck in UGR are given in Table 13 and those for 1977 in Table 14. In each case data are pooled to give yearly means. In 1976 the mean conversion factor for undercounting was 1,75:1 and in 1977 1,91:1, indicative of 43 per cent and 48 per cent undercounting respectively, assuming a 500 m census strip.

The population estimate for 1976 is 796 $\pm$ 415 (2 SE) and for 1977 is 907 $\pm$ 266 (2 SE). The overlap shown by these approximate 95 per cent confidence limits shows that no significance can be placed on the difference between years. The 1976 total represents a crude density of 1,6 per km^2 and that of 1977 a crude density of 1,8 per km^2.

Helicopter censuses

Results of the annual helicopter censuses of UGR made by NPB staff are shown in Figs. 22 to 24 for the nine main herbivore species. Two questions need to be answered for waterbuck: first by what fraction is the 1976 count of 319 an underestimate and second, is the series of seven counts a valid index of population trend?

Tables 15 and 16 compare results of helicopter counts in the study area with the results of ground censuses. Results of the slow helicopter count of July 1977 are given in Table 17 and a summary of undercounting is given in Table 18. On average the helicopter count for waterbuck represented 66 per cent of the ground census, with a large increase on slower aerial counting. If as has been argued above, the maximum number seen estimate is the most accurate ground method, then the normal helicopter census recorded 40 per cent of waterbuck present in July 1976, the ground census being 61 per cent of the maximum number seen estimate during that month. Using this figure as a conversion factor produces a corrected 1976 helicopter count for waterbuck of 787, which compares very favourably with the stratified fixed wing estimate of 796. The only other census over all of UGR apart from helicopter counts is one for 1967 made by Bourquin (1967, *In*: Mentis 1970) who estimated 820 waterbuck in UGR.

The fractions of ground census results counted from the helicopter for other species given in Table 18 are used below to produce corrected species estimates for UGR which are used in biomass calculations.

Table 13. Results of stratified fixed wing sampling for waterbuck in the Umfolozi Game Reserve during 1976.

Stratum	N_h	n_h	$\frac{N_h(N_h-n_h)}{n_h}$	s^2y_h	$\bar{y}_h$	$Y_h=N_h\bar{y}_h$
<2 km to permanent water	180,10	38	673,5	63,84	4,38	787,9
>2 km to permanent water	66,69	14	250,9	0,22	0,12	8,2
						Y = 796,1

Standard error of Y = $h \quad \frac{N_h(N_h-n_h)}{n_h} \quad s^2y_h = 207,5$

therefore $\underline{Y = 796,1 \pm 415 \ (2\ SE)}$

where: All symbols refer to stratum h.

N_h = total number of 2 km^2 sampling units,

n_h = number of units sampled,

$\bar{y}_h$ = mean number of animals per unit sampled,

$s^2\bar{y}_h$ = variance of numbers between sampled units,

$Y_h=N_h\bar{y}_h$ = estimated total number of animals in the stratum, and

Y = estimated total number of animals in the UGR population.

Table 14. Results of stratified fixed wing sampling for waterbuck in the Umfolozi Game Reserve during 1977.*

Stratum	N_h	n_h	$\frac{N_h(N_h-n_h)}{n_h}$	s^2y_h	$\bar{y}_h$	Y_h
$<$ 2 km to permanent water	180,10	57	388,9	39,73	4,43	797,8
$>$ 2 km to permanent water	66,69	21	145,10	15,48	1,64	109,4
						Y = 907,2

Standard error of Y = 133

Y = 907,2 ± 266 (2 SE)

* Symbols as in Table 13.

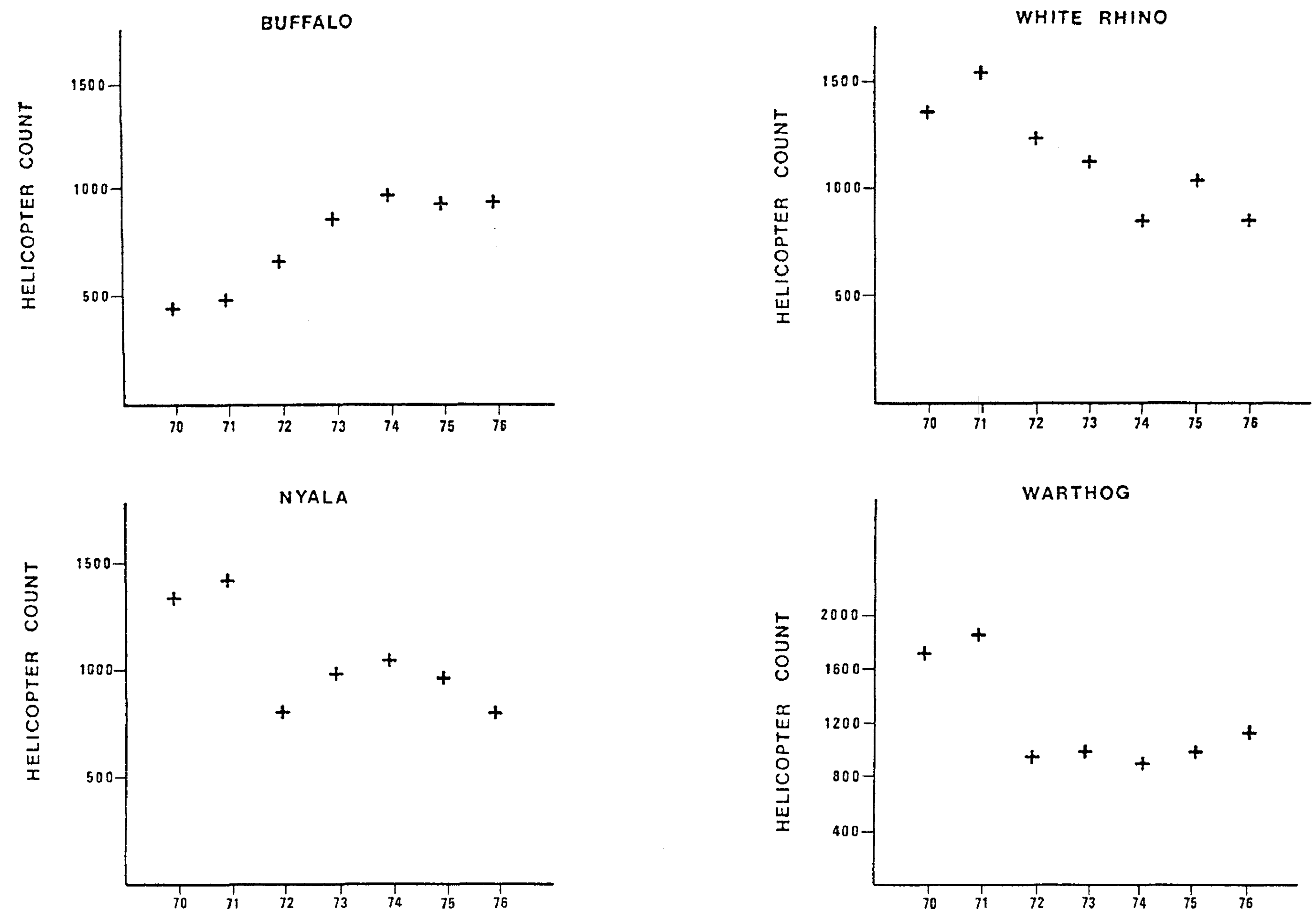


Figure 22. Helicopter counts of large herbivores in the Umfolozi Game Reserve between 1970 and 1976: buffalo, white rhino, nyala and warthog.

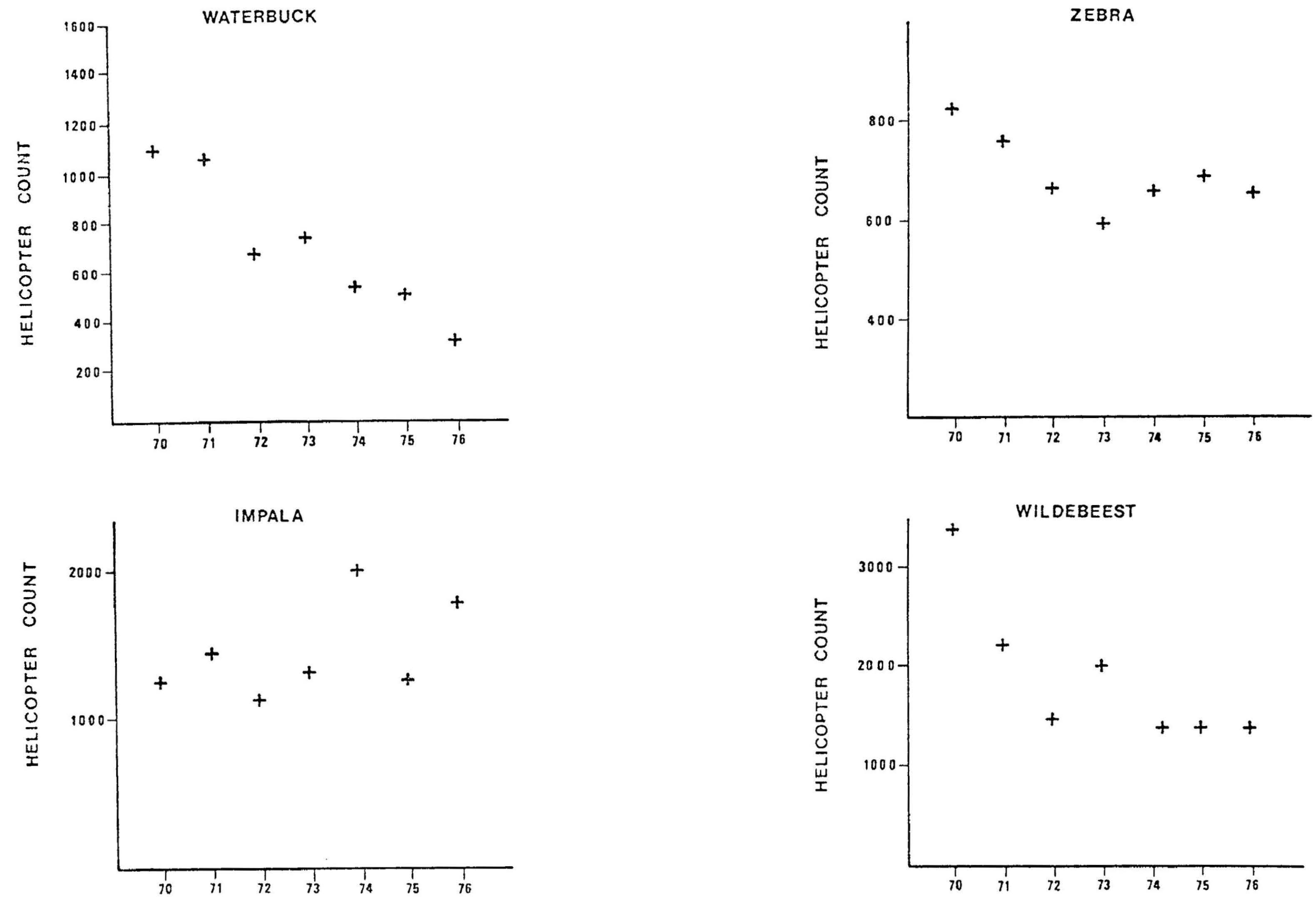


Figure 23. Helicopter counts of large herbivores in the Umfolozi Game Reserve between 1970 and 1976: waterbuck, zebra, impala, wildebeest.

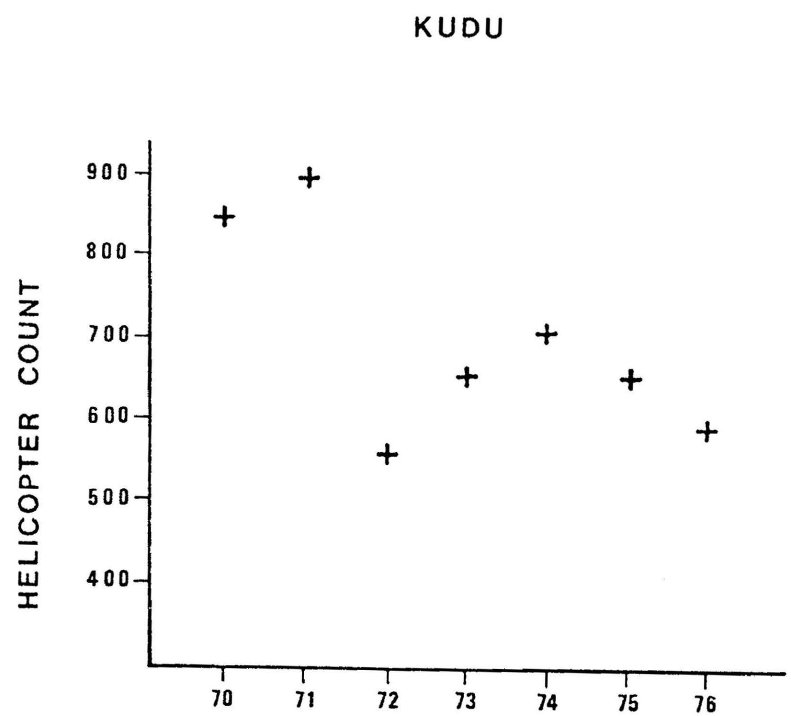


Figure 24. Helicopter counts of kudu in the Umfolozi Game Reserve between 1970 and 1976.

Table 15. Numbers of animals seen during ground counts and normal helicopter counts in the main study area.

	July 1976		July 1977			
Species	Sontuli ground	Sontuli helicopter	Sontuli ground	Sontuli helicopter	Thobothi ground	Thobothi helicopter
White Rhino	15	22	20	41	30	42
Buffalo	0	2	66	3	3	22
Wildebeest	9	16	40	27	13	23
Zebra	21	24	4	0	30	15
Impala	175	47	212	53	104	61
Kudu	19	1	7	21	19	9
Waterbuck	28	23	11	7	24	13
Baboon troop	1	1	1	0	0	0
Black rhino	1	1	3	2	0	1
Nyala	72	25	88	39	66	46
Warthog	92	65	66	29	50	20
Grey duiker	3	1	1	0	2	0
Steenbok	0	0	1	0	0	0
Cheetah	0	1	0	0	0	0

Table 16. Percentage of the main study area ground count seen from the helicopter.

Species	July 1976 Sontuli	July 1977 Sontuli	July 1977 Thobothi
White rhino	146%	205%	140%
Buffalo	+[1]	4,5%	733%
Wildebeest	178%	67,5%	177%
Zebra	114%	-[1]	50%
Impala	27%	25%	59%
Kudu	5%	300%	47%
Waterbuck	82%	64%	54%
Baboon troop	100%	66%	+[1]
Black rhino	100%	66%	+[1]
Nyala	34%	44%	70%
Warthog	71%	44%	40%
Grey duiker	33%	-[1]	-[1]
Steenbok	=[1]	-[1]	=[1]
Cheetah	+[1]	=[1]	=[1]

1. Zero counts recorded: - zero from helicopter; = zero from helicopter and ground; + zero from ground.

Table 17. Comparison of ground, normal helicopter and slow helicopter counts of Sontuli during July 1977. Helicopter counts are expressed as a percentage of the ground count.

Species	Ground count	Helicopter normal		Helicopter slow	
	no	no	per cent	no	per cent
White rhino	20	41	205%	41	205%
Buffalo	66	3	4,5%	3	4,5%
Wildebeest	40	27	67,5%	10	25%
Zebra	4	0	-[1]	4	100%
Impala	212	53	25%	124	58%
Kudu	7	21	300%	13	186%
Waterbuck	11	7	64%	37	336%
Baboon troop	1	0	66%	1	100%
Black rhino	3	2	66%	3	100%
Nyala	88	39	44%	50	57%
Warthog	66	29	44%	49	74%
Grey duiker	1	0	-[1]	2	200%
Steenbok	1	0	-[1]	0	-[1]
Cheetah	0	0	-[1]	0	-[1]

1. Zero counts recorded either during ground census, helicopter census or both.

Table 18. Summary of results on helicopter undercounting.

Species	Mean percentage of the ground count seen from helicopter	Does a slower helicopter count give an increase in numbers?	Constancy of helicopter count (per cent seen)	Is short term movement a problem?
White rhino	164%	No	Good	No
Buffalo	369%	No	Poor	Yes
Wildebeest	141%	No	Poor	Yes
Zebra	82%	Yes	Moderate	Yes
Impala	37%	Yes	Moderate/good	No
Kudu	71%	No	Poor	Yes
Waterbuck	66%	Yes	Moderate/good	No
Baboon troop	83%	Yes	Moderate/good	No
Black rhino	83%	Yes	Moderate/good	No
Nyala	49%	Yes	Moderate/good	No
Warthog	52%	Yes	Moderate/good	No
Grey duiker) Steenbok) Cheetah)	Sample size too small for comment			

A table has been drawn up to help assess the validity of the censuses as indices of trend; it gives variations in procedure and other factors likely to influence the degree of undercounting from a helicopter (Table 19). Four of these variable factors are also graphed in Fig. 25.

By comparing Fig. 25 with the results of the helicopter censuses it can be seen that for many species a relationship exists between the duration of the census and the numbers of animals counted. Species showing the closest correlation are those that are undercounted the most from the helicopter (Table 18). The more obvious of these relationships are graphed in Fig. 26, where the correlation is shown to positive for nyala, warthog, kudu and waterbuck.

The importance of flying time to this census method can be crudely quantified by using the slow and normal helicopter counts of Sontuli during July 1977 to compute the increase in number of animals seen, per unit area, per per cent increase in counting time (Table 20). The four species showing the greatest increase in number with slower speed, impala, waterbuck, warthog and nyala, are those most undercounted from the helicopter as judged by the ground census. These results mean that, for example, a 25 per cent reduction in helicopter speed causes 2,0 more waterbuck to be counted per km^2. If this trend were constant over all UGR an additional 988 waterbuck would be counted. Little reliance can be placed on these figures because of the small sample size used in their calculation and also it is not known over what speeds or what habitat types the relationship holds. They do, however, indicate the large variation in densities that can be expected when the mean speed of the census changes.

By using a single factor (duration of count) much of the variation in census estimates of certain species has been accounted for, particularly the high counts of 1970 and 1971 and the low count of 1972. This does not mean that if the counts are corrected to a standard time they can be used as valid indices of trend. Rather it points to the susceptibility of total counts to error from this and other unidentified sources, particularly for those species like waterbuck which are undercounted the most from a helicopter. For example all species in Fig. 26 show the same pattern of two or three low counts for moderately high flying times ($\pm$ 1 040 min). In each case these are for the years 1974, 1975 and 1976. This strongly suggests that an additional important source of variability has come into being

Table 19. Details of helicopter counts in the Umfolozi Game Reserve-Corridor-Hluhluwe Game Reserve Complex in Zululand.

	1970	1971	1972	1973	1974	1975	1976
Observers, UGR[1]	JV,PMH	PMH,JF	PMH,JF	PMH,JF	AW,JF	AW,JF,JBK	AW,JF
Helicopter type	Bell G-5	Bell G-5	Bell 47 G-4a	Bell 47 G-4a	Hiller HU 12e	Hughes 300c	Hughes 300c
Suitability for counting (visibility)	Very good	Very good	Very good	Very good	Very good	Fair	Fair
Average counting speed, UGR (ha/min)	43,3	40,1	63,6	55,1	47,7	47,5	47,4
Flying time, UGR	20 h 15 min	20 h 32 min	12 h 57 min	14 h 57 min	17 h 15 min	17 h 20 min	17 h 23 min
Flying time, Complex	49 h 45 min	52 h 45 min	32 h 40 min	41 h 50 min	42 h 55 min	26 h 5 min[2]	45 h 25 min
Suitability of observers	-	Nausea reported		-	-	-	-
Dates	10-13/8	5-13/8	23-29/8	30/6-2/7	28/7-5/8	1-5/7	21-29/7
Cloud	Some cloud	Clear	Overcast	Some cloud	Clear	Some cloud	Overcast
Wind	Light breeze	Light breeze	Moderate/ strong	Light breeze	Light breeze/ moderate	Light breeze/ moderate	Moderate/ strong
Rain	No rain	No rain	Drizzle	No rain	No rain	No rain	No rain
Temperature	-	-	Bitterly cold in UGR count	-	-	-	Cold in west UGR

continued

1. JV=J. Vincent; PMH=P.M. Hitchens; JF=C.J. Forrest; JBK=J.B. Kemp; AW=A. Whateley.
2. UGR and southern corridor only.

Table 19, continued

	1970	1971	1972	1973	1974	1975	1976
Observers' recorded weather index	Two days not ideal, others good	Ideal	Poor, unsatis-factory for counting	Ideal	UGR ideal	Ideal	Fair/poor UGR
Other factors observers noted	-------Searching for black rhino-------				-	-	-
Notes	-	Nausea meant stops plus broken flight pattern could have caused under or over counting		-	-	*A. nigrescens* in leaf and full flower; reduced visibility	-

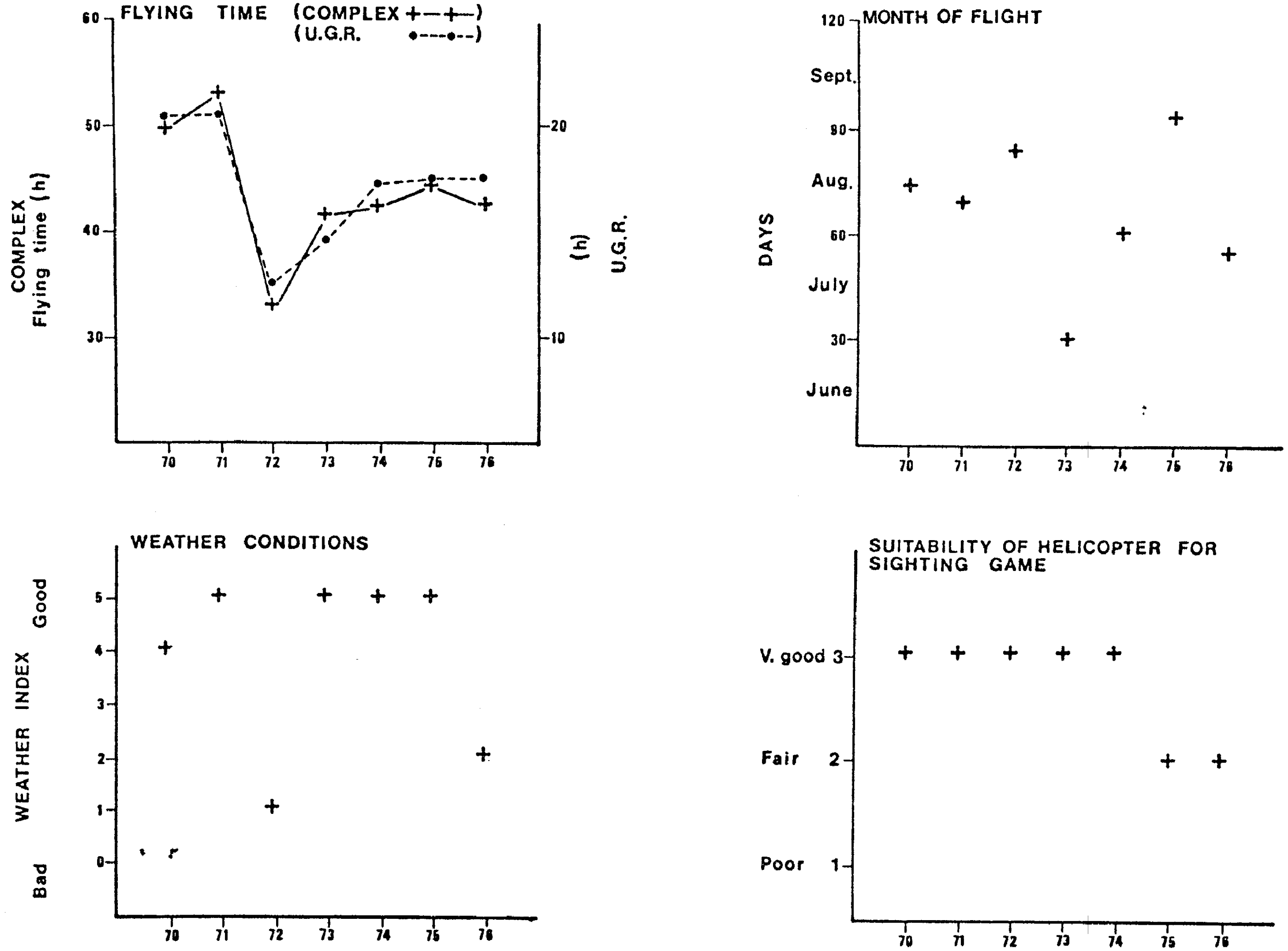


Figure 25. Factors likely to affect undercounting from a helicopter graphed for the 1970 to 1976 censuses of the Umfolozi Game Reserve: duration of count (note that the 1975 time for the Complex is a proporational estimate): month of flight; weather conditions; suitability of helicopter for sighting game.

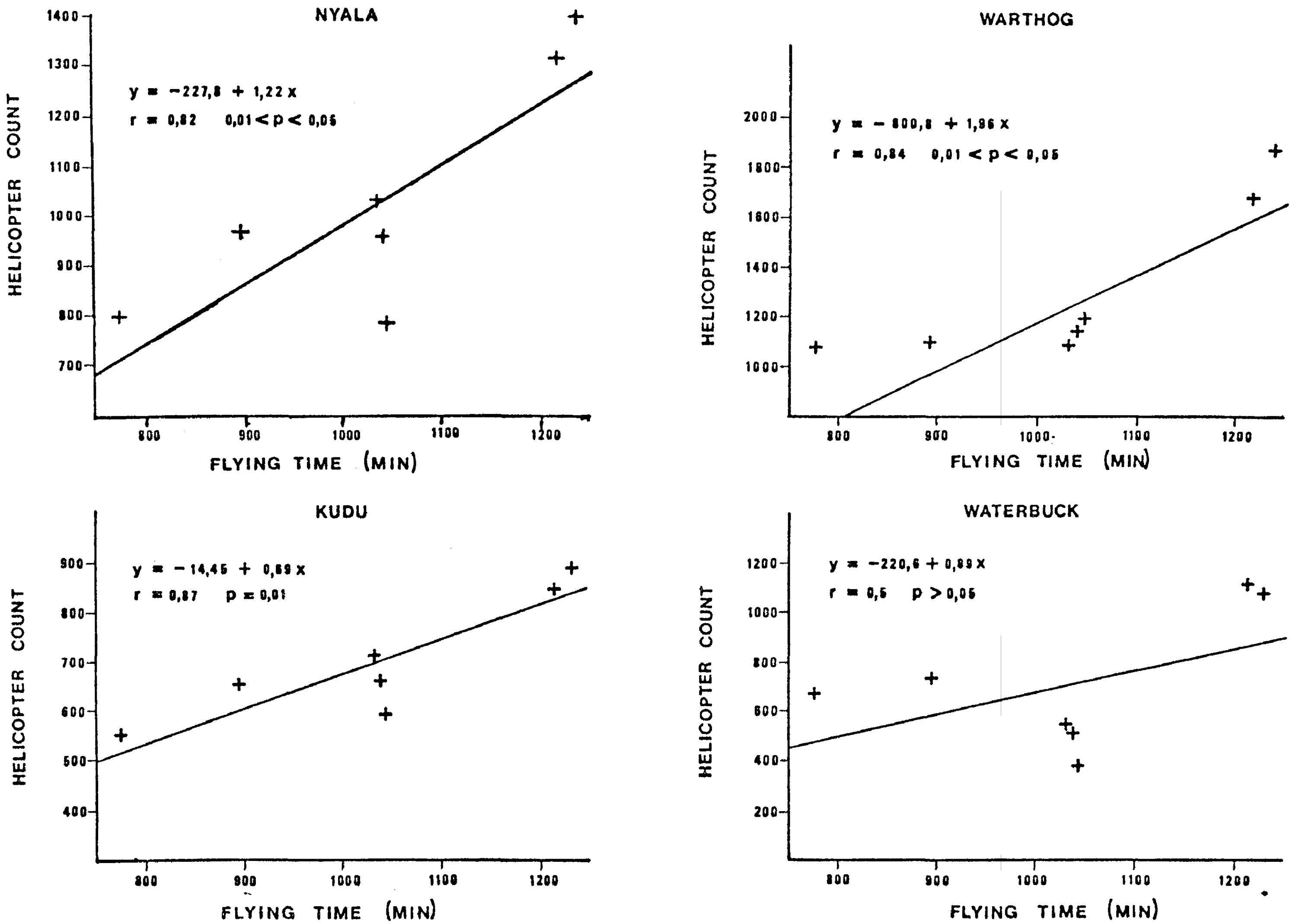


Figure 26. The relationship between the numbers of animals counted and the duration of the helicopter census for four species in the Umfolozi Game Reserve.

Table 20. The increase in number per unit area of animals counted, if the duration of the helicopter count is doubled.

Species	Additional animals counted per km^2 when the flying period is doubled
White rhino	0
Buffalo	0
Wildebeest	-*
Zebra	0,5
Impala	9,0
Kudu	-*
Waterbuck	4,0
Nyala	1,0
Warthog	3,0

* Movement confounded calculation.

causing low counting in these three years compared to the previous four. Such low counting would obviously further invalidate the use of these data as indices of trend for waterbuck. The following changes are suggested as possibly contributing to low counts over these three recent years.

1. From 1970 to 1973 (inclusive) observers were particularly interested in black rhino (*Diceros bicornis*) (Forrest[1] pers. comm.). This meant that black rhino habitat, particularly riverine forest in UGR at that time, was searched more slowly than other areas and when a black rhino was encountered the helicopter came down very low so that the animal could be age determined, sexed and individually identified. These activities likely caused additional game to be flushed and recorded in thicker vegetation (Table 19).

2. In 1975 and 1976 the helicopter used was judged less suited for counting than in previous years (Fig. 25).

3. Weather conditions were bad in 1976. The only time similarly poor conditions occurred was in 1972 when undercounting owing to bad weather would have reinforced low counting attributable to fast flying time (Fig. 25).

4. In general the dates of counts were timed to give good visibility during the leaf fall period of winter (Brooks pers. comm.). The 1975 count, however, was the latest during any year (Fig. 25) and it was noted that *Acacia nigrescens* woodland and riverine woodland were in leaf and the former also in flower, both reducing visibility (Table 19).

5. Bush encroachment had been steadily increasing in UGR prior to 1972 (Downing 1972) and probably since then. This may have caused progressively increased undercounting.

6. Certain species, particularly those which have been subject to helicopter capture attempts as well as censusing, may become increasingly intolerant of a helicopter and seek thicker vegetation on its approach.

1. Mr C.J. Forrest, Warden UGR.

Waterbuck have been seen to move to dense riverine woodland plus shrubs on the approach of a helicopter. Certainly individual animals captured using a helicopter, marked and then released can become "helicopter shy", retiring into thicker vegetation on its approach whereas non-marked animals do not (Brooks pers. comm.).

It is concluded that factors are varying between counts making the helicopter census estimates of waterbuck invalid as indices of trend. It is probable that the population has been declining but not at such a high rate as the counts suggest, the recent densities being greater underestimates than the former.

Biomass of herbivores

Interpretation of biomass data involves the use of two parameters: the total biomass of animals in an area and the proportionate contribution of individual species.

The importance of the first figure has been recognised for a long time, its use being its relationship to the term carrying capacity. Caughley (1976) clarified somewhat the concept of carrying capacity by defining two types. First is economic carrying capacity, which is the number of animals that produce a maximum sustained offtake, but cause no vegetational trends. Second is ecological carrying capacity, which is the maximum number of animals that can be sustained indefinitely without causing changes in vegetation. Both of these capacities represent equilibria, but different equilibria; the ecological carrying capacity represents a higher standing crop of animals and a lower standing crop of vegetation. So in the past assessment of whether an area is overstocked or understocked in relation to either carrying capacity has largely involved consideration of grassland condition. A significant advance has been the demonstration of an empirical relationship between rainfall, primary production, carrying capacity of herbivores and energy expenditure of herbivores (Coe *et al.* 1976). Their work has emphasised the need for better predictive models for rainfall and carrying capacities, so that objective limits for stocking rates can be set.

The importance of knowing the percentage contribution to biomass or better still energy expenditure (i.e. metabolic biomass) was shown by what Geist (1974) termed the Jarman-Bell principle (Jarman 1974, Bell 1971). This principle is explained as follows. The daily energy and protein requirements of mammals are approximately equivalent to their mass^{0,75} (Kleiber 1975). Thus smaller species require more energy and protein per unit body mass than large species. Their higher metabolism can only be sustained on highly digestible, high protein and low fibre forage such as fruits, seeds, and sprouting shoots. Since these items represent a small percentage of primary production, so the biomass of these selective feeders represents a small proportion of the total biomass of herbivores. The reverse argument holds for large bodied animals, which can be termed bulk and roughage feeders. The importance of using mass^{0,75} units follows directly from this. A small species will be utilizing a greater proportion of primary production than that represented by its per cent crude biomass estimate because of its higher energy requirements per unit body weight over a large species.

Estimates of total biomass

Biomass calculations for herbivores in the main study area and over all UGR are given in Tables 21 and 22. The mean masses of species used in these calculations and in calculating biomasses in other areas of Africa are shown in Table 23. The total crude biomass and total metabolic biomass of herbivores in the main study area are 56,00 kg per ha and 12,05 kg per ha. The corresponding figures for UGR are 68,80 kg per ha and 15,98 kg per ha. The predictive relationship of Coe *et al.* (1976) between rainfall and ecological carrying capacity suggests a carrying capacity of 54 kg per ha for UGR. Mentis and Duke (1976) produce a second prediction of ecological carrying capacity by calculating what they consider to be probable maximal carrying capacities for wild ungulates for the various bioclimatic regions of Natal as given by Phillips (1973), using modifications of agriculturalists' domestic stocking rates. The predicted stocking rate for UGR is approximately 6,6 ha per animal unit (AU), where an AU equals a domestic animal of 456 kg and the number of a given species "x" making up one AU =

$$\frac{456^{0,75}}{(\text{mean mass of species x})^{0,75}} .$$

Using this formula for all herbivores in UGR gives a present stocking rate of 6,31 ha per AU.

These two crude predictions suggest that the present biomass of herbivores in UGR is close to or slightly above the ecological

Table 21. Mean biomass of herbivores in the main study area during 1976-1977.

Species	Density* no/km^2	Biomass kg/ha	Per cent biomass	Metabolic biomass kg/ha	Per cent metabolic biomass	Per cent metabolic biomass, grazers only
White rhino	1,83	31,60	56,4	4,90	40,7	42,6
Buffalo	0,85	4,25	7,6	0,90	7,5	7,8
Zebra	1,20	2,59	4,6	0,68	5,6	5,9
Waterbuck	2,53	5,19	9,3	1,37	11,4	11,9
Wildebeest	1,39	2,53	4,5	0,69	5,7	6,0
Warthog	3,54	1,06	1,9	0,45	3,7	3,9
Impala	9,03	3,70	6,6	1,46	12,1	12,7
Nyala	4,21	3,07	5,5	1,05	8,7	9,1
Steenbok	0,07	0,01	0,02	0,01	0,08	0,09
Kudu	1,10	1,50	2,7	0,44	3,7	
Grey duiker	0,08	0,01	0,02	0,01	0,08	
Black rhino	0,06	0,49	0,9	0,09	0,7	
		56,00		12,05		

* Mean ground census multiplied by 1,25 (see text for explanation).

Table 22. Biomass of herbivores in the Umfolozi Game Reserve during 1976.

Species	Helicopter count	Corrected* helicopter count	Density (no/km^2)	Biomass (kg/ha)	Per cent biomass	Metabolic biomass (kg/ha)	Per cent metabolic biomass	Per cent metabolic biomass, grazers only
White rhino	849	849	1,72	29,70	43,2	4,61	28,8	31,7
Buffalo	921	921	1,86	9,30	13,5	1,97	12,3	13,5
Zebra	650	793	1,61	3,48	5,1	0,91	5,7	6,3
Waterbuck	319	787	1,59	3,26	4,7	0,86	5,4	5,9
Wildebeest	1347	1347	2,73	4,97	7,2	1,35	8,5	9,3
Warthog	1162	3643	7,37	2,21	3,2	0,94	5,9	6,5
Impala	1746	7692	15,57	6,38	9,3	2,52	15,8	17,3
Nyala	783	2605	5,27	3,85	5,6	1,32	8,3	9,1
Steenbok	16	-[1]	-	-	-	-	-	-
Reedbuck[2]	83	205	0,41	0,16	0,2	0,07	0,4	0,5
Giraffe	31	31	0,06	0,49	0,7	0,09	0,6	
Kudu	584	1443	2,92	3,97	5,8	1,16	7,3	
Black rhino	29	57	0,12	0,98	1,4	0,18	1,1	
Grey duiker	14	-[1]	-	-	-	-	-	
Bushbuck	3	-[1]	-	-	-	-	-	
				68,75		15,98		

* Corrected for aerial undercounting to values equivalent to ground census and corrected with respect to the ground census being an underestimate (see text).

1. Not included in biomass terms because of low percentage contribution and unknown degree of undercounting.

2. Common reedbuck and mountain reedbuck.

Table 23. Mass data used for biomass calculations.

Species	Mass (kg)	Metabolic* mass (kg)	Reference
Elephant	1725	267,7	1
Zebra	216	56,3	2
Bushpig	55	20,2	2
Warthog	30	12,8	2
Giraffe	818	153,0	2
Buffalo	500	105,7	2
Eland	385	86,9	2
Greater kudu	136	39,8	1
Bushbuck	30	12,5	1
Tsessebe	91	29,5	1
Roan	220	57,1	1
Sable	185	50,2	1
Gemsbok	150	42,9	1
Waterbuck	205	54,2	2
Common reedbuck	55	20,2	2
Impala	41	16,2	2
Common duiker	12	6,5	2
Steenbok	12	6,5	2
Grysbok	7	4,3	2
Blue wildebeest	182	49,6	2
White rhino	1727	267,9	2
Nyala	73	25,0	2
Black rhino	816	153,0	2
Mountain reedbuck	28	12,2	2
Thompson's gazelle	15	7,6	1
Grant's gazelle	40	15,9	1
Bubal hartebeest	182	49,6	2
Bohor reedbuck	36	14,7	3
Hippopotamus	1000	177,8	1
Kirk's dik dik	5	3,4	3
Lesser kudu	70	24,2	1
Springbok	26	11,5	1
Blesbok	53	19,6	1
Black wildebeest	120	36,3	1
Klipspringer	10	5,6	2

* $\text{Mass}^{0,75}$

1. Coe *et al.* (1976)
2. Mentis and Duke (1976)
3. Dorst and Dandelot (1970)

carrying capacity of the area.

Table 24 includes estimates of previous biomasses in UGR made by Mentis (1970). The present estimate is not as low as those for 1929-1930 or 1942-1950, but it is lower than that of 1967. The suggested decline since 1967 is probably a real one, especially considering the increased removal of many species since that year, particularly white rhino and wildebeest (Table 10). A biomass figure of 131,1 kg per ha for part of the main study area during 1972-1973 given by Porter (1975) is considered an overestimate, though the biomass may have peaked between 1967 and 1976 at a higher value than those estimated for these two years.

Percentage contributions to biomass

The use of mass^{0,75} values emphasises the contributions of smaller species and lessens those of larger ones, but white rhino still predominate contributing 42,6 per cent of the metabolic biomass of grazers in UGR. Results from the study area are similar (Table 21) but with more white rhino and waterbuck and less buffalo and nyala than over all UGR.

The percentage contributions to crude biomass for grazing species in the study area are similar to 1972-1973 estimates (Porter 1975), with white rhino contributing 58 per cent in each case (Table 25). The main change is for an increase in buffalo, which agrees with density data from helicopter censuses. More significant changes can be seen by comparing present data with estimates for earlier periods made by Mentis (1970) (Table 24). In 1929-1930 UGR was dominated by zebra with white rhino a distant second in terms of contribution to biomass. There were no nyala or impala at this time and as explained before (see Chapter 2) it is in doubt as to whether they were endemic to UGR (Bourquin *et al.* 1971). By the 1940's white rhino were the dominant species, with buffalo second and zebra third. 1967 shows a marked increase in total biomass with white rhino the main contributor to biomass. The present results indicate a reduction in white rhino and a marked increase in impala, nyala and buffalo. Considering the total period from the 1930's to the 1970's there is possibly a 50 per cent increase in total standing crop of herbivores. This is attributable mainly to increases in white rhino, impala, nyala and buffalo. Impala and nyala are shown later (Chapter 8) to prefer

Table 24. Comparison of species' contributions to grazing biomass in the Umfolozi Game Reserve during 1976-1977 with previous estimates.

Species	Per cent crude biomass 1929-1930*	Per cent crude biomass 1942-1950*	Per cent crude biomass 1967*	Per cent crude biomass 1976-1977
White rhino	8,4	32,1	57,9	46,9
Buffalo	1,5	18,6	7,5	14,7
Zebra	79,6	11,4	2,9	5,5
Waterbuck	2,6	5,1	7,8	5,1
Wildebeest	3,0	5,4	12,8	7,9
Warthog	2,6	6,1	4,2	3,5
Impala	0	0,03	1,0	10,1
Nyala	0	0,1	2,9	6,1
Reedbuck[1]	0,5	7,5	1,8	0,3
Steenbok	0,1	0,4	0,2	trace
Bushbuck	1,6	13,4	1,1	trace
Total grazing biomass in above years (kg/ha)	46,0	36,3	76,6	63,3

* Recalculated from Mentis (1970).

1. Mountain and common reedbuck.

Table 25. Comparison of 1972-1973 biomass data for part of the main study area with those of 1976-1977 presented here for grazing species.

Species	Per cent crude biomass 1972-1973*	Per cent crude biomass 1976-1977
White rhino	58,1	58,5
Buffalo	2,2	7,9
Zebra	9,5	4,8
Waterbuck	12,0	9,6
Wildebeest	6,4	4,6
Warthog	0,9	2,0
Impala	3,8	6,9
Nyala	7,1	5,7

* Porter (1975)

short grassed often overgrazed lowland areas. The food habits of white rhino ally this species with these two small selective short grass grazers (Owen-Smith 1973). Thus only the increase in buffalo is considered in keeping with the Jarman-Bell principle. Putting it another way zebra have been replaced as the dominant herbivore by a species mix that largely feed selectively on short grass areas. On theoretical grounds such a change is expected to accompany a reduction in total biomass but a 50 per cent increase has occurred. Such situations with a preponderance of short grass grazers have been found by Mentis and Duke (1976) in many private game areas in Natal, often accompanied by poor condition of grassland and animals.

What are the consequences of these findings for waterbuck though? Table 26 compares the percentage contributions to biomass by waterbuck for other areas in Africa with the 1976-1977 position in UGR. Waterbuck represent a mean value of 15,3 per cent metabolic biomass of grazers for 15 samples considered to reflect the ecological abundance of waterbuck. When the high value of 76,1 per cent from Lake Nakuru is omitted this reduces to 11,0 per cent, which compares well with the present value of 11,9 per cent in UGR.

These data suggest that the present density of waterbuck in UGR represents the maximum which can be expected to maintain itself, considering that the total stocking rate is near the ecological carrying capacity. Waterbuck do not usually attain high percentage contributions to biomass (Table 26). The high figure of 76,1 per cent at Lake Nakuru is attributable to a number of factors: hunting causing decreased competition and predation; control of poaching; fencing not adversely affecting the species because of its non-migratory habits; and a resulting favourable habitat (Kutilek 1974). Results from Chapters 8 and 9 indicate that a high contribution to total biomass should not be expected for two reasons. First waterbuck have strict habitat requirements for a healthy population and such habitats occur as a low percentage of any game area in Africa. Second competition from other species such as nyala and impala is high in waterbuck favoured areas and waterbuck can be classed as a poor competitor. Indeed it is concluded in Chapter 10 that competition is the likely ultimate factor affecting the numbers of waterbuck in UGR at present. The widespread distribution of impala through eastern and south-eastern Africa allows a comparison to be made between waterbuck and impala in terms of their percentage contributions to biomass (Table 26 and Fig. 27). A significant

Table 26. Metabolic biomasses and percentage contributions by waterbuck and impala for the Umfolozi Game Reserve and other locations in eastern and southern Africa where waterbuck occur. Data for other areas were recalculated from data in the references given.

Area	Metabolic biomass of all herbi-vores kg/ha	Per cent metabolic biomass of all herbi-vores: waterbuck	Metabolic biomass of grazers kg/ha	Per cent metabolic biomass of grazers: waterbuck	Per cent metabolic biomass of grazers: impala	Ecological or crude waterbuck abundance	Annual rainfall (mm)
UGR 1976[1]	16,0	5,4	14,6	5,9	17,3	crude	647[a]
UGR 1976-1977[2]	12,1	11,4	11,5	11,9	12,7	ecological	647[a]
Henderson ranch, Rhodesia[3]	8,9	1,7	7,2	2,1	36,3	crude	406[b]
Fort Tuli, Rhodesia[3]	17,8	1,1	17,5	1,1	71,5	ecological	502[c]
Wankie, Rhodesia[3]	28,3	23,6	25,0	26,8	19,7	ecological	548[c]
Victoria Falls, Rhodesia[3]	6,0	36,1	5,3	41,2	2,2	ecological	716[c]
Central Estates, Rhodesia[3]	2,5	3,2	1,9	4,2	28,3	ecological	668[c]
Timbavati, S. Africa[4]	13,9	1,2	8,8	1,8	42,3	crude	566[4]
Kafue, Zambia[5]	3,3	13,9	3,1	14,9	0,1	crude	889[d]
Kafue, Zambia[5]	8,8	9,9	8,3	9,8	0,1	ecological	889[d]
Kruger N.P., S. Africa[6]	4,2	2,7	3,8	2,9	45,9	crude	481[c]
Kruger N.P. South,S. Africa[6]	12,6	3,3	11,5	3,7	39,2	ecological	650[b]
Nairobi N.P., Kenya[7]	11,4	3,5	10,0	4,0	28,4	ecological	844[b]
Lake Nakuru N.P., Kenya[8]	22,3	75,7	22,2	76,1	6,6	ecological	878[b]
Rwenzori N.P., Uganda							
1956-1957[9]	52,2	4,5	51,5	4,5	0	ecological	1010[b]
1963-1967[10]	43,9	13,6	43,4	13,8	0	ecological	1010[b]
1968[11]	67,5	7,4	67,0	7,5	0	ecological	1010[b]
Tarangire, Tanzania[12]	18,9	5,1	16,6	5,8	19,3	ecological	915[b]*

1. This study.
2. Main study area, this study.
3. Dasmann and Mossman (1962a).
4. Hirst (1975).
5. Dowsett (1966).
6. Pienaar *et al.* (1966).
7. Foster and Kearney (1967).
8. Kutilek (1974).
9. Petrides and Swank (1965).
10. Field and Laws (1970).
11. Eltringham (1974).
12. Lamprey (1964).

a. Porter (1975).
b. Coe *et al.* (1976), *Manyara.
c. Weather bureau, Pretoria (pers. comm.)
d. Hanks (pers. comm.)

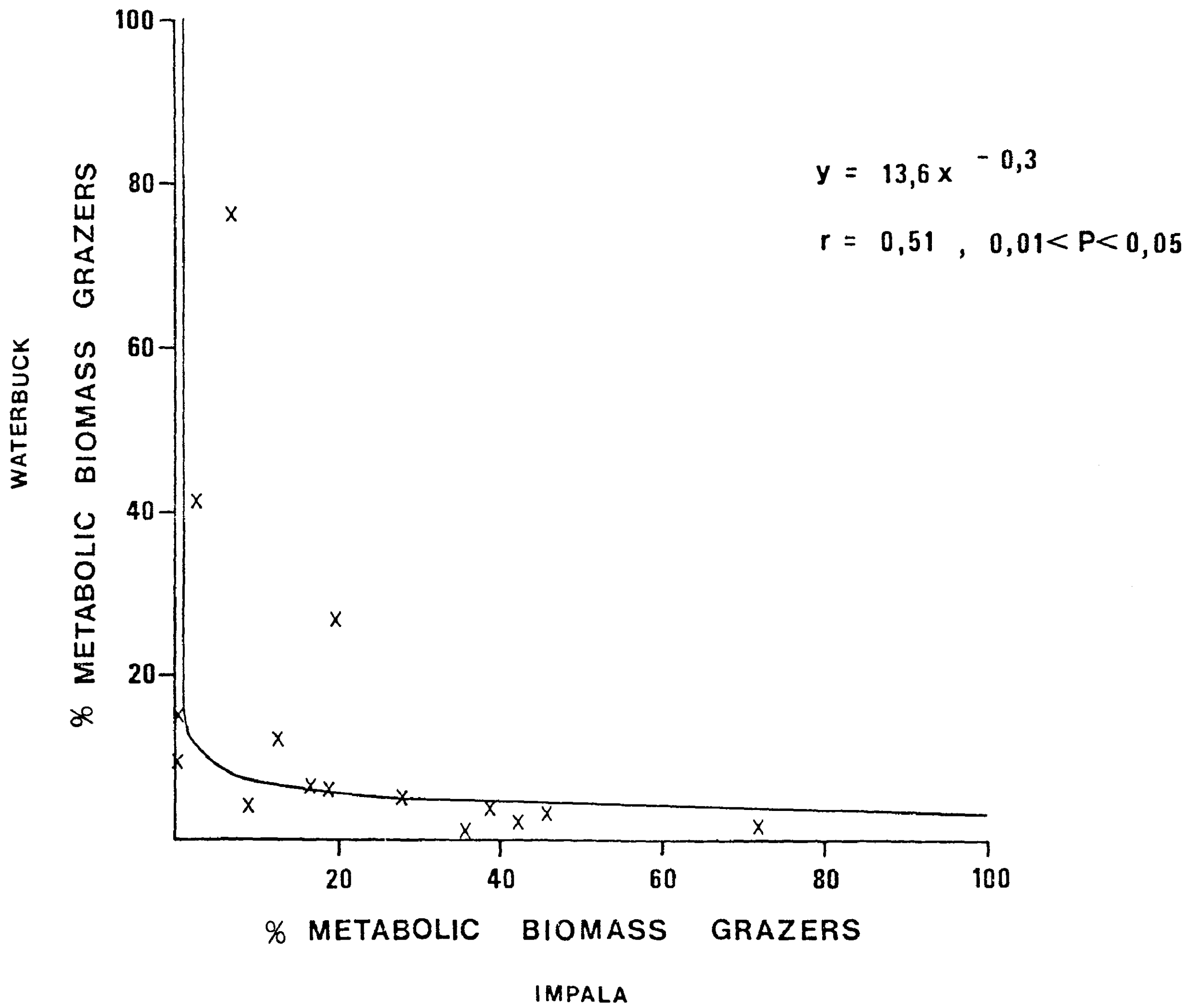


Figure 27. A comparison of the contributions of waterbuck and impala to grazing communities, as shown by 15 samples from eastern and southern Africa.

($P < 0,05$) inverse relationship holds; areas with many impala having few waterbuck and vice-versa. It may be possible to generalise and label impala as equivalent to the botanist's weedy species, since it is one of few that prefer grassland in a near-overgrazed and overgrazed condition. A similar assessment of impala was made by Savory (1969). Such a species can then be used to gauge the suitability of an area for poorly competing species such as waterbuck. These data suggest that competition as quantified by the index species impala may be the overriding limiting factor on waterbuck irrespective of habitat type. This subject will be explored further in Chapters 8 and 9.

CONCLUSIONS

There are at present between 700 and 900 waterbuck in UGR, which represents an ecological density of 2,5 per km^2 and a crude density of 1,6 per km^2. On an energy expenditure basis the ecological abundance of waterbuck represents 11,9 per cent of grazers which compares well with a mean value of 11,0 per cent for 14 other samples over eastern and southern Africa. This density is the maximum which can be expected to maintain itself at the present near ecological carrying capacity stocking rate of 63,3 kg per ha. However, the species' proportionate contributions to total biomass in the reserve are far from optimal in terms of basic physiological principles. Considering the poor competitive status of waterbuck (see Chapter 8) this is one of the first species expected to be adversely affected by this abundance of selective short grass feeders. This statement is supported by an analysis of many areas in Africa with respect to per cent contributions to metabolic biomass of waterbuck and impala.

CHAPTER 4

AGE DETERMINATION AND GROWTH

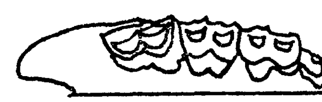
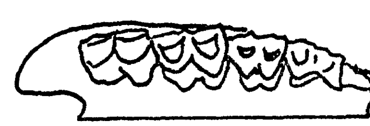
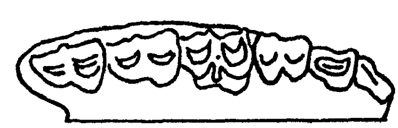
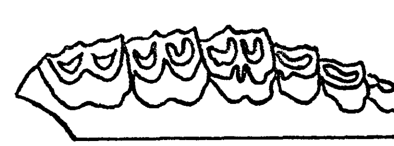
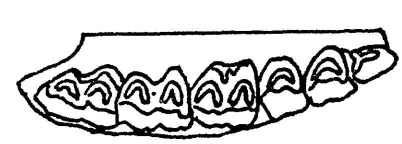
INTRODUCTION

Age determination of Umfolozi waterbuck is important for a number of reasons. First, it enables the construction of a d_x based life table whereby the age-specific reasons for the decline in density described in the last chapter can be investigated. Second, a combination of age determination and growth studies form the basis of field age classification. This classification means that the age structure of the population can be monitored and recruitment to the adult segment followed. A study of growth with age also allows growth rates of animals living in different environments to be compared. Third, age determination and field age classification enable data on movement and habitat utilization to be viewed with respect to the age of individuals.

Age determination of skulls by tooth replacement and attrition

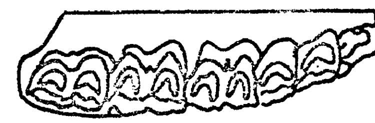
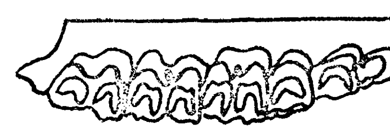
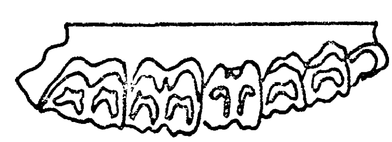
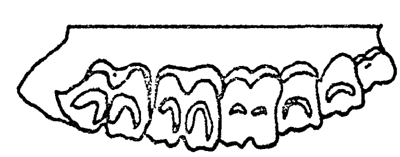
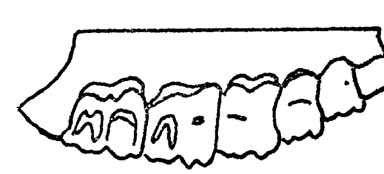
The use of eruption and replacement times in age determination are usually only applicable to young animals, while attrition of the permanent teeth is a method of age estimation in adult animals. Morris (1972) and Spinage (1973) review some of the many studies that have adopted these methods. The procedure involves assigning skulls to arbitrary age classes based on the appearance of the teeth and later calibrating these to chronological ages by one of a number of methods. For the present study the process is somewhat simplified owing to a previous study on age determination in the Uganda defassa waterbuck (Spinage 1967). Spinage assigned chronological ages to his arbirary age classes by using maxillary tooth row impressions taken at yearly intervals from a group of animals of varying ages. In this way he was able to determine the age of an animal up to ten years and to within six months. Older animals were assigned to an 11 year class (Fig. 28). Two factors caution against the straight adoption of Spinage's wear criteria. The rate of attrition can vary significantly between different localities (Severinghaus 1949) and although the time sequence of eruption appears more constant, as described by Miller (1972) for *Rangifer* from Lapland, U.S.S.R., Alaska and Newfoundland, it too can change with genetic and environmental variation (Morris 1972).

Figure 28. Replacement and attrition of waterbuck teeth by age class, modified slightly from Spinage (1967); see text for details.

Age (years)	Teeth characteristics (all molars referred to are maxillary)	Appearance of maxillary tooth row
0	Birth; pm_1, pm_2 and pm_3 present.	
0,5	pm_1 to $_4$ present with pm_1 to $_3$ in use; M_1 below gum.	
1,0	M_1 erupted and in use but not full height.	
2,0	M_2 completely erupted in oldest case.	
3,0	I_1 fully erupted, i_{2-4} still present. M_3 cutting gum in youngest, completely erupted in oldest; pm_1 and $_2$ may be lost; pm_3 present but very worn.	
4,0	Pm_4 at full height; occlusal surface of Pm_2 usually slightly worn.	
5,0	Pm_2 still little worn, exposed dentine confluent in typical "Y" shape.	

continued

Figure 28, continued.

Age (years)	Teeth characteristics (all molars referred to are maxillary)	Appearance of maxillary tooth row
6,0	Crown of Pm_2 just concave; infundibulum of Pm_3 and $_4$ very shallow; M_1 cusps levelling.	
7,0	Dentine completely exposed in Pm_2; infundibulum of Pm_3 and $_4$ very shallow.	
8,0	As 7 year class but occlusal surfaces of all teeth broader.	
9,0	Infundibula of M_1 in typical "J L" pattern.	
10,0	Infundibula of M_1 reduced to very shallow c-shapes; occlusal surfaces of M_2 and M_3 broader.	
11,0	M_1 and possibly M_2 infundibula lost; plus all stages of wear greater than this, for instance M_1 may be almost absent.	

Age determination of skulls by cementum line counts

Age determination methods for mammals based on the rate of deposition of cementum in teeth as viewed in thin sections were largely developed by Laws (1952) working with marine mammals. The method has been the subject of a number of reviews including Klevezal and Kleinenberg (1967), Morris (1972), Spinage (1973), Steenkamp (1975) and Spinage (1976), and is now widely used.

Unfortunately the physiological reasons for the production of growth lines in cementum are still poorly understood, which hampers interpretation of line counts. In temperate studies it is usual to find two lines laid down per year, as was done in the early North American study of Low and Cowan (1963). One line is narrow and darkly staining, the other is broad and lightly staining. It is generally held that the narrow line represents a period of slowed growth during winter months while active growth causes a broad less-dense band during summer. A similar although more uncertain interpretation has been made of cementum layers in tropical studies. Thus Spinage (1976) could conclude that buffalo teeth show one darkly staining line per year in areas with unimodal rainfall and two per year in areas with two wet seasons. Simpson and Elder (1969), however, report two darkly staining lines per year in kudu (*Tragelaphus strepsiceros*) teeth in Rhodesia, where a single rainy season occurs each year. Anomalies also occur in temperate regions. The very strong effects of hibernation on growth of tooth cementum is well documented (Mayer and Bernick 1963), but Stoneberg and Jonkel (1966) found in the black bear (*Ursus americanus*) that the winter cementum line was laid down before an animal entered the den and therefore presumably before the food supply became limiting. Even with such anomalies and with doubt as to their actual cause, cementum lines have proved successful in many studies in giving estimates of absolute age (Morris 1972).

METHODS

Age determination of skulls

Both of the complimentary methods described above have been employed: an examination of waterbuck tooth replacement and attrition and a study of incremental lines in the cementum of the first maxillary molar (M_1). All references to molar teeth examined in this study are to maxillary molars.

Tooth replacement and attrition

The method used here was first to classify skulls to Spinage's year classes and then to check and if necessary modify these absolute ages by taking tooth impressions from immobilised individuals. Second samples were planned to come from both reimmobilised animals and from the recovery of skulls of previously immobilised animals dying naturally at a later date. Details of immobilisation are given in Chapter 7.

Tooth impressions were taken using the basic method of Barnes and Longhurst (1960). Three workers were employed; one opened the mouth by hand, if necessary using a blunt softwood rod as a lever. Another held the tongue to one side while a third inserted the metal impression tray filled with modelling clay and positioned it over an upper tooth row. The mouth was closed and held tight to allow no lateral chewing movement and then reopened and the tray removed. Positive casts were made of Plaster of Paris, including a deep base made by building up the sides of a tray with cardboard.

During 1976 tooth impressions were taken from 21 individuals. Impressions were obtained from another two in 1977 and two of the 1976 animals were recaptured and second impressions made.

Tooth measurements were taken to supplement Spinage's qualitative wear criteria in order to compare objectively age by wear with age by cementum line estimates. A number of measurable characters have been described that change continuously with tooth wear in mammals (Morris 1972, Spinage 1973). Six measurements were used here; linear measurements were made with calipers to 0,1 mm and mass was measured to 0,1 g.

1. The height of the crown (enamel) of the first permanent incisor (I_1).

2. The buccal height of M_1 measured at the mid-point on the anterior-posterior axis from the cingulum to the crown.

3. The widths of the four occlusal surfaces of M_1, each taken from the margin of the infundibulum to the corresponding buccal or lingual cusp. If an infundibulum was missing due to wear then this measurement was not made. The four widths were summed.

4. The weight of M_1.

5. The weight of M_2.

6. The maximum depth of infundibula of M_1, measured after the tooth was sectioned as done prior to cementum studies.

Enquiries for known age material have been made to the main conservation bodies in South Africa and with advertisements in a national periodical. At the time of writing none have been acquired.

Cementum line counts

The tooth chosen here was M_1 since it is the first permanent upper tooth to erupt. A maxillary tooth was desired because the majority of skulls recovered in the field have the mandibles missing owing to scavengers. A number of M_2 and M_3 teeth were also sectioned to compensate somewhat for the lack of known age material, as done by Simpson and Elder (1969). It is likely that the time sequence of eruption of M_1, M_2 and M_3 in Umfolozi waterbuck will be as described by Spinage (1967), any variation being insignificant for the year class accuracy required (Spinage 1973). Thus the increase in number of lines expected to be found in the earlier erupted M_1 compared with an M_2 or M_3, will have been laid down over an essentially known interval of either one or two years (Fig. 28).

Teeth were removed with a hacksaw or hammer and fine chisel. They were cut with a rotating diamond-dusted disc cooled by a water bath. The first cut was vertical along the mid-line anterior-posterior axis, thus traversing the wide cementum pad between the roots. The smaller lingual half of the tooth was trimmed at the crown and sometimes at the root tip to make it a convenient size for sectioning. Decalcification and staining followed Ludbrook (1977), a procedure arrived at after consultation with J.C. Austin[1]; the full method is given in Appendix 1. Tooth pieces were fixed in buffered neutral formalin for a minimum of four days. They were then decalcified in five per cent nitric acid, the process usually being complete after five days. Wax was infiltrated into the material using an autotech-

1. Dr J.C. Austin, University of the Witwatersrand Oral and Dental Hospital (Research Section).

nician (Elliot Liverpool ltd.) followed by vacuum infiltration. Longitudinal sections of 7 µm were cut using a Reichert rotary microtome with a bevelled blade. Longitudinal sections are necessary in order to view splitting and compression of lines and so obtain a maximum count (Spinage 1967, Grimsdell 1973). Sections were stained with Erlich's Haematoxylin, followed by routine mounting with a synthetic resin. Fifty M_1 teeth, five M_2 teeth and six M_3 teeth were processed.

As described by Hall-Martin (1976) a standard counting procedure was found necessary because split lines and accessory lines occurred, particularly in the thick pad and root tip. Lines also became compressed along the length of the root. Stained sections were viewed using a Zeiss binocular microscope at x100 magnification. Slides were also projected onto a white wall using a Leitz Wetzlar projection microscope as described by Grimsdell (1973). In general the ordinary microscope method was preferred because of the better quality image. Counts were confined to the extreme upper root and molar pad. Five fields were viewed in this area for each section and the maximum number of dark staining continuous bands recorded for each field. This was repeated for between two and five sections per tooth. The mean of these maximum counts gave the mean number of cementum lines for the tooth.

Growth and field age classification

Body measurements were taken from 32 immobilised animals and seven fresh carcasses. Details of male horns also came from 47 fresh skulls.

The measurements chosen were those expected to be most helpful in field age estimation and those most useful for comparing growth rates with populations elsewhere. Measurements that attain their asymptote at a particularly early age, such as hind foot length and tail length (Howells and Hanks 1975), were therefore omitted. Methods of measurement follow Ansell (1965) and Spinage (1967). Lengths were recorded to the nearest 1,0 cm using a 4,0 m flexible tape. The measurements were:

1. Neck girth measured at the approximate mid-point minimum.

2. Shoulder height taken from the top of the withers to the base of

the foot.

3. Head plus body length taken over the body contours from nose to base of tail.

4. Body girth measured around the body immediately posterior to the forelegs.

5. Horn length of males measured on the anterior (concave) surface of both horns and a mean calculated.

6. Mean number of horn annuli.

RESULTS AND DISCUSSION

Age determination of skulls

The dental formula for waterbuck has been given previously by Spinage (1967). That of the deciduous teeth is:

$$i\,\frac{0}{4}\quad c\,\frac{0}{0}\quad pm\,\frac{3}{3}\quad m\,\frac{0}{0}\,.$$

That of the permanent teeth is:

$$I\,\frac{0}{4}\quad C\,\frac{0}{0}\quad Pm\,\frac{3}{3}\quad M\,\frac{3}{3}\,.$$

The appearance of the molariform teeth for each of Spinage's (1967) age classes has already been given in Fig. 28 along with a description of important features. The only modification over his results is the interpolation of a nine year class based on a distinctive "JL" pattern.

At the time of writing no skulls from previously immobilised animals have been recovered after a period greater than two months. Therefore the tooth impressions from two reimmobilised animals are the only second samples of wear obtained over a substantial known period. Both of these animals do, however, show an amount of wear equivalent to that expected from Spinage's wear criteria. Female 1 was classed as 3,5 years in May 1976 and five years in July 1977; Male 2 was classed as nine years in May 1976 and 10 years in July 1977. Even though this sample is very small, the fact that these individuals are at opposite extremes of the adult age series adds weight to their support of Spinage's wear criteria. The wear classes are therefore used as given in Fig. 28 for comparison with cementum line age estimates.

Figures 29 to 40 show the six wear measurements graphed against age by wear for males and females, with regressions predictive for wear age based on tooth data. Similar graphs for cementum lines are given in Figs. 41 to 52. On some occasions teeth showed distinctive characters representative of two contiguous age classes, in which case an intermediate age was assigned. Linear regression gave the most satisfactory fit for all tooth parameters where skulls had full permanent dentition, which is where the wear model supercedes age prediction based on replacement. When younger age classes were included linear relationships were still satisfactory for infundibula depth of M_1, mass of M_1, and buccal crown height of M_1. Linear regressions could not adequately be fitted to weight of M_2 and height of I_1 data when young age classes were added, since maximum values for these parameters are not reached until approximately three years of age. The relationships of occlusal surface width of M_1 with both age by wear and cementum lines are curvilinear when all age classes are considered, indicative of a decreased rate of wear with age. For the cementum age comparison the best fit is a power curve for males ($y=0{,}01x^{1{,}81}$, n=37, r=0,72, $0{,}001 < P < 0{,}01$) and an exponential curve for females ($y=0{,}03e^{3{,}14x}$, n=11, 4=0,95, $P < 0{,}001$). Spinage (1973) and Grimsdell (1973) describe curved wear relationships; Hall-Martin (1976) found a slightly improved fit when a second degree polynomial was used for some giraffe measurements but concluded that linear regression was adequate for predictive purposes. Here the nature of the curve relies heavily on the few young skulls used. It is probable that variation will occur because of this small sample size that would negate any added accuracy that would come from fitting of non-linear regressions. For this reason only linear relations will be used for predictive and comparative purposes.

Figure 53 shows the mean number of cementum lines graphed against age by wear. The significant ($P < 0{,}001$) predictive relationship of lines from wear age suggests that both systems can be used for age determination, with cementum lines being laid annually after eruption. The 95 per cent confidence limits indicate that cementum age could in general be predicted to within one year from the wear series. The

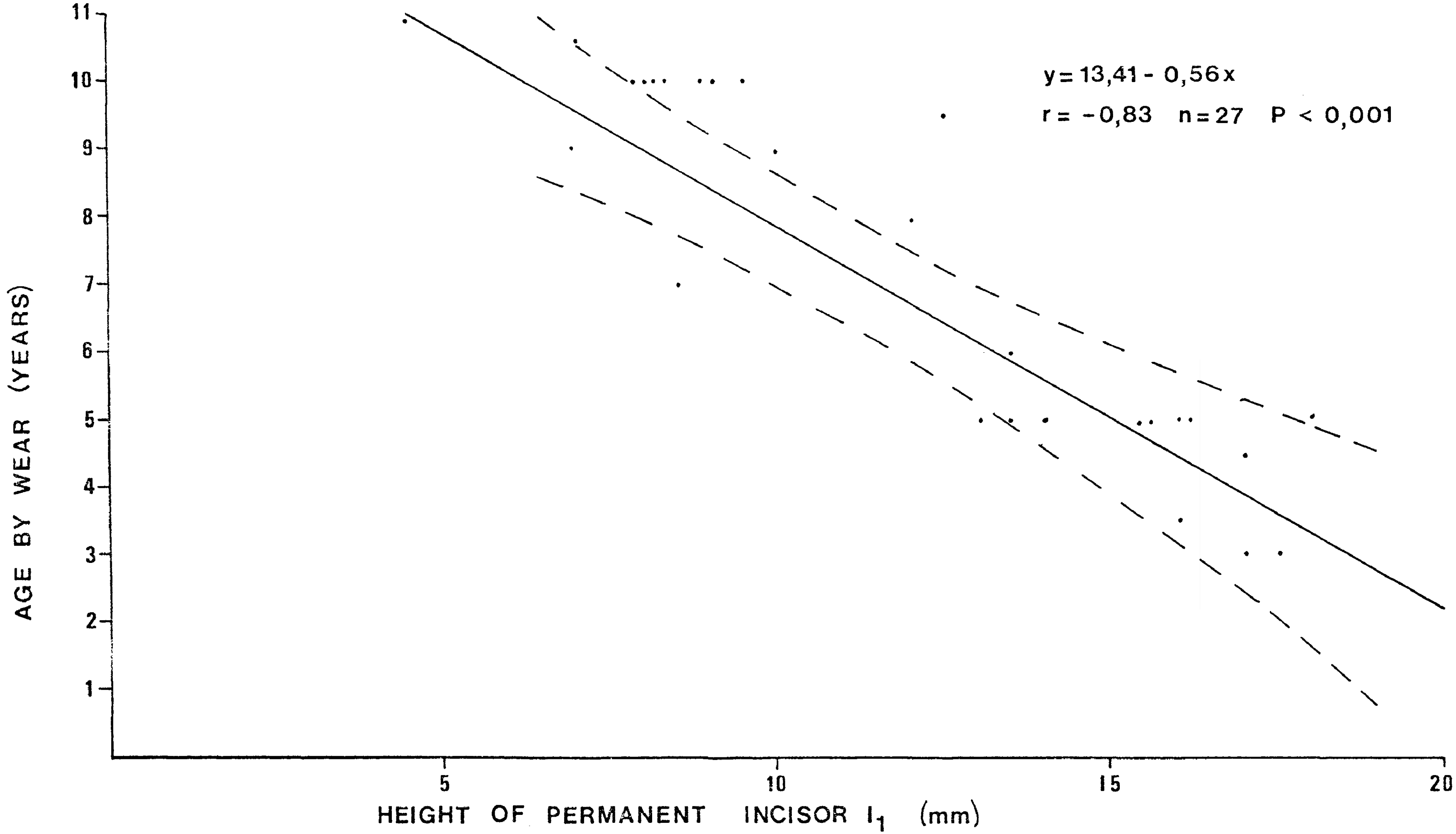


Figure 29. A comparison of the height of I_1 with age by wear; male waterbuck. Broken lines are 95 per cent confidence limits.

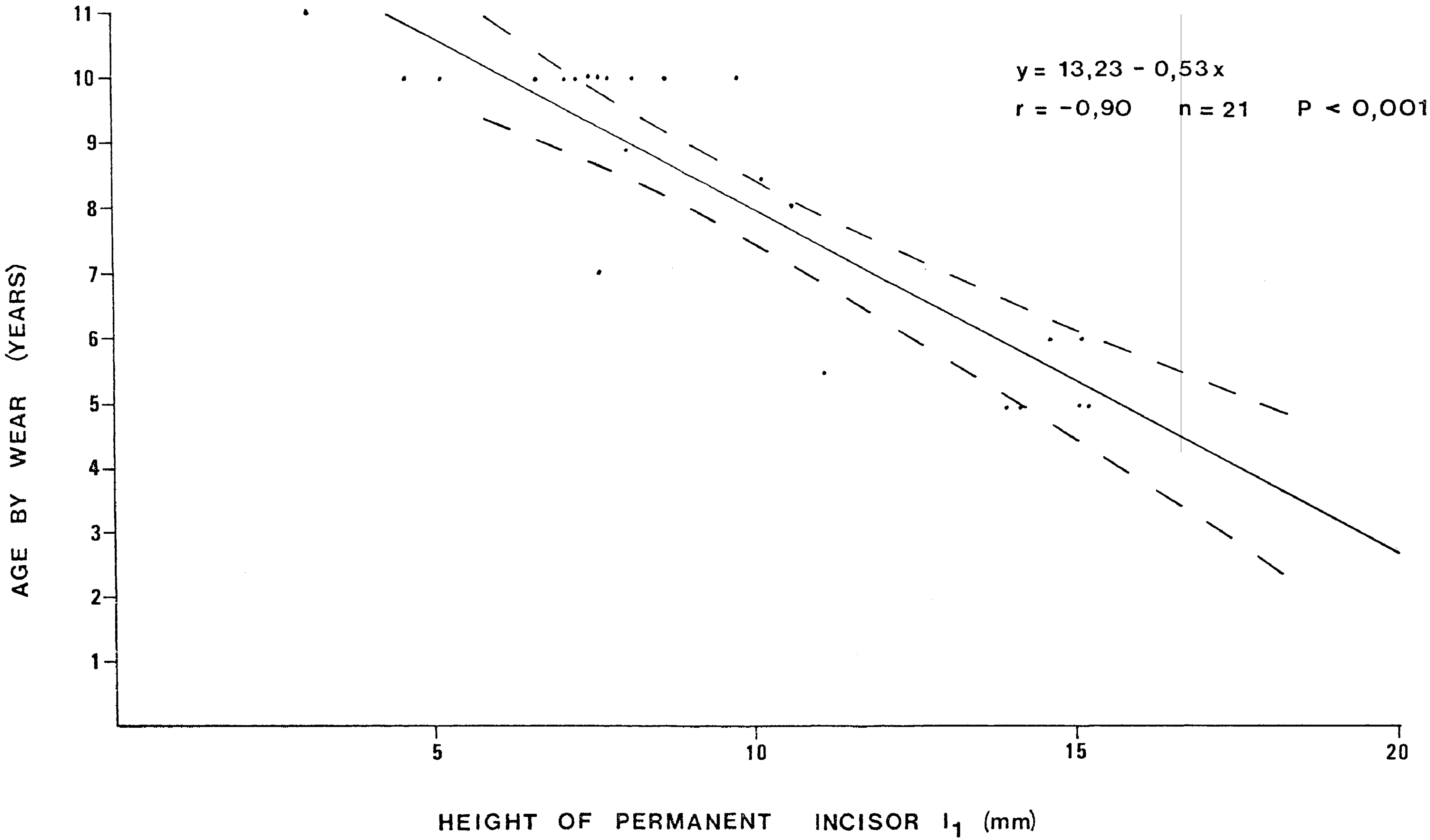


Figure 30. A comparison of the height of I_1 with age by wear; female waterbuck. Broken lines are 95 per cent confidence limits.

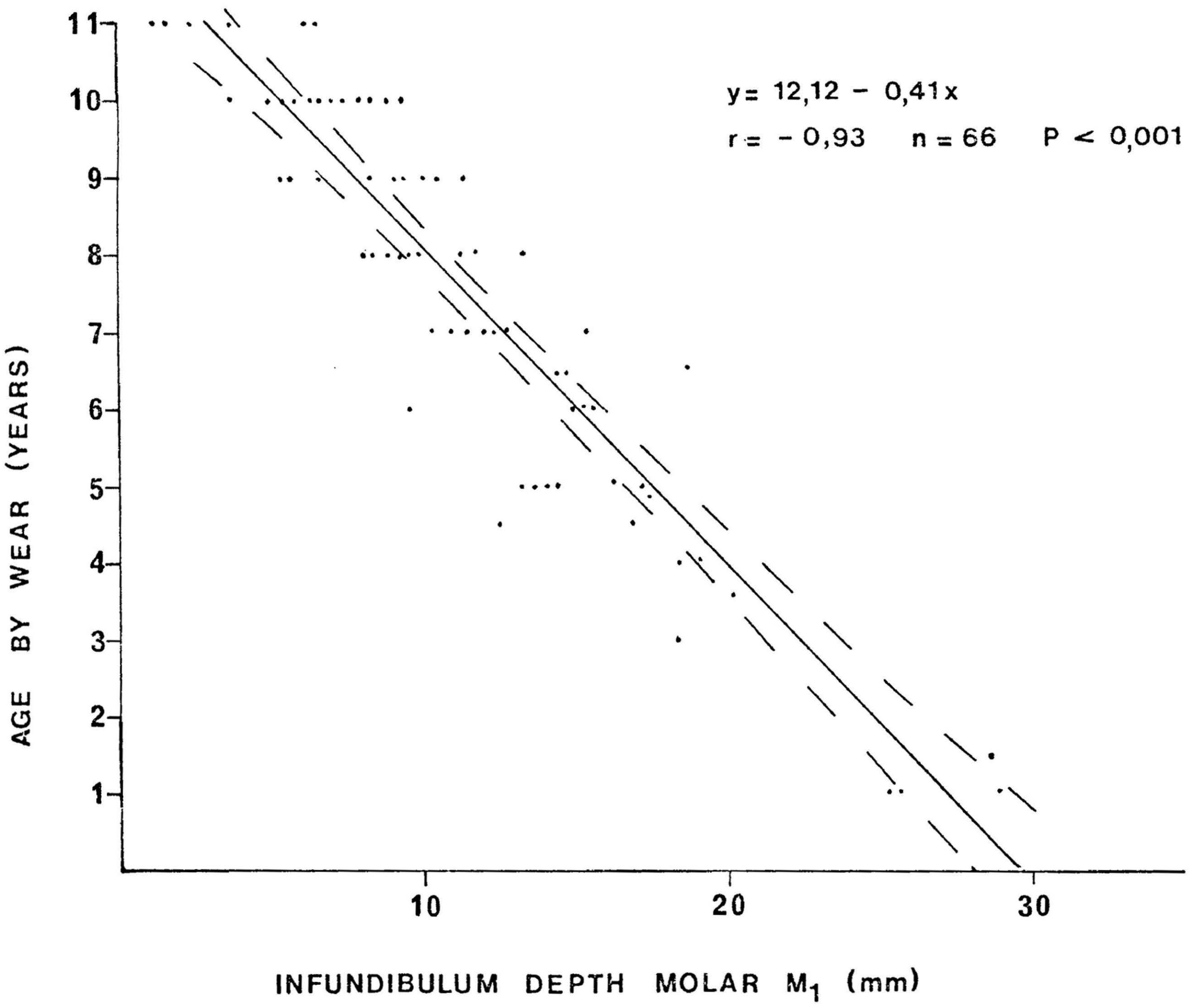


Figure 31. A comparison of the infundibulum depth of M_1 with age by wear; male waterbuck. Broken lines are 95 per cent confidence limits.

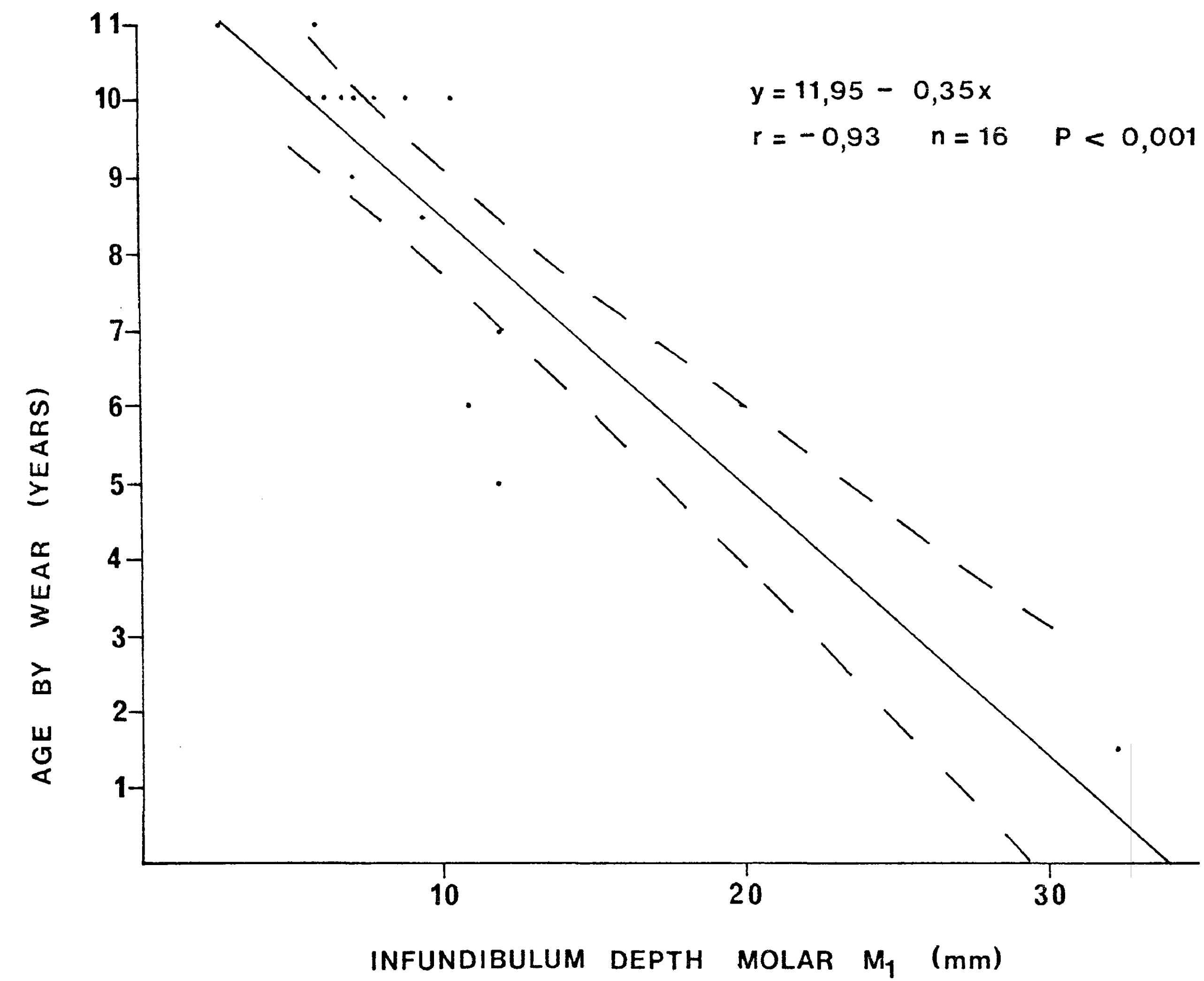


Figure 32. A comparison of the infundibulum depth of M_1 with age by wear; female waterbuck. Broken lines are 95 per cent confidence limits.

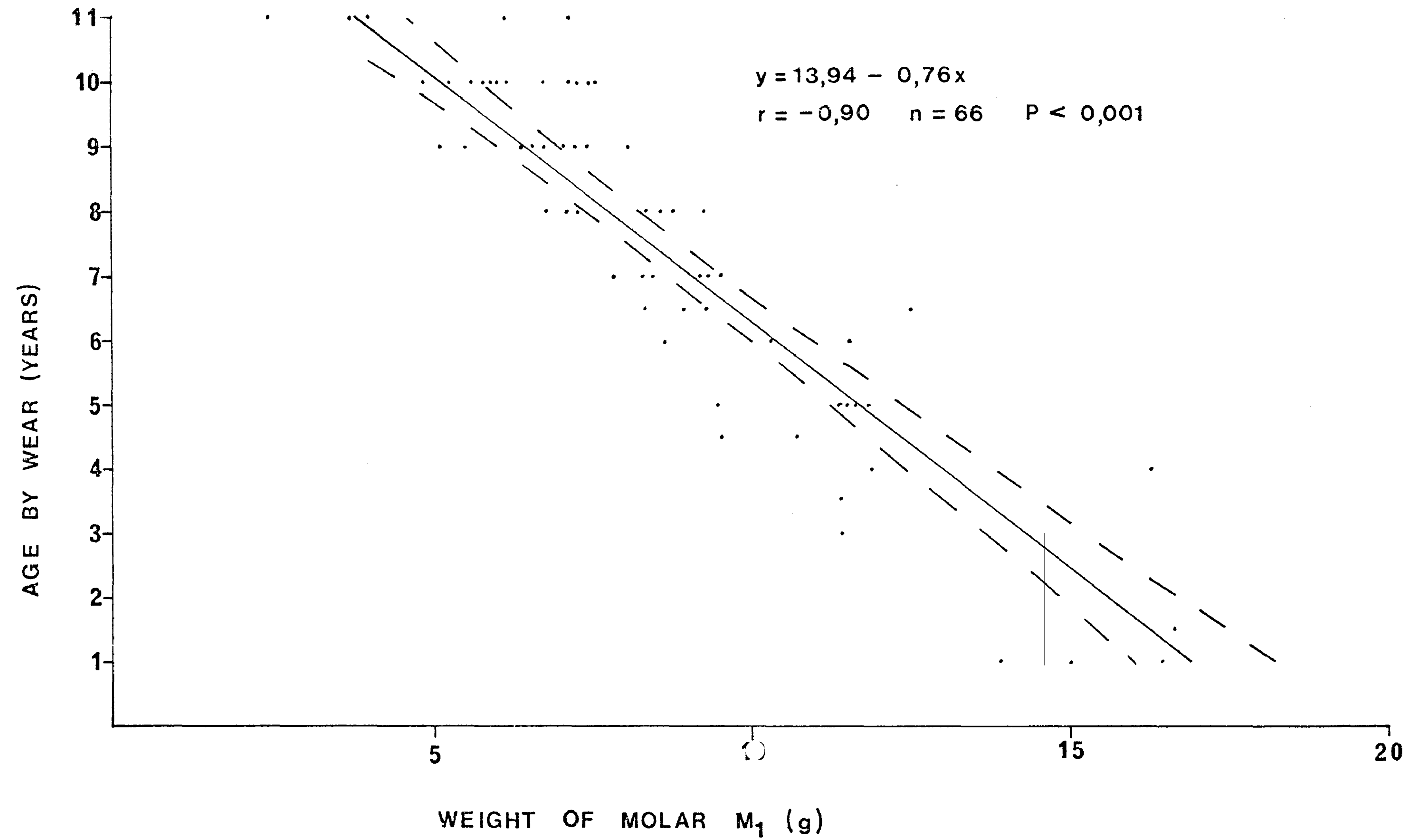


Figure 33. A comparison of the weight of M_1 with age by wear; male waterbuck. Broken lines are 95 per cent confidence limits.

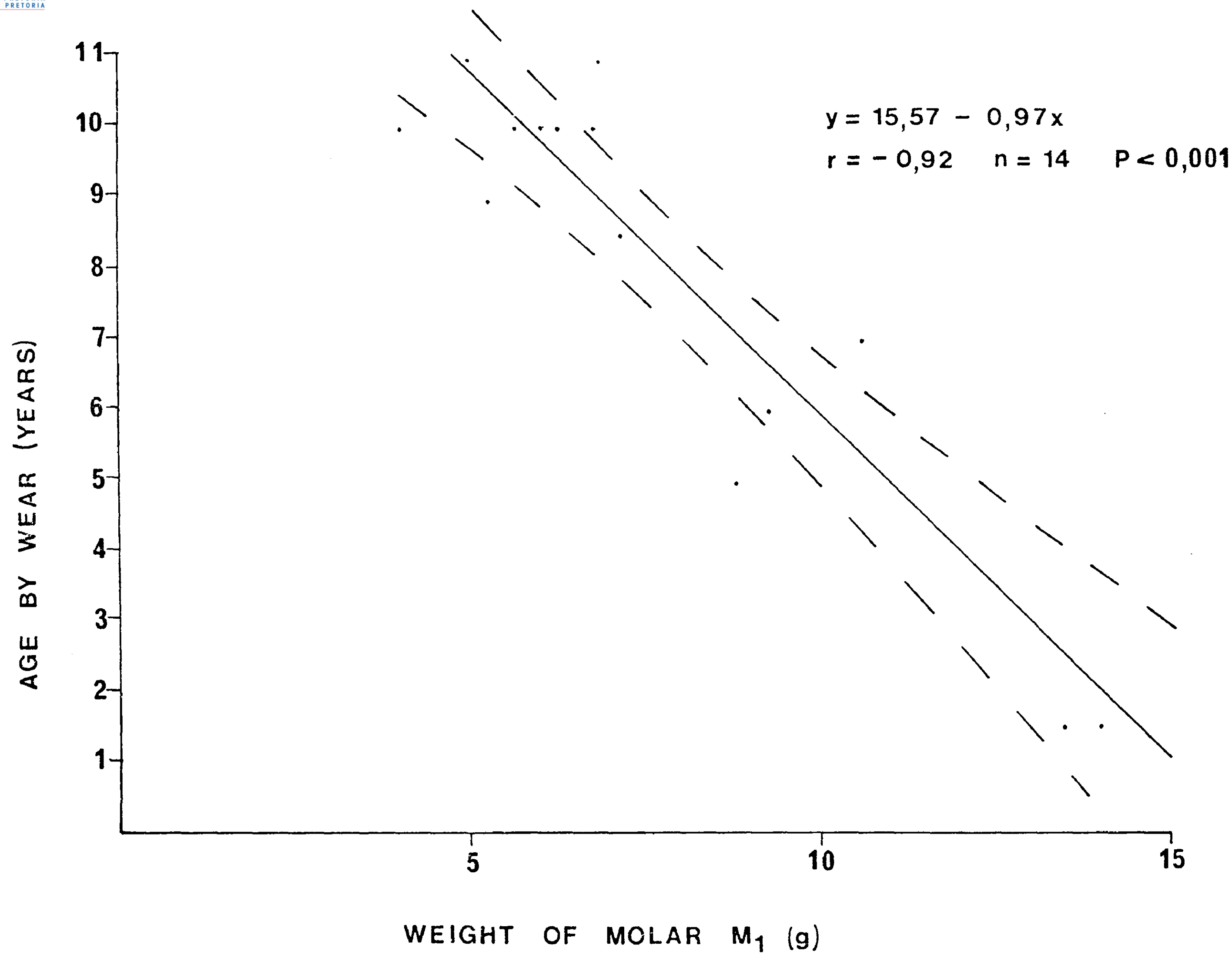


Figure 34. A comparison of the weight of M_1 with age by wear; female waterbuck. Broken lines are 95 per cent confidence limits.

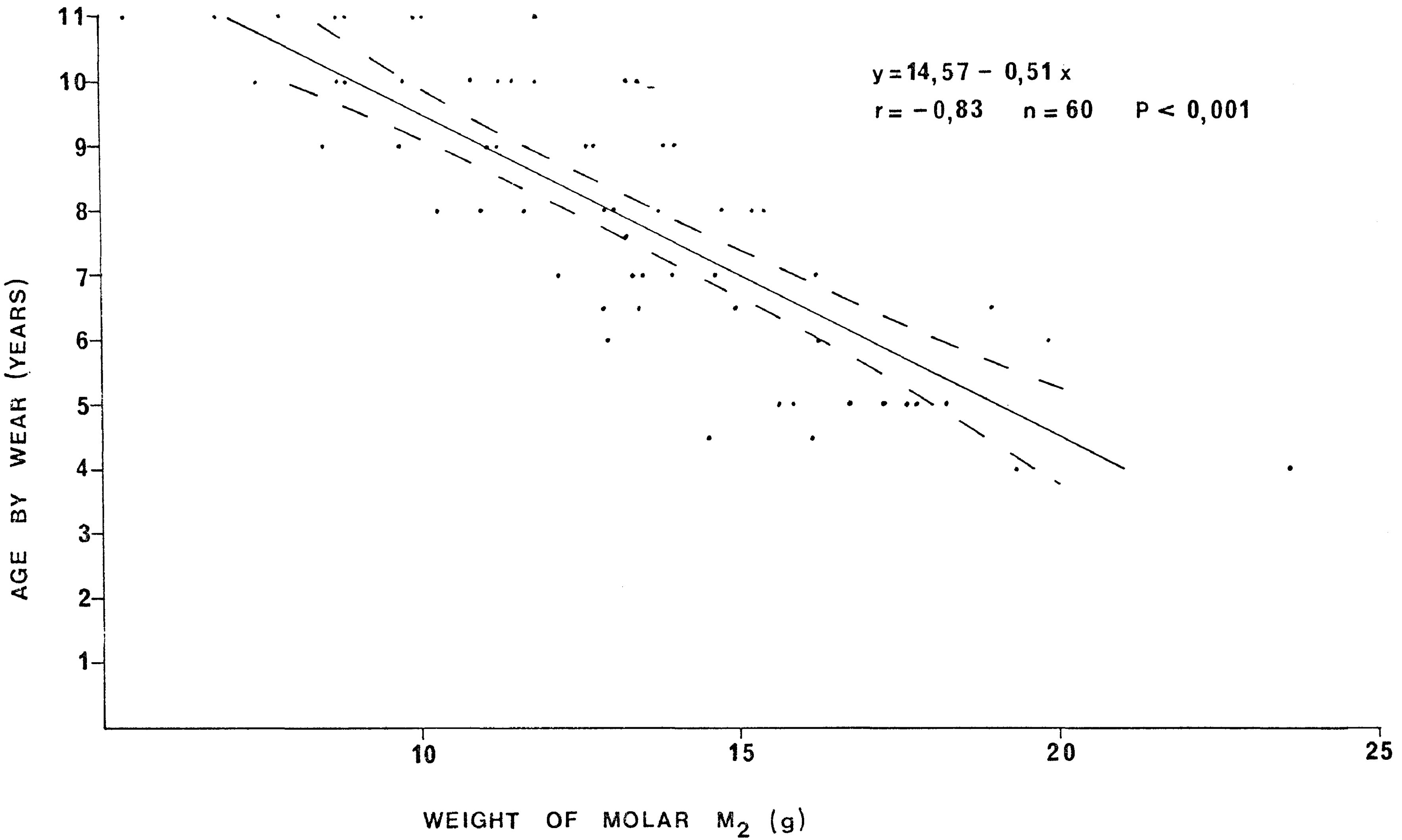


Figure 35. A comparison of the weight of M_2 with age by wear; male waterbuck. Broken lines are 95 per cent confidence limits.

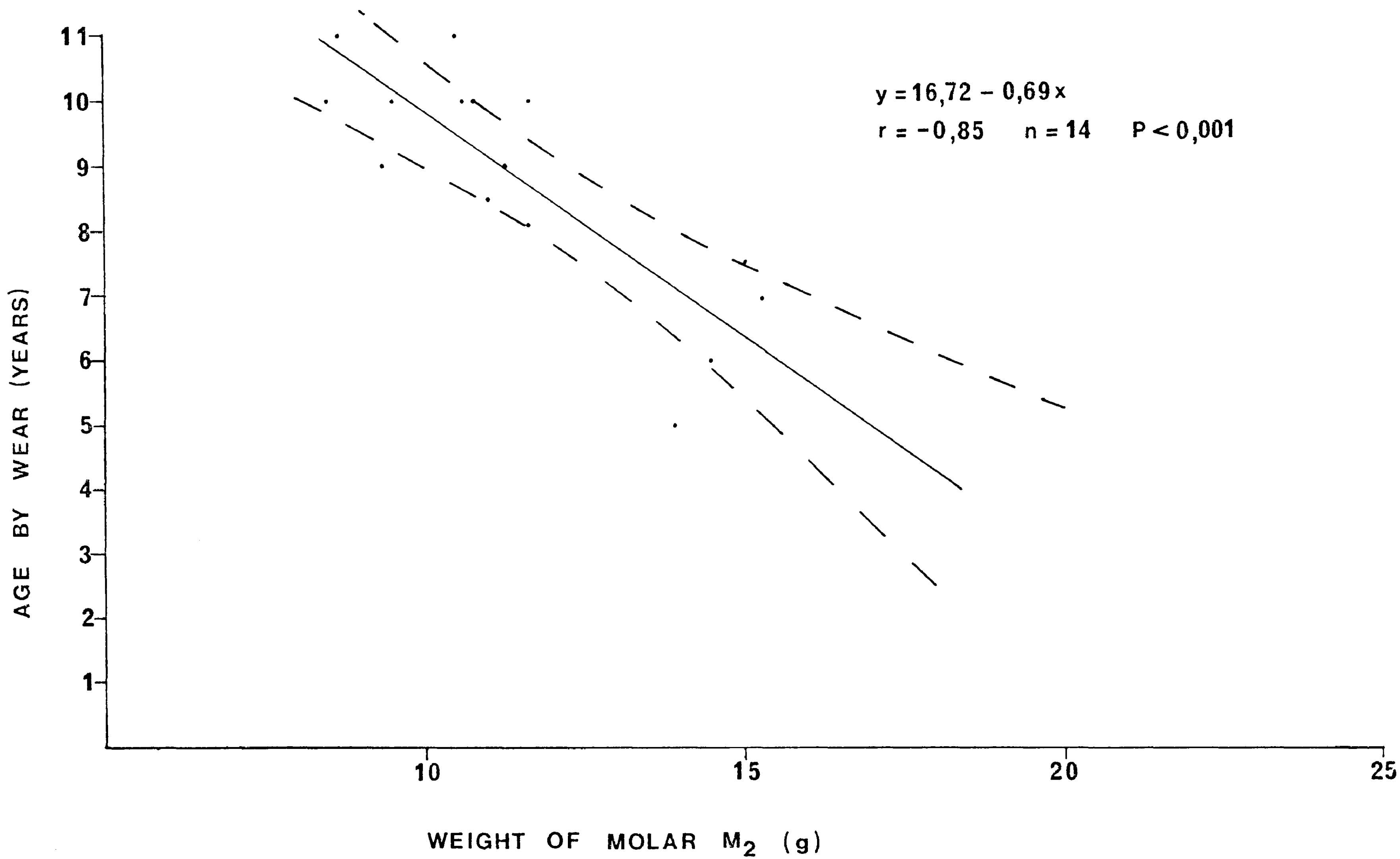


Figure 36. A comparison of the weight of M_2 with age by wear; female waterbuck. Broken lines are 95 per cent confidence limits.

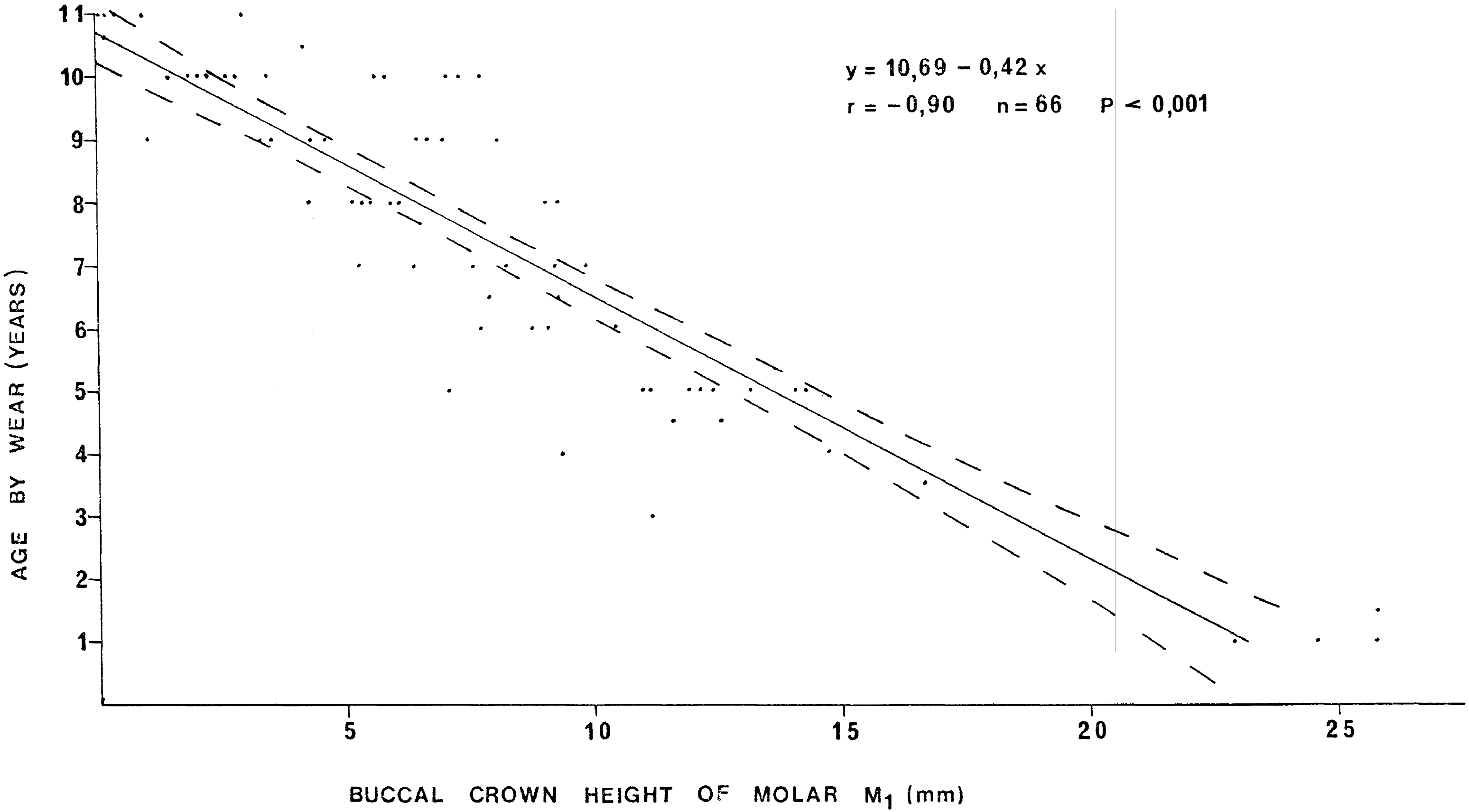


Figure 37. A comparison of the buccal crown height of M_1 with age by wear; male waterbuck. Broken lines are 95 per cent confidence limits.

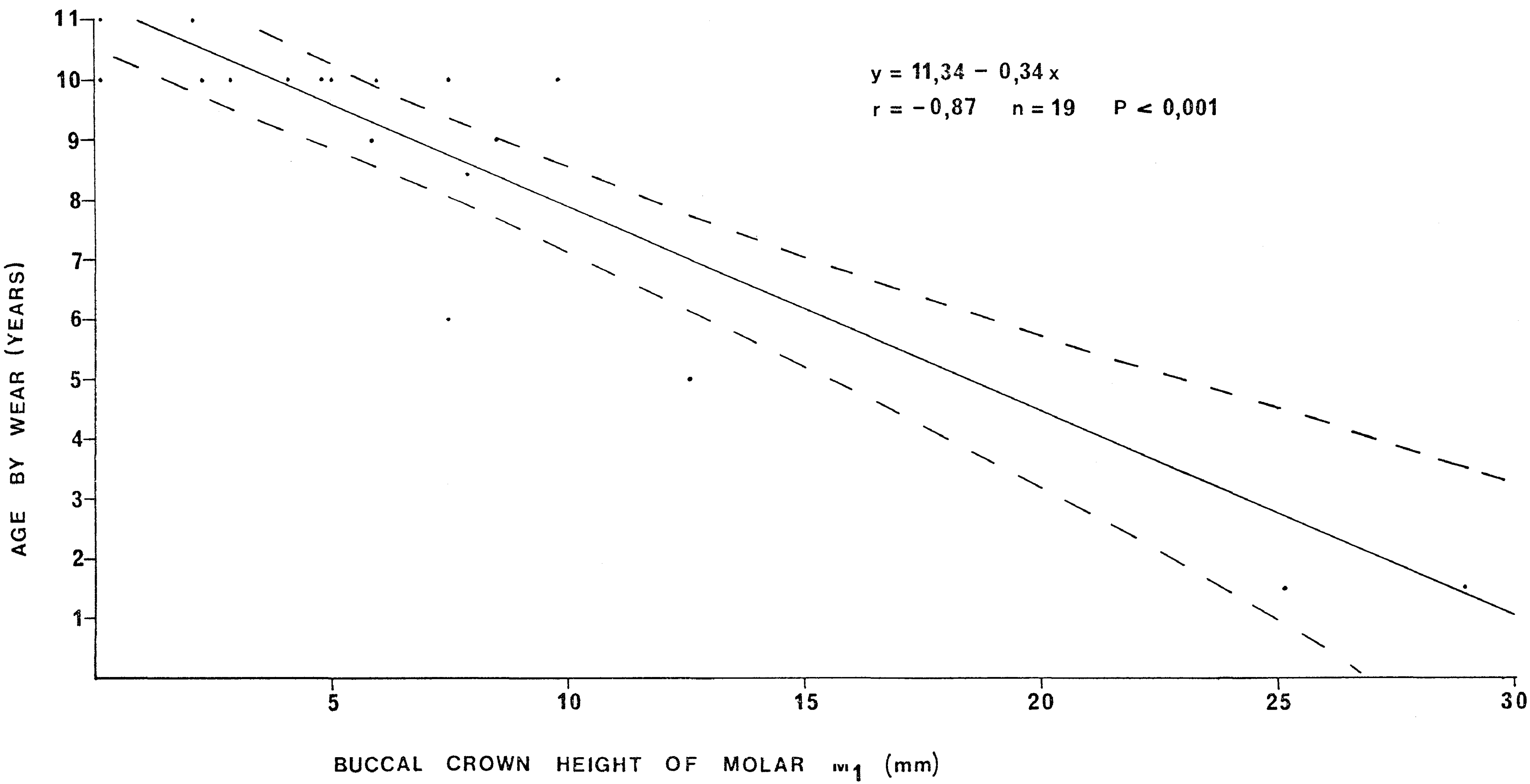


Figure 38. A comparison of the buccal crown height of M_1 with age by wear; female waterbuck. Broken lines are 95 per cent confidence limits.

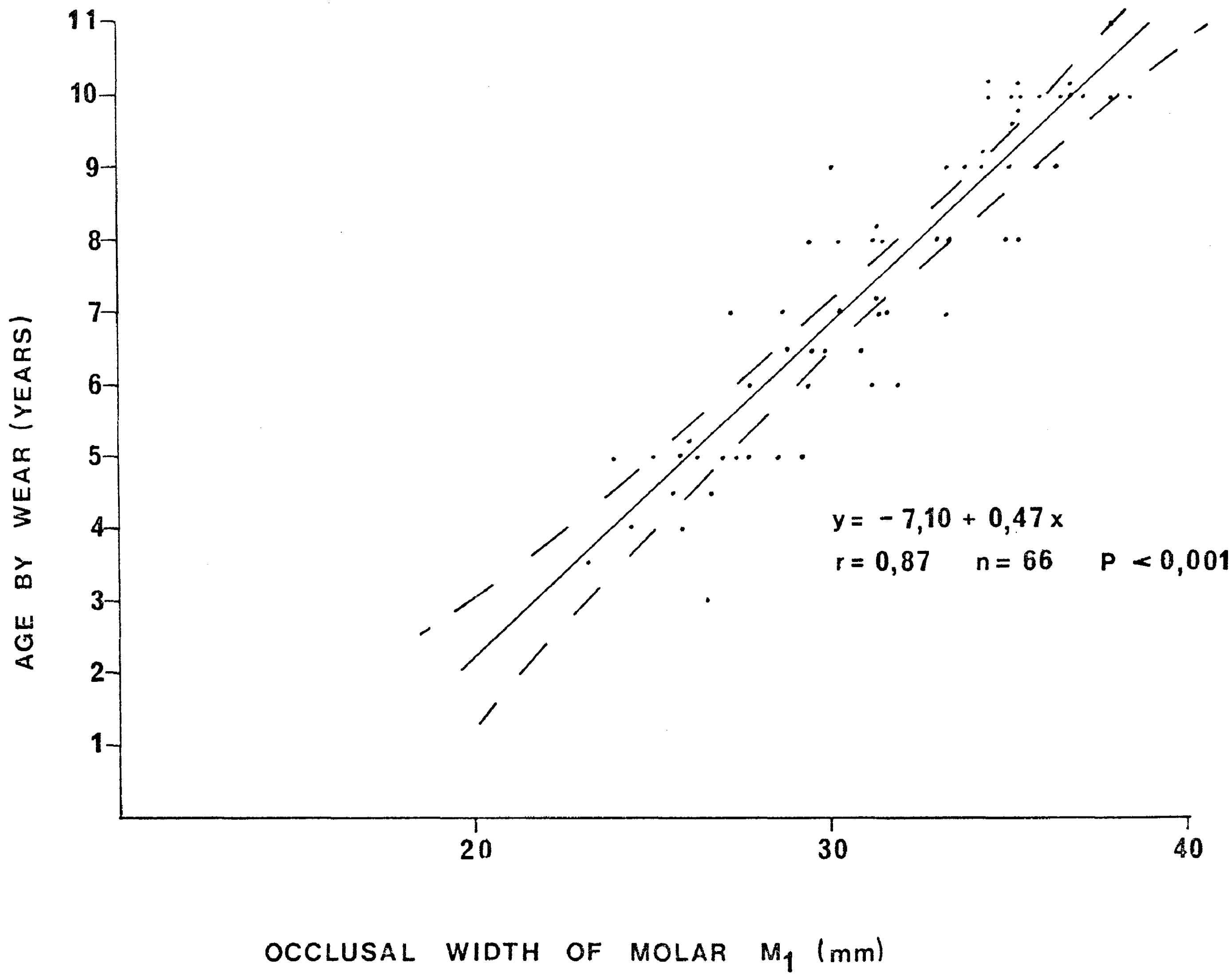


Figure 39. A comparison of the occlusal width of M_1 with age by wear; male waterbuck. Broken lines are 95 per cent confidence limits.

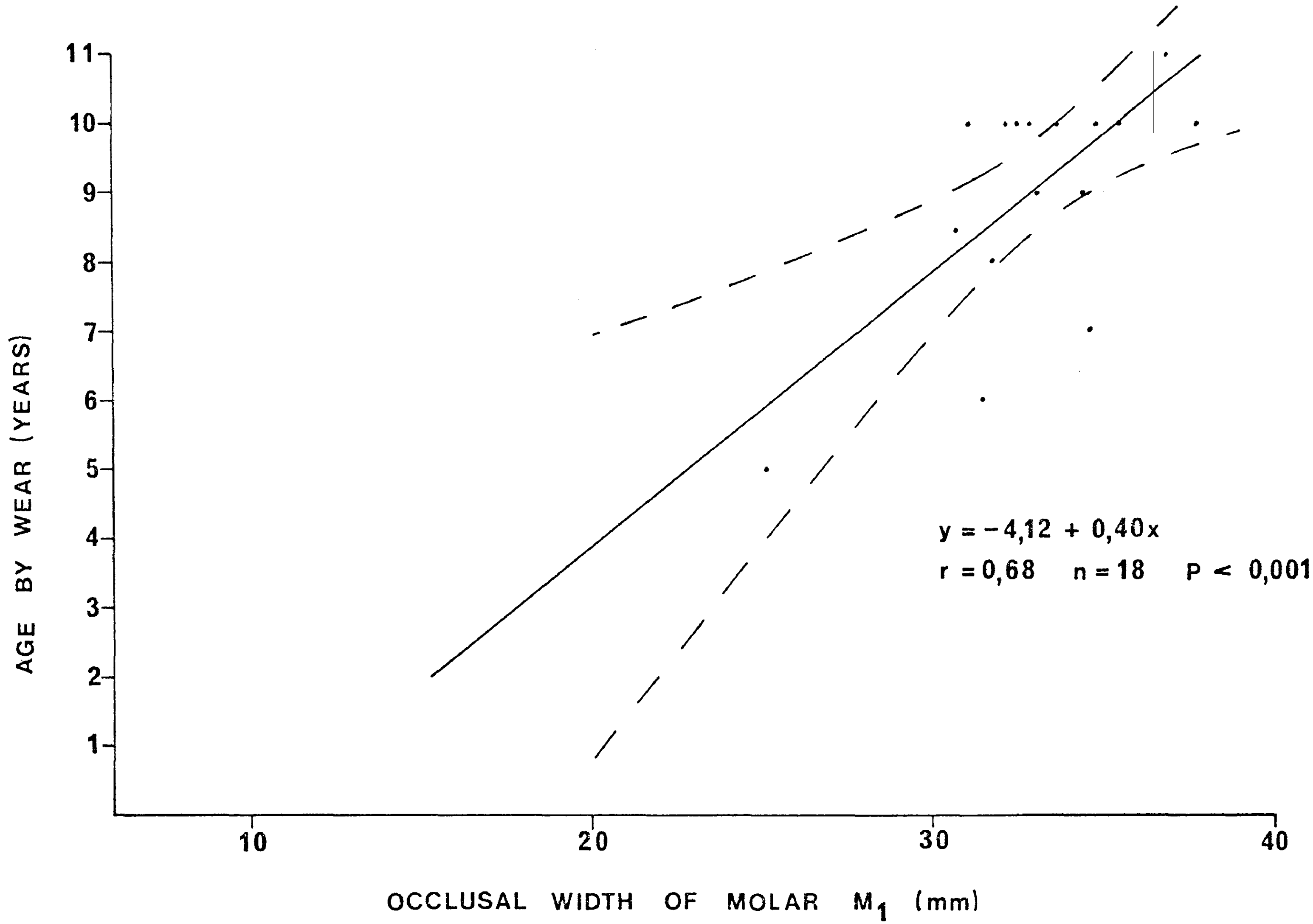


Table 40. A comparison of the occlusal width of M_1 with age by wear; female waterbuck. Broken lines are 95 per cent confidence limits.

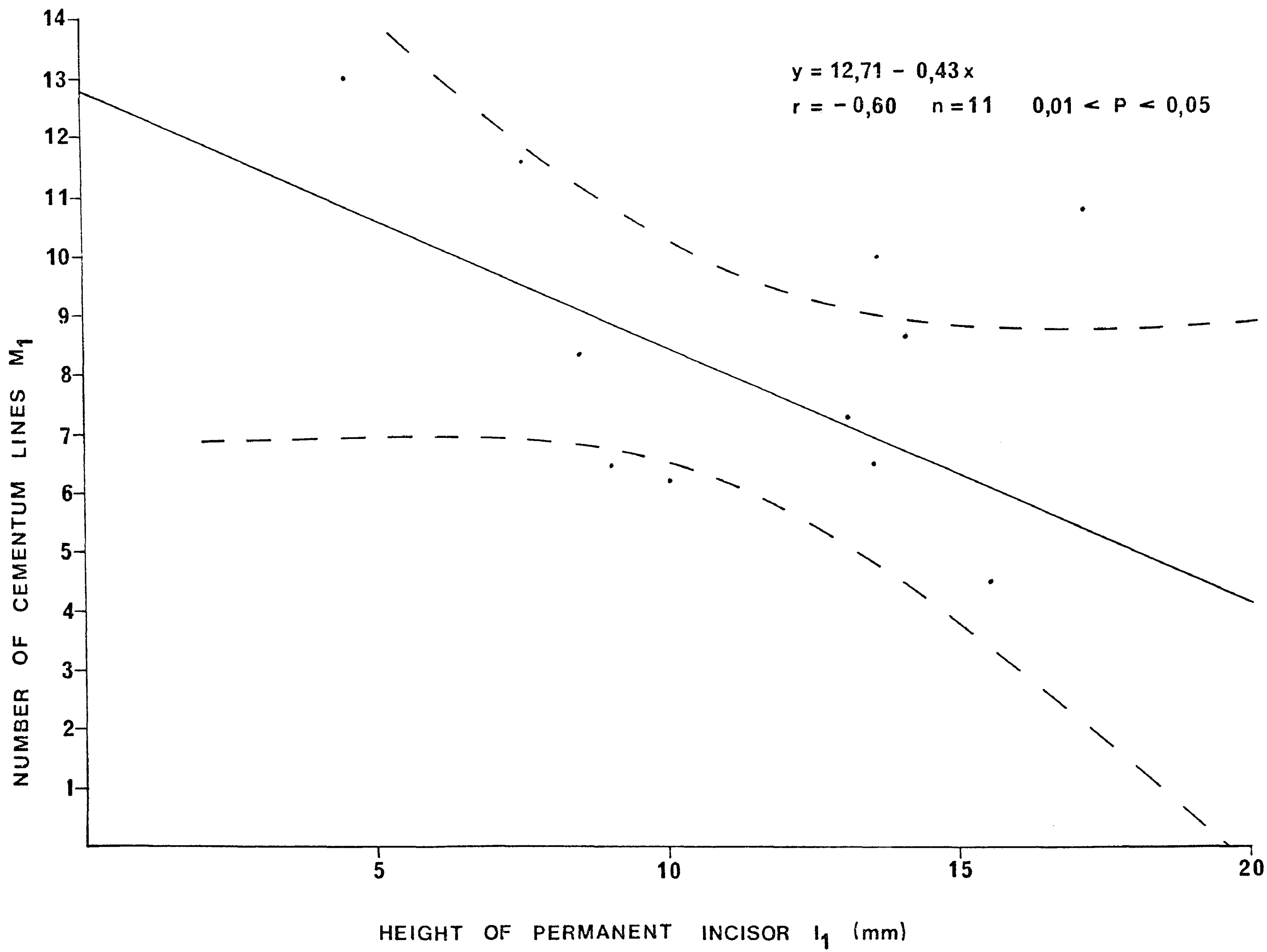


Figure 41. A comparison of the height of I_1 with cementum age; male waterbuck. Broken lines are 95 per cent confidence limits.

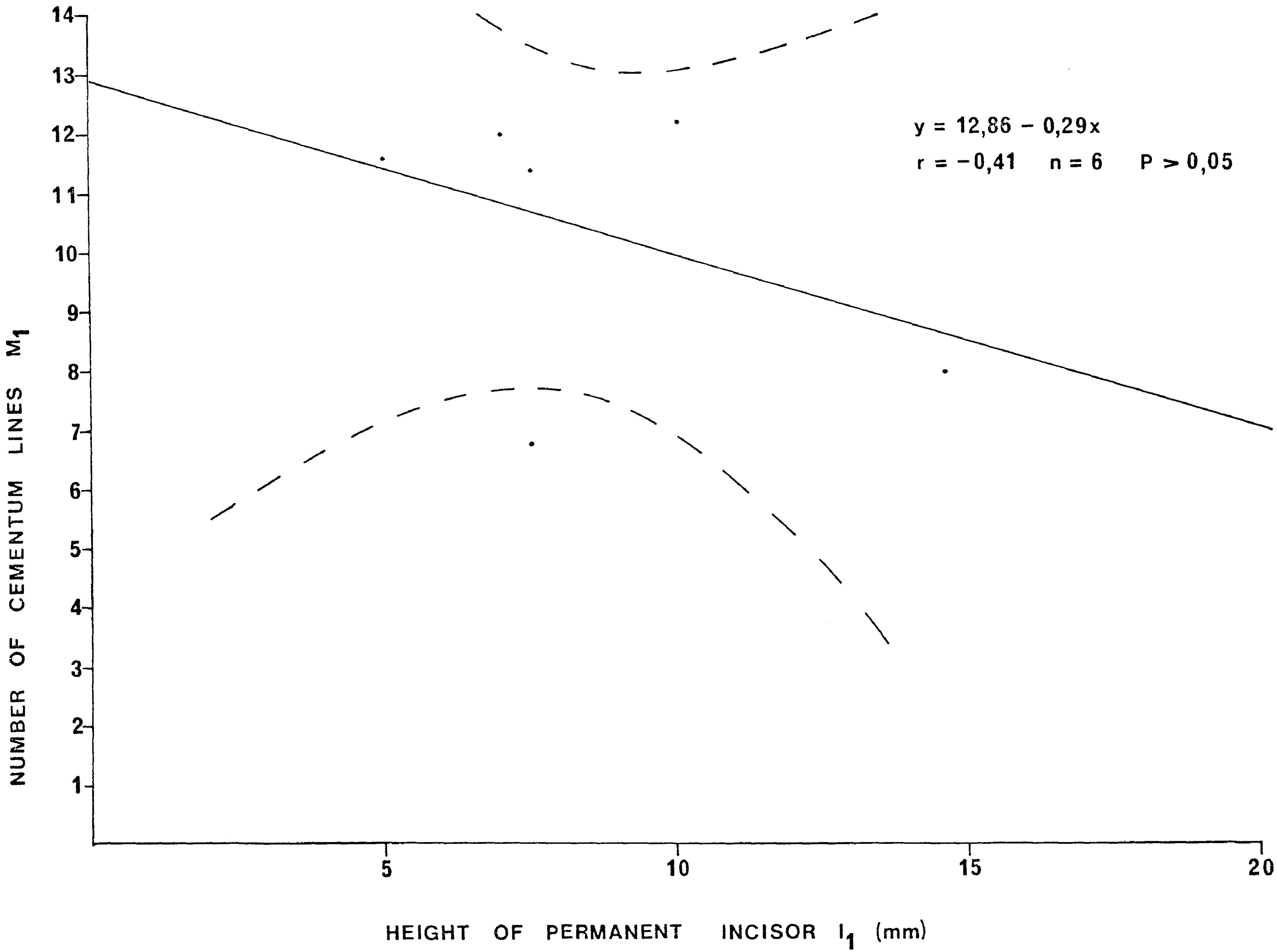


Figure 42. A comparison of the height of I_1 with cementum age; female waterbuck. Broken lines are 95 per cent confidence limits.

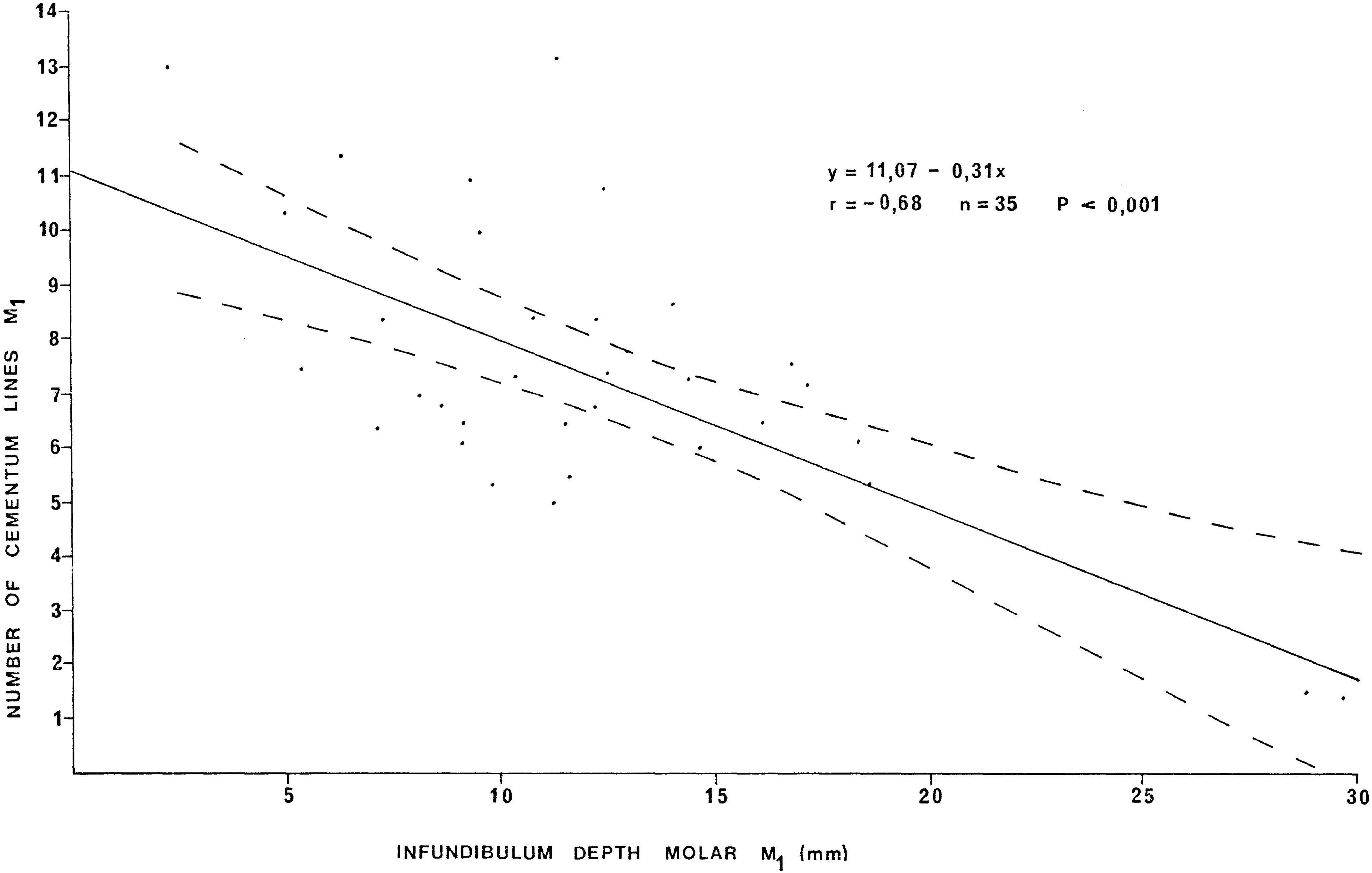


Figure 43. A comparison of the infundibulum depth of M_1 with cementum age; male waterbuck. Broken lines are 95 per cent confidence limits.

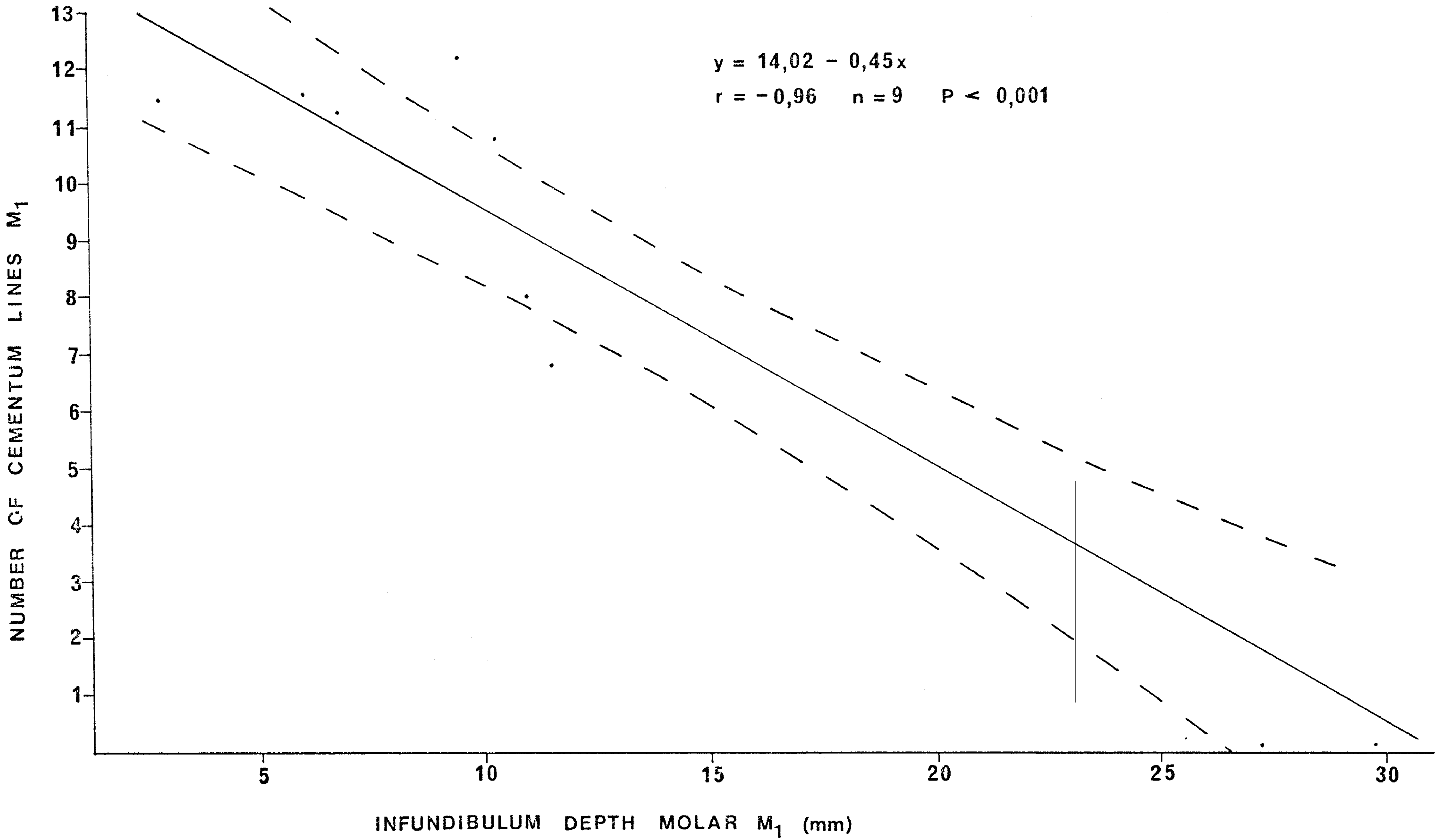


Figure 44. A comparison of the infundibulum depth of M_1 with cementum age; female waterbuck. Broken lines are 95 per cent confidence limits.

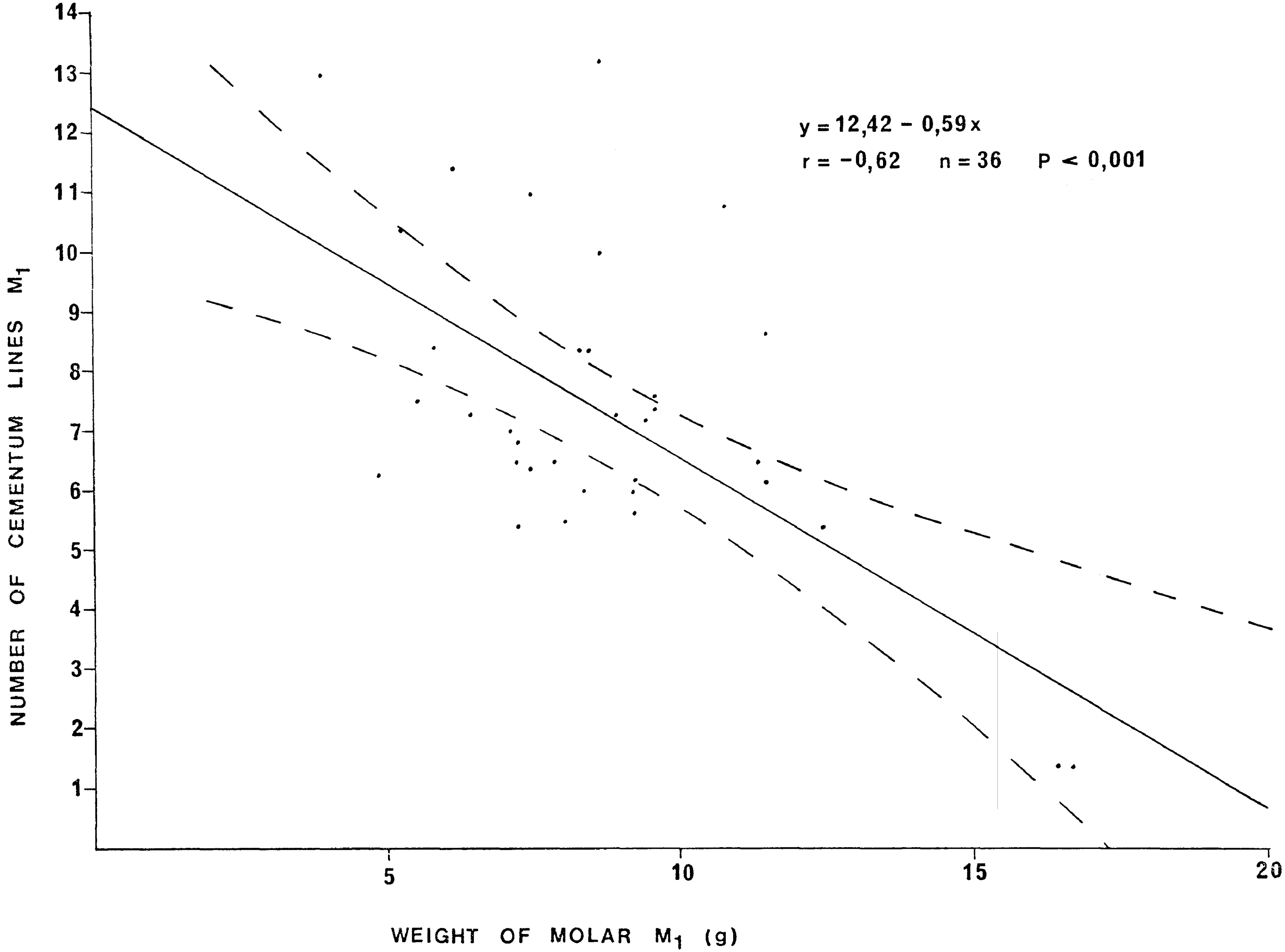


Figure 45. A comparison of the weight of M_1 with cementum age; male waterbuck. Broken lines are 95 per cent confidence limits.

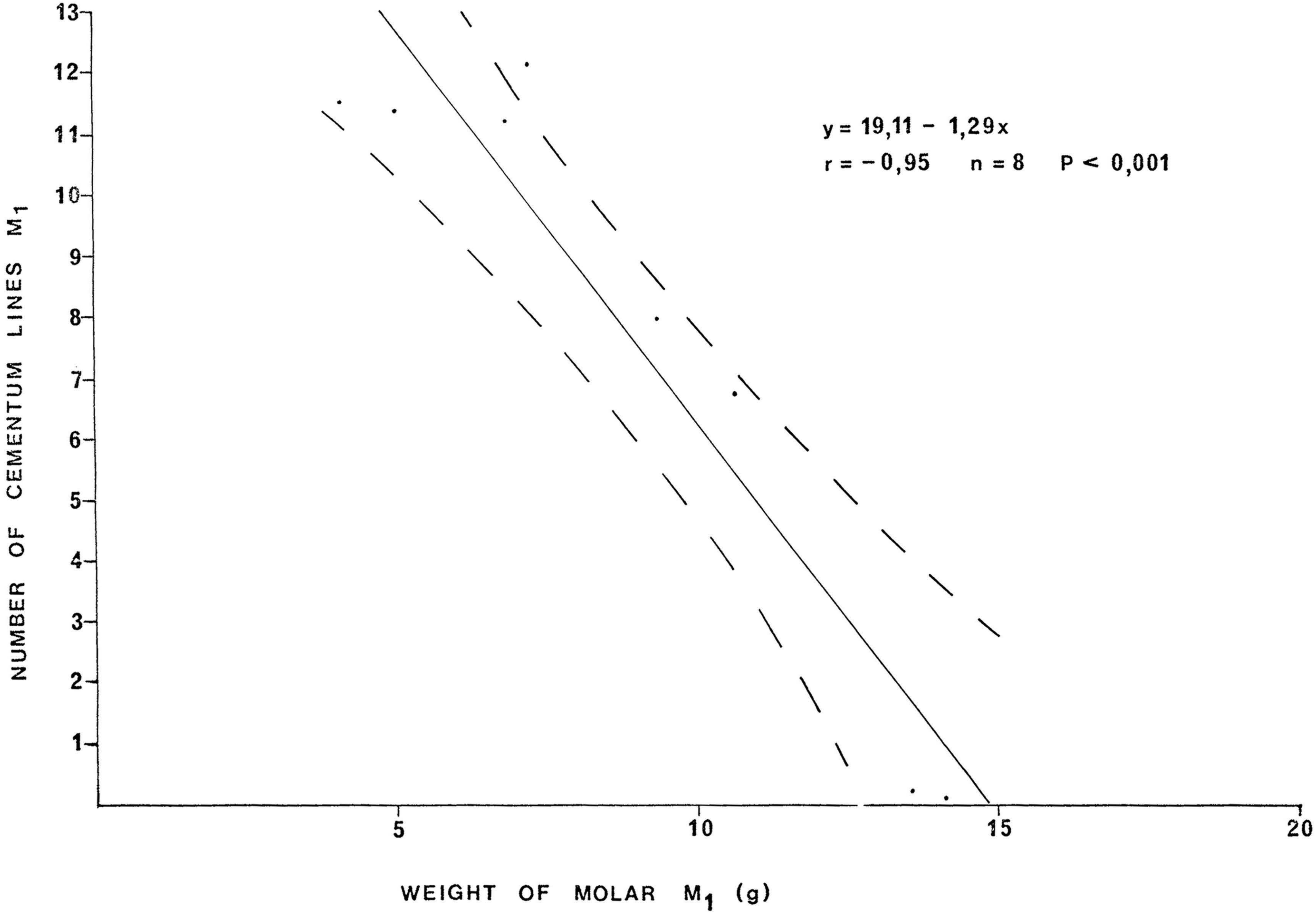


Figure 46. A comparison of the weight of M_1 with cementum age; female waterbuck. Broken lines are 95 per cent confidence limits.

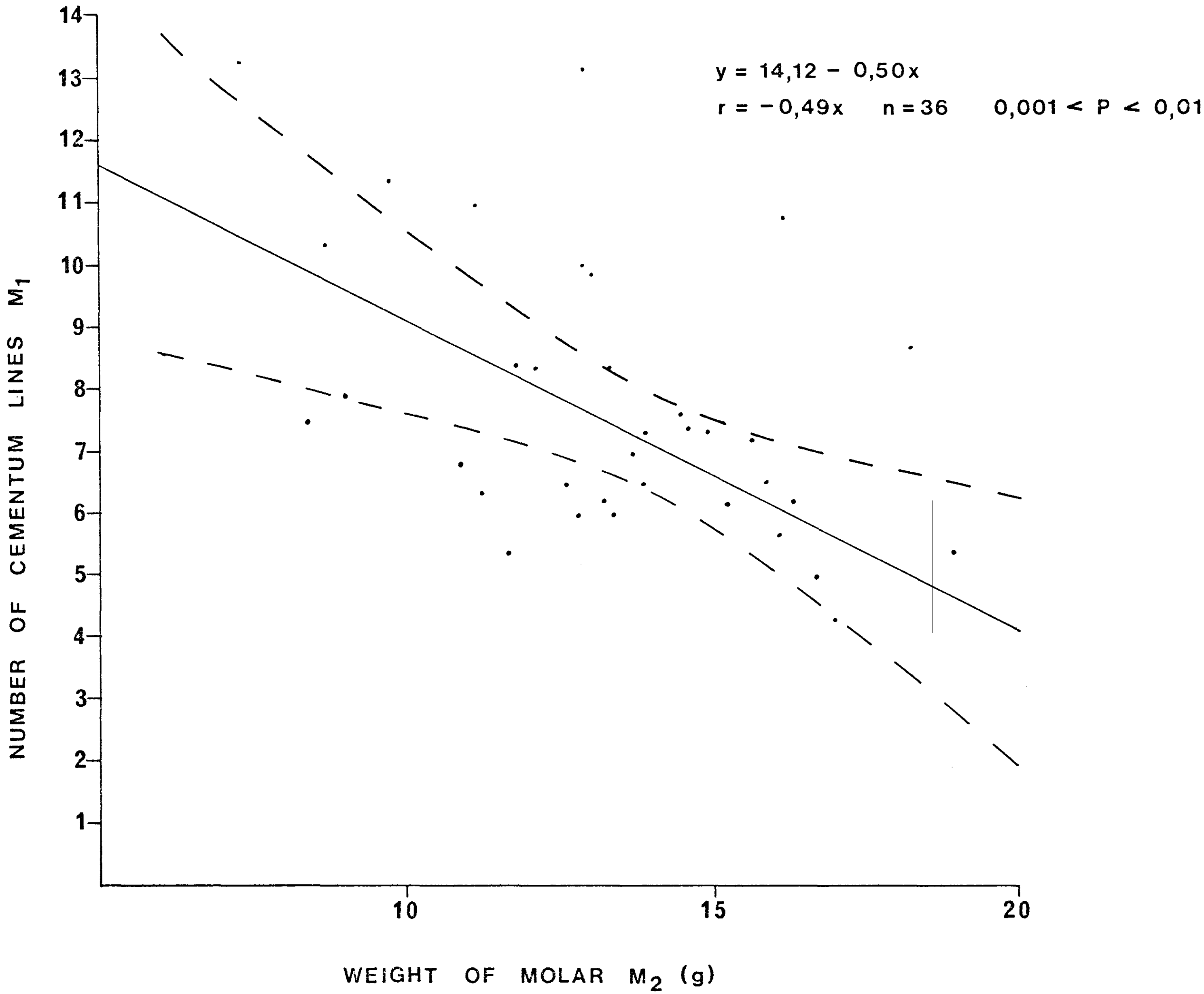


Figure 47. A comparison of the weight of M_2 with cementum age; male waterbuck. Broken lines are 95 per cent confidence limits.

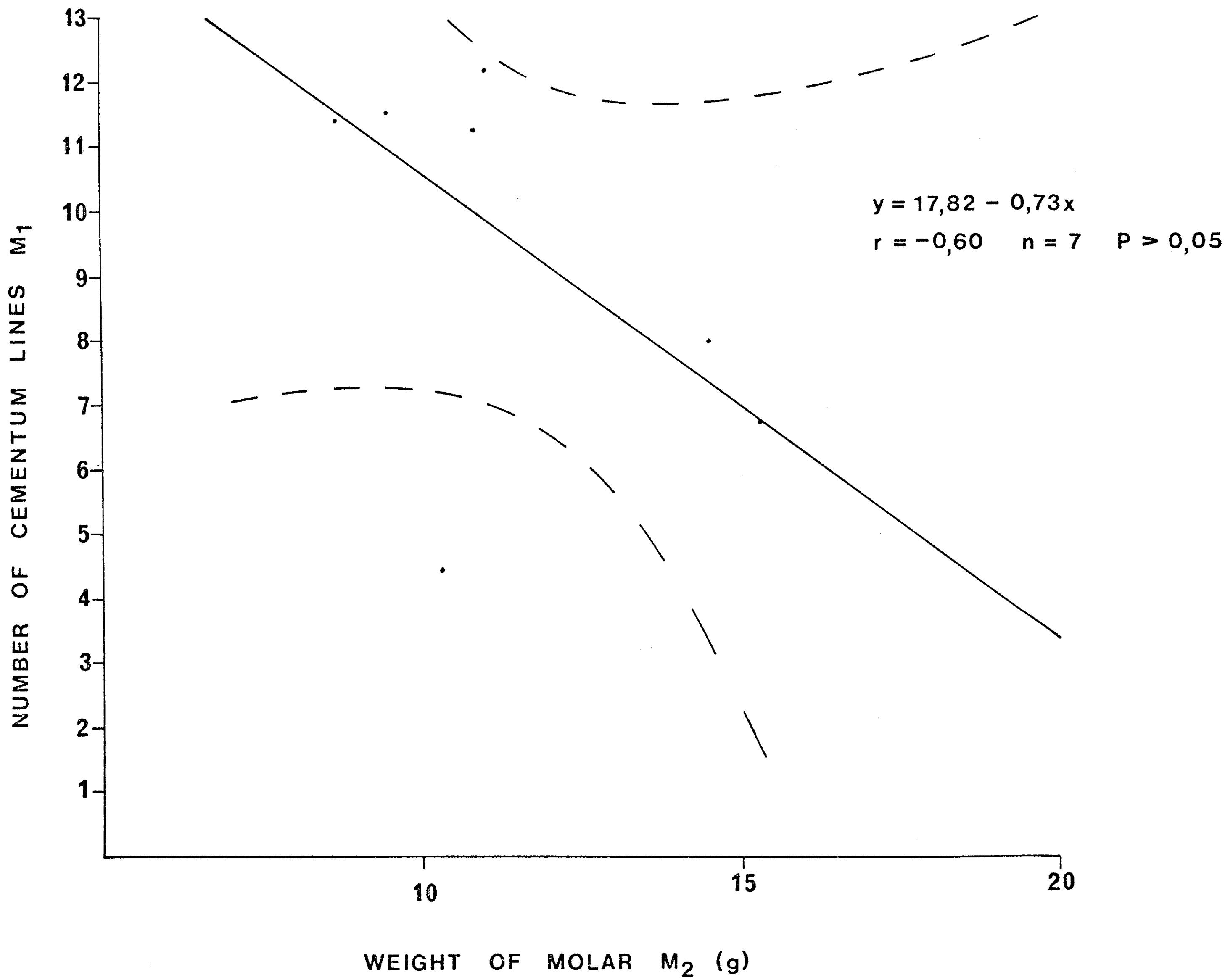


Figure 48. A comparison of the weight of M_2 with cementum age; female waterbuck. Broken lines are 95 per cent confidence limits.

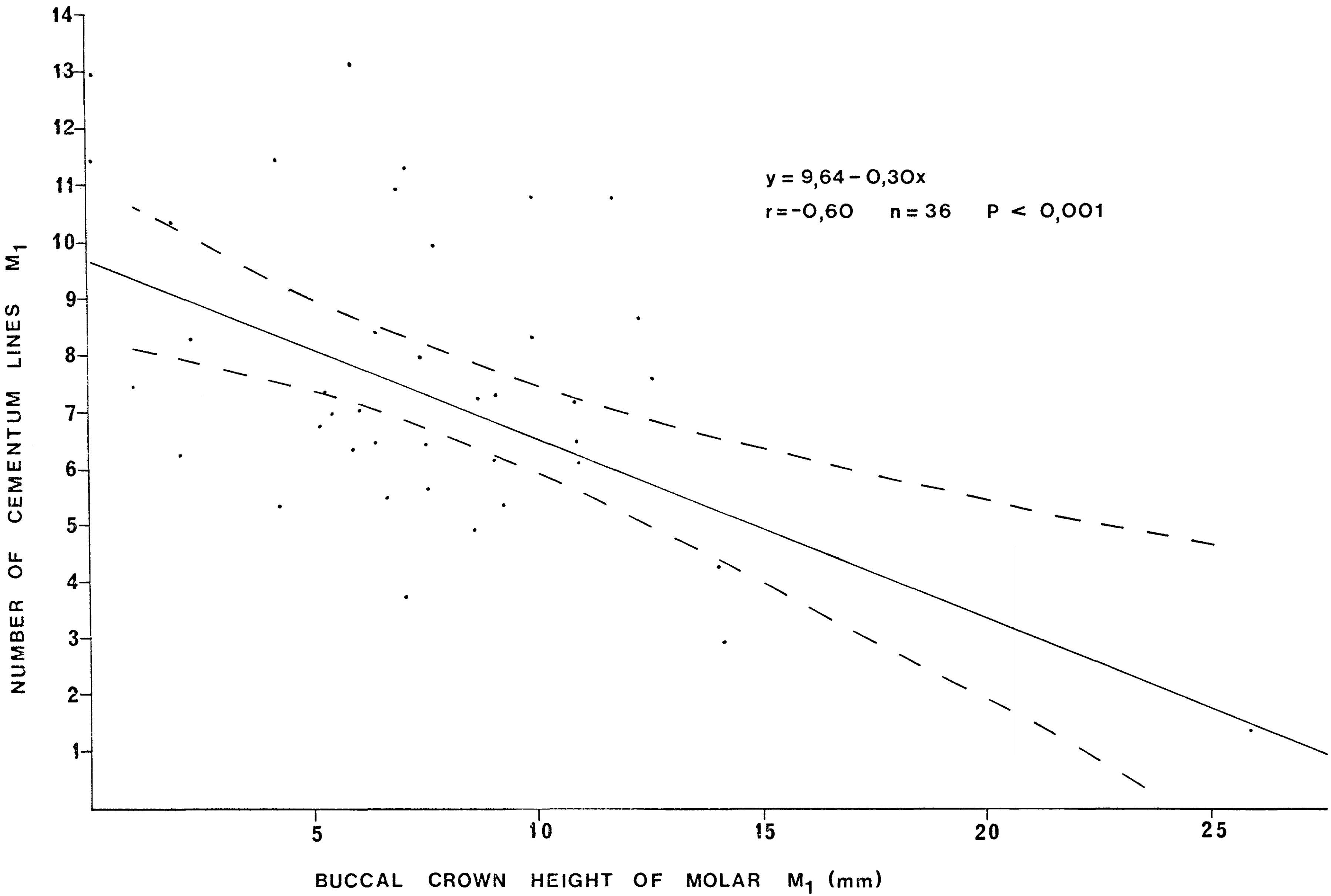


Figure 49. A comparison of the buccal crown height of M_1 with cementum age; male waterbuck. Broken lines are 95 per cent confidence limits.

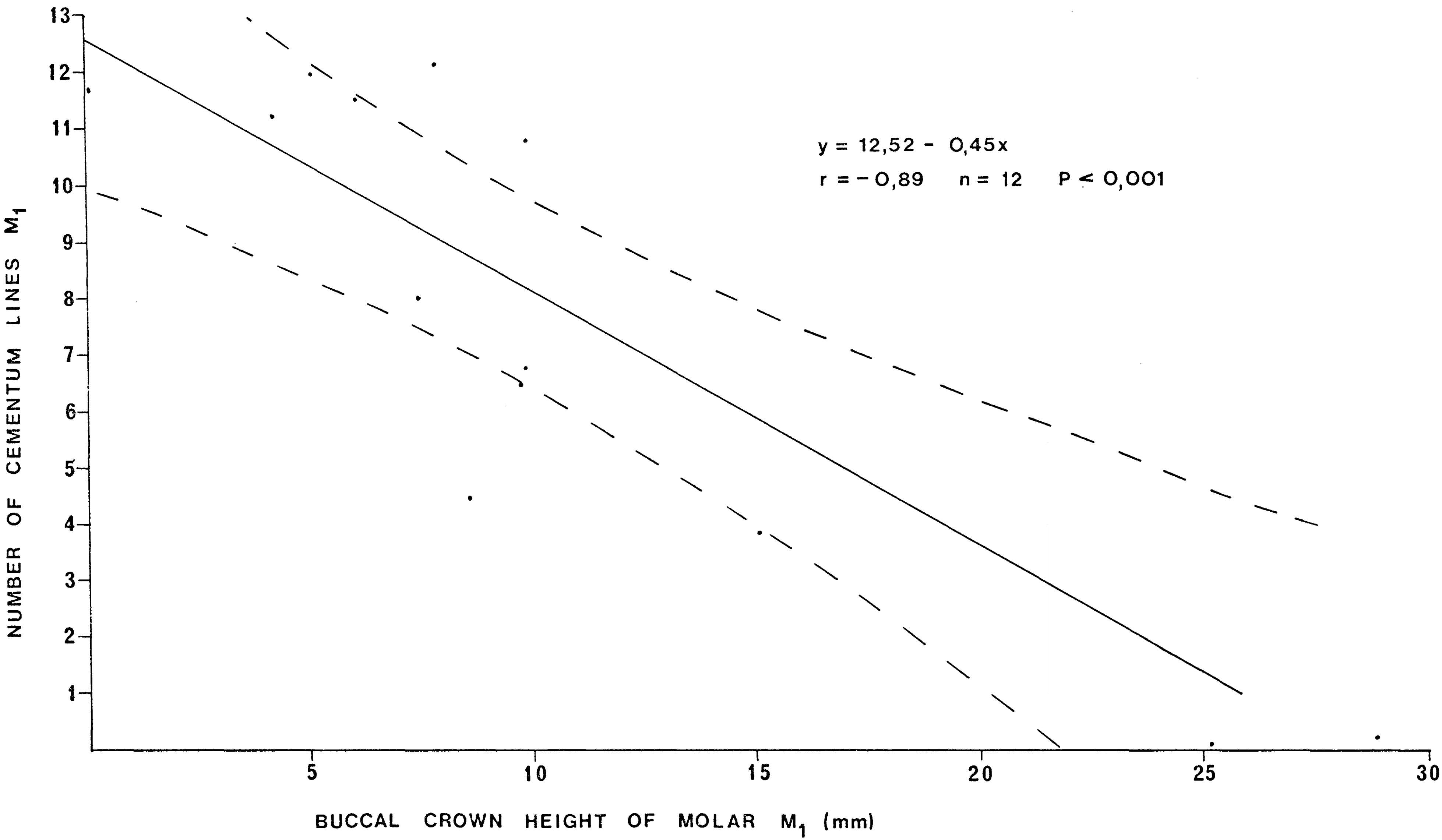


Figure 50. A comparison of the buccal crown height of M_1 with cementum age; female waterbuck. Broken lines are 95 per cent confidence limits.

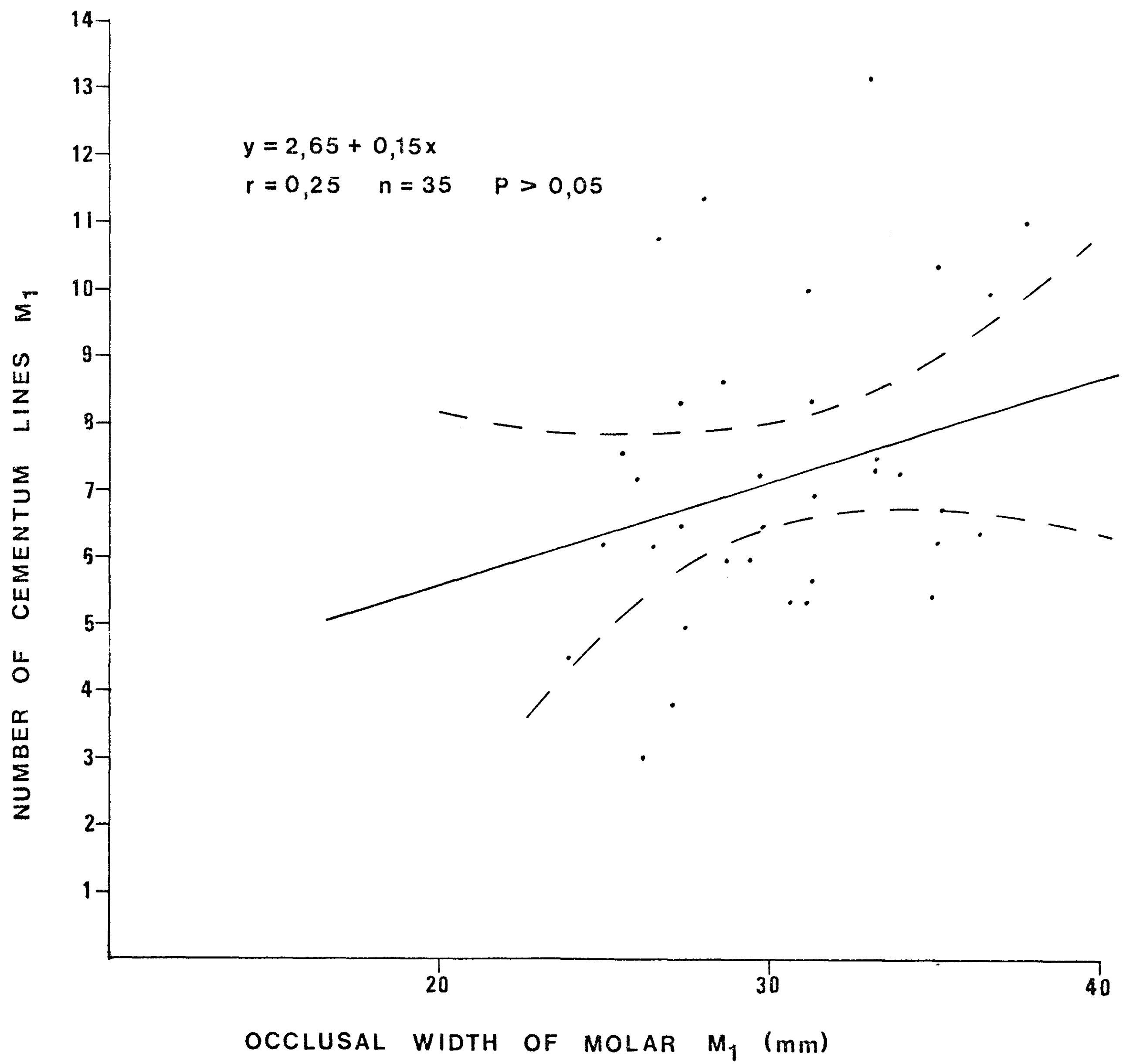


Figure 51. A comparison of the occlusal width of M_1 with cementum age; male waterbuck. Broken lines are 95 per cent confidence limits.

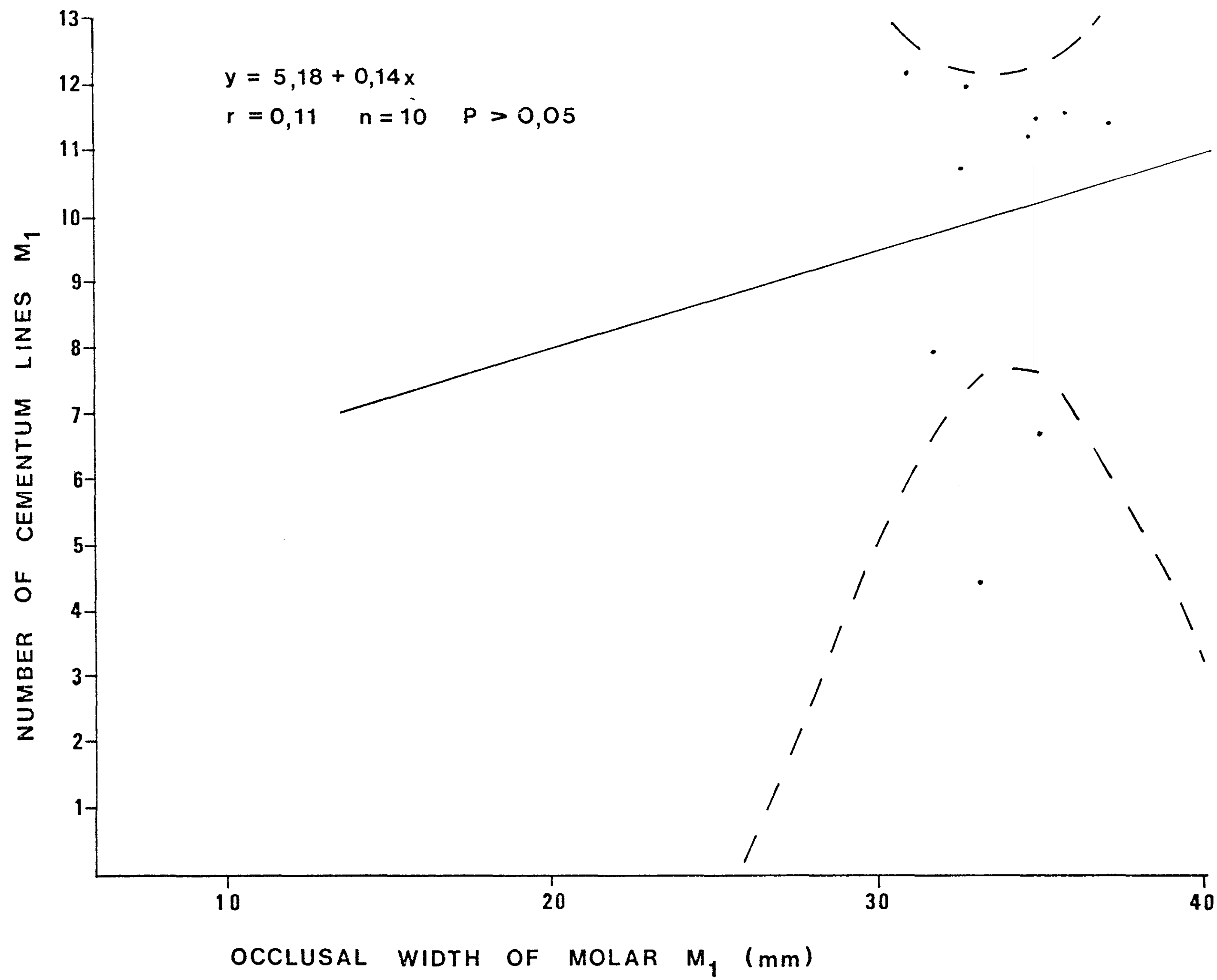


Figure 52. A comparison of the occlusal width of M_1 with cementum age; female waterbuck. Broken lines are 95 per cent confidence limits.

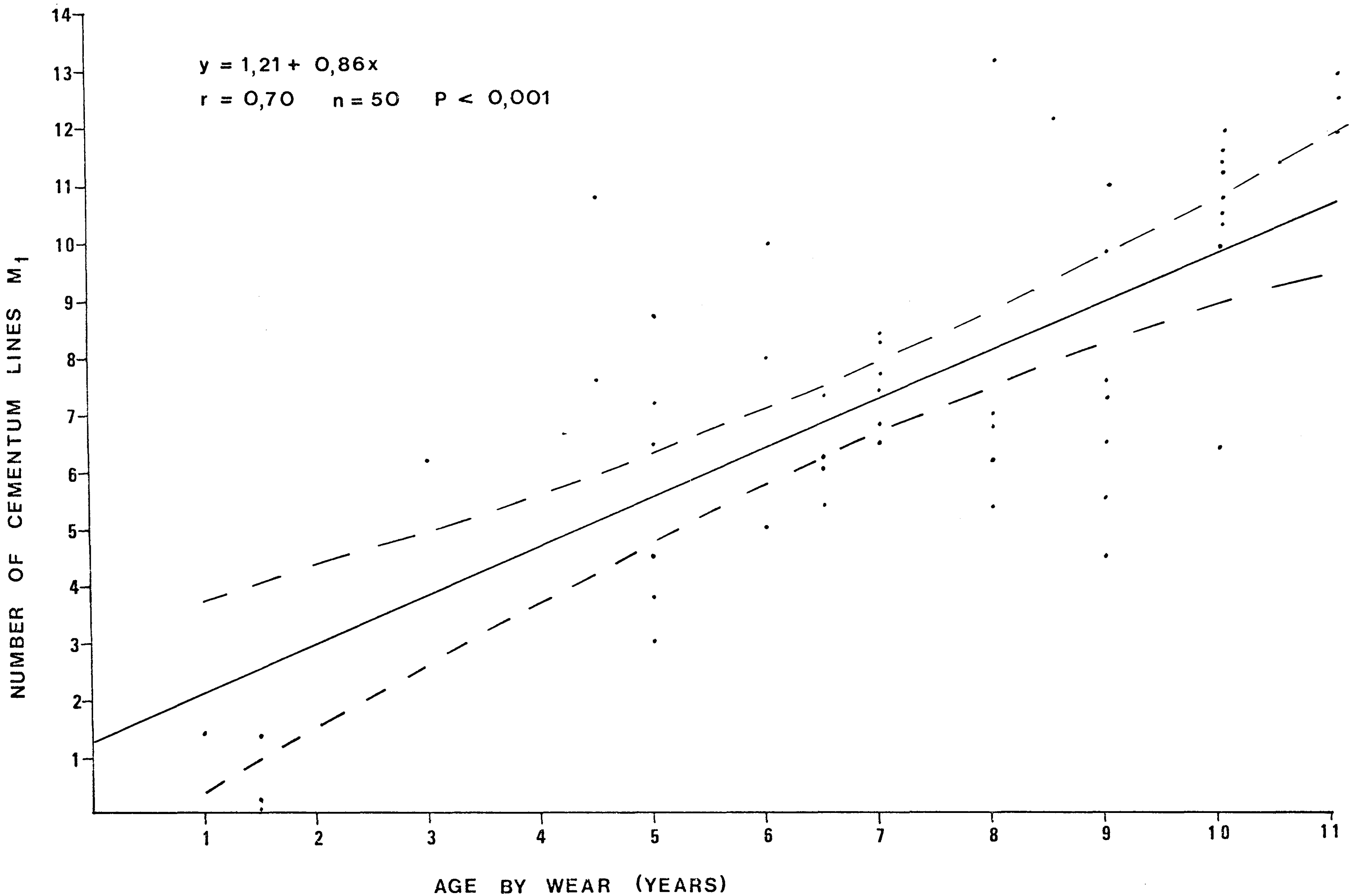


Figure 53. A comparison of age by wear with cementum age for male and female waterbuck. Broken lines are 95 per cent confidence limits.

annual nature of cementum lines starting after eruption is supported by four one year-old skulls examined. The skulls came from animals that were age determined to between 1,0 years and 1,5 years based on body size and the following through of cohort groups from the late summer birth peak (see Chapter 5). The number of lines seen in these known age animals ranged from 0 to 1,4 with a mean of 0,8. No definite eruption line was seen as described by Spinage (1967). A wide range in the number of lines does occur for some age classes; for example teeth classified to eight years by wear have between 5,0 and 13,2 cementum lines. This variability could either be owing to inaccuracy in the wear model, variability in the amount of attrition with age, or variability in either the number of lines laid down or actually observed. An indication of which is the main cause of inconsistancy comes from comparing the graphs of wear measurements versus wear age (Figs. 29 to 40) with those of wear measurements against cementum age (Figs. 41 to 52). In nine of the 12 comparisons tooth measurements have higher correlation coefficients with age by wear than with cementum age and in the other three the values are equal. Thus the precision with which tooth mensural data predicts age by wear is greater than that with which they predict cementum age. This is shown more precisely in Table 27 by comparing 95 per cent confidence limits of y (where y is cementum age and age by wear). This is done at their minimum confidence range, which occurs at $\bar{x}$ (Snedecor and Cochran 1967). The y values are similar for cementum age and wear age, but for all 12 tooth measurements the confidence limits are smaller for the wear age figure, usually be at least half. For example the y value for $\bar{x}$ M_1 occlusal surface (females) is 10,0 years cementum age and 9,1 years age by wear, but the 95 per cent confidence range is 7,99 to 12,07 for cementum age and 8,51 to 9,76 for age by wear.

These results strongly suggest that it is the number of cementum lines that is varying with age, either because of real variability or error in observation. This conclusion is supported by considering the number of lines in M_1, M_2 and M_3 teeth. The argument given above predicts that in the same skull M_2 should have one cementum line less than M_1, and M_3 two lines less than M_1, because of the yearly sequence of eruption. Table 28 shows that the mean difference in numbers of lines between M_1 and M_2 is 1,6 and between M_1 and M_3 2,5. Considering the small sample size these results can be taken as supporting the

Table 27. Comparison of the precision with which waterbuck tooth mensural data predict age by wear and age by cementum lines.

Tooth measurement (x)	Cementum line age (y)			Age by wear (y)		
	Mean x*	y at $\bar{x}$	95 per cent confidence range for y	Mean x	y at $\bar{x}$	95 per cent confidence range for y
Height of permanent incisor I_1 (M)	10,7	8,2	6,4-9,0	10,8	7,3	6,6-8,1
Height of I_1 (F)	8,6	10,4	7,7-13,1	9,5	8,2	7,7-8,7
M_1 infundibulum depth (M)	12,3	7,3	6,6-8,0	11,5	7,4	7,2-7,7
M_1 infundibulum depth (F)	13,22	8,1	6,9-9,2	10,83	8,2	7,5-8,8
M_1 weight (M)	8,81	7,3	6,54-7,98	8,61	7,3	7,08-7,65
M_1 weight (F)	8,81	7,7	6,17-9,24	7,92	7,9	7,19-8,61
M_2 weight (M)	13,71	7,3	6,46-8,06	13,15	7,92	7,67-8,23
M_2 weight (F)	11,59	9,41	6,86-11,96	11,56	8,75	8,12-9,37
M_1 crown height (M)	8,33	7,2	6,40-7,91	8,06	7,30	7,01-7,58
M_1 crown height (F)	9,66	8,21	6,51-9,91	7,55	8,74	8,08-9,40
M_1 occlusal surface (M)	30,77	7,25	6,50-8,00	31,25	7,44	7,17-7,70
M_1 occlusal surface (F)	33,59	10,03	7,99-12,07	33,19	9,14	8,51-9,76

* Linear measurements were taken in millimetres, mass in grams.

M = male

F = female

Table 28. Cementum line counts from M_1, M_2 and M_3 teeth of waterbuck.

Skull number	Mean number of cementum lines, M_1	Mean number of cementum lines, M_2	Mean number of cementum lines, M_3	Number of cementum lines, M_1-M_2	Number of cementum lines, M_1-M_3
2	6,2	5,0	-	1,2	-
R7	10,8	8,8	-	2,0	-
258	6,0	5,7	-	0,3	-
B101	11,0	6,2	6,3	4,8	4,7
G30	6,5	7,0	6,0	-0,5	1,5
406	13,2	-	9,2	-	4,0
G240	11,4	-	6,0	-	5,4
261	8,4	-	8,3	-	0,1
G45	6,2	-	6,7	-	-0,5
Mean	-	-	-	1,6	2,5

hypothesis of one line per year. However, they also show the wide variation in the number of lines observed to be laid down over these essentially known time intervals. Thus skull 2 showed 6,2 lines in M_1 and 5,0 in M_2 as expected, but skull B101 had 11,0 lines in M_1 but only 6,2 in M_2.

The percentage agreement between cementum age and age by wear, including ± one year latitude, is only 36 per cent, compared to a value of 76 per cent of Spinage (1967); with ± two years latitude agreement is 74 per cent in UGR compared to 93,5 per cent in Uganda. It is believed that this low agreement is due to variation in the number of cementum lines recorded which results from uncertainty as to what constitutes an annual line in stained sections. Figure 54 shows how clearly lines can be viewed in most sections; however, annual layers are difficult to count because of splitting of lines and the presumed presence of accessory lines which may stain as strongly as annual lines (Spinage 1976). Elliott (1977) found 46,6 per cent agreement (± one year latitude) between cementum age and age by wear for waterbuck in Kenya and also noted much variation within sections.

Waterbuck in UGR have been shown to exhibit annual cementum layers as compared to biannual layers in waterbuck from Uganda, a bimodal rainfall area (Spinage 1967). This supports the hypothesis that layers are related to periods of nutritional stress which are in turn related to rainfall. Although bands can be seen clearly in stained decalcified sections, difficulties in their interpretation cause variability that makes it undesirable to adopt cementum line counts as estimates of age for individual animals. In contrast age by wear has been shown to concur with cementum age in predicting absolute age, but with much narrower confidence limits. For these reasons ages based on the age by wear classification given in Fig. 28 will be used in all future data analyses.

Growth

As an animal grows older its various body measurements increase in a fairly regular manner. When measurements are taken from a sample of variously aged individuals and plotted against age a particular type of curve is obtained. The basic shape of this growth curve has been found to be constant, typified by an initial high rate of increase, then slowing to an asymptote. A number of purely empirical mathematical expressions could be used to produce the smooth line of

Figure 54. Longitudinal section through the cementum pad of a waterbuck maxillary M_1 tooth. Cementum lines are dark staining and the cementum-dentine interface is seen at the bottom. Scale approximately x 80.

a growth curve; or a line could be fitted by eye as done by many workers. Indeed no curve need be fitted at all as advocated by Caughley (1971) who backs this decision by stating that to his knowledge no curve adequately tracks the growth of mammals. The value of curve fitting is that it allows quantification of the growth process which defines asymptote values and is convenient for comparing growth processes. Beverton and Holt (1957) suggested a curve based on the work of von Bertalanfly (1938). For linear measurements the equation takes the general form:

$$N_t = N_\infty(1 - e^{-K(t-t_0)})$$

where N_t = measurement value at age t,

N_∞ = asymptote value of measurement,

K = a constant, the coefficient of catabolism, which represents catabolism of body materials per unit mass and time,

t = age of an animal, and

t_0 = theoretical age at which an animal would have zero value of measurement.

The equation resulted from experiments on the physiology and growth of animals, where the constant K had the biochemical significance given above. As a generalisation, however, Hanks (1972) has argued well that this coefficient can have little biological meaning. The t_0 value is also seen to be artificial as the adult growth pattern is not found at the earliest ages. This equation has to be regarded as an essentially empirical one. It has been used by a number of workers including Beverton and Holt (1957), Laws and Parker (1968), Laws, Parker and Johnstone (1970), Hanks (1972) and Howells and Hanks (1975).

No attempt is made here to investigate further recent literature on growth because it is likely that for this study, and for most field studies with large mammals, measurements are not sufficiently precise to distinguish between the possible alternative relationships (Needham 1964). Spinage (1969a) used the logistic equation to describe growth in mass with age for defassa waterbuck. The basic form of the equation is:

$$N_t = \frac{N_\infty}{1 + e^{-K(t-t_0)}}$$

using notation as above. Like the von Bertalanfly equation the logistic is an exponential expression modified to produce an asymptote. They also both have two points of inflexion, the first early and positive, the second negative towards the asymptote.

In this study lines were fitted to all measurement data using the theoretical von Bertalanfly equation. In addition the logistic curve was fitted to two sets of data, horn length and horn rings, which were the two poorest fits with von Bertalanfly's equation as judged by the residual sums of squares. Curve fitting was carried out using a program developed by S.H.C. du Toit[1], on the University of Pretoria IBM 370 computer. For both equations the constants were determined via transformations of the basic equations, using three additional constants x_1, x_2 and x_3. For the von Bertalanfly equation:

$$N_t = N_\infty(1 - e^{-K(t-t_o)}) \qquad (1)$$

or $$N_t = N_\infty(1 - e^{Kt_o} \cdot (e^{-K})^t)$$

or $$N_t = e^{x_1}\left[1 - \frac{1}{(1+e^{x_2})} \cdot \left(\frac{1}{(1+e^{x_3})}\right)^t\right]$$

Using pairs of measurement-age data the program calculated the three constants x_1, x_2 and x_3. The coefficient K and the values of N_∞ and t_o necessary for fitting a curve using equation (1) were calculated as follows:

$$N_\infty = e^{x_1}$$

$$Kt_o = \log e \left(\frac{1}{(1+e^{x_2})}\right)$$

$$K = -\log e \left(\frac{1}{(1+e^{x_3})}\right)$$

$$t_o = \frac{Kt_o}{K}$$

Similar calculations were carried out with the logistic equation in the transformed state:

$$N_t = \frac{e^{x_1}}{\left(1 + \frac{1}{(1+e^{x_2})} \cdot \left(\frac{1}{(1+e^{x_3})}\right)^t\right)}$$

1. Mr S.H.C. du Toit, Statistics Department, University of Pretoria.

The ages at which asymptotic values are reached are taken as those where 97,5 per cent of the value has been attained, as done by Attwell (1977).

Growth in neck girth with age (Fig. 55)

The theoretical von Bertalanfly equation for males is:

$$N_t = 94{,}12(1 - e^{-0{,}2140(t+2{,}123)})\ \text{cm.}$$

For females the equation is:

$$N_t = 55{,}07(1 - e^{-0{,}9256(t+0{,}680)})\ \text{cm.}$$

Neck girth is the body measurement which shows the maximum difference in asymptotic value between sexes, which is presumably related to fighting in males. For males it is also the parameter that continues to increase for the longest period, probably because of the increased use of horns for fighting in older territorial animals. For defassa waterbuck Spinage (1969a) records a maximum neck girth in males of 95 cm and for females of 62 cm, compared with values of 95 cm and 60 cm in this study. The delayed attainment of asymptotic values for this measurement is reflected in Spinage's (1969a) finding that in describing allometry of size for both sexes, neck girth was the single parameter that most accurately predicted weight.

Growth in shoulder height with age (Fig. 56)

The theoretical von Bertalanfly equation for males is:

$$N_t = 124{,}23(1 - e^{-0{,}9068(t+0{,}881)})\ \text{cm.}$$

For females the equation is:

$$N_t = 115{,}13(1 - e^{-1{,}8294(t+0{,}408)})\ \text{cm.}$$

The asymptote is reached at four years in males and two years in females. Sachs (1967) working with defassa waterbuck in Serengeti gave a mean adult male shoulder height of 131,5 cm with a range from 126,0 cm to 136,0 cm. For females he recorded a mean of 123,7 cm and a range of 122,0 cm to 126,7 cm. His values came from a small

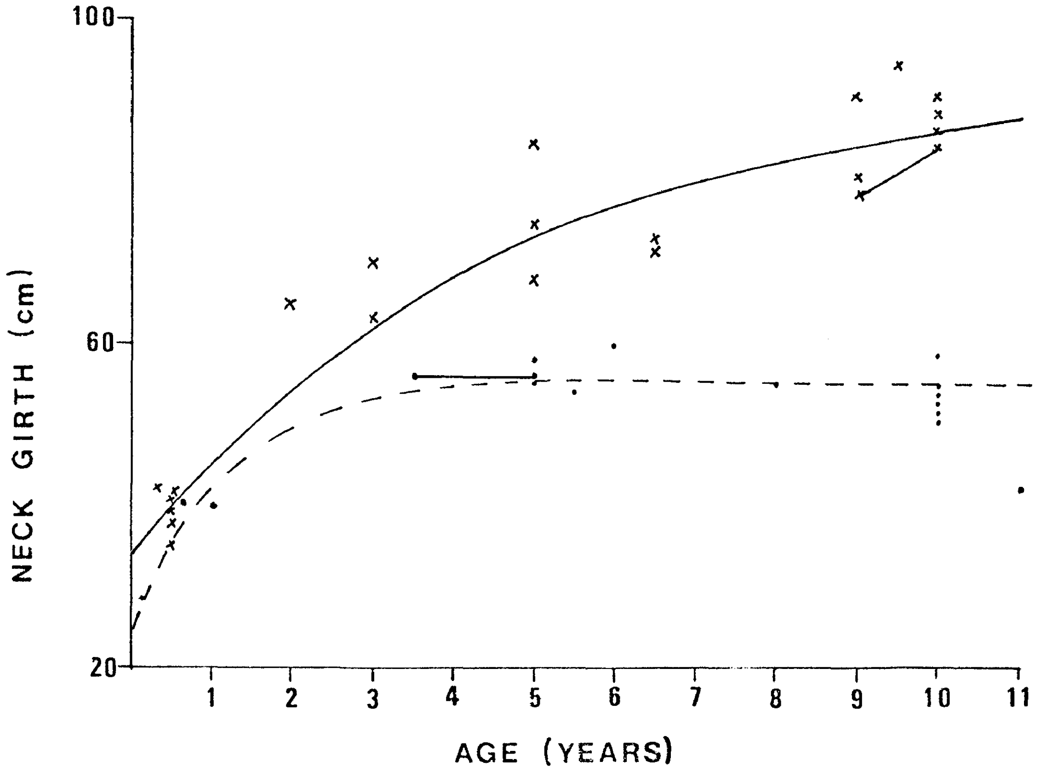


Figure 55. Theoretical von Bertalanfly growth in neck girth curves for male (—x—) and female (- • -) waterbuck, together with measurements from individual animals; see text for equations. Joined data points refer to reimmobilised individuals.

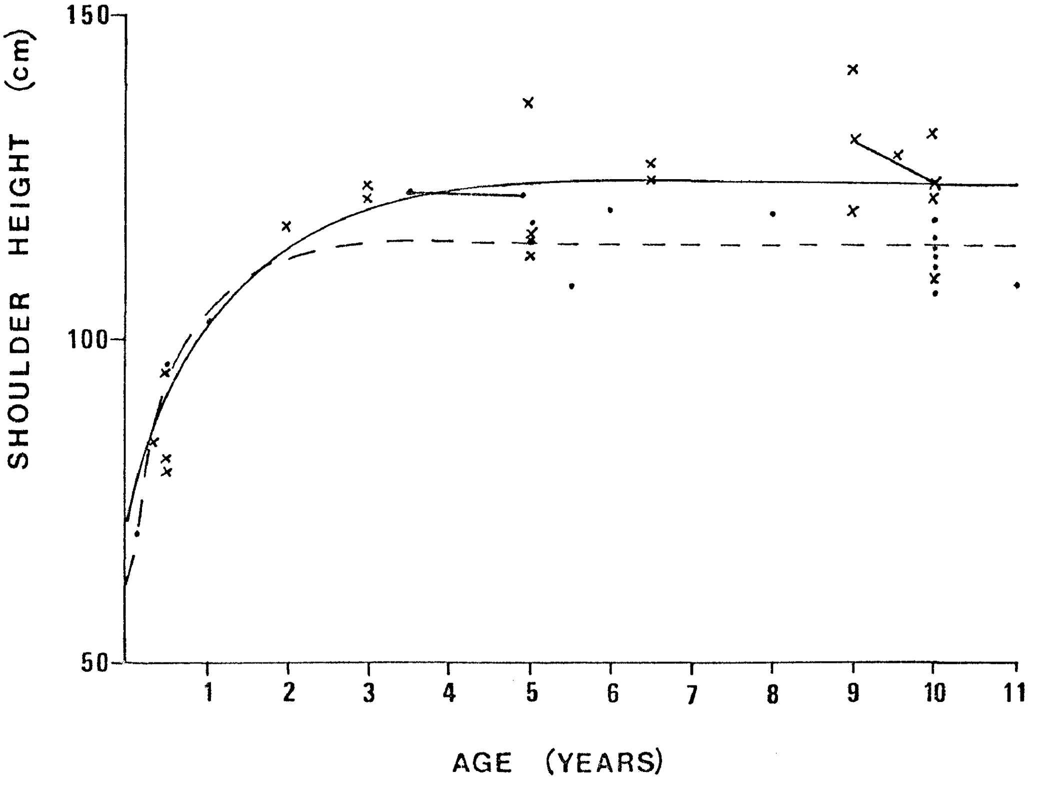


Figure 56. Theoretical von Bertalanfly growth in shoulder height curves for male (—x—) and female (–• –) waterbuck, together with measurements from individual animals; see text for equations. Joined data points refer to reimmobilised individuals.

sample size, so it is not known if Serengeti waterbuck are generally taller at the shoulder than UGR waterbuck. Hanks, Price and Wrangham (1969) gave the shoulder heights of three neonates as 63,5 cm, 62,5 cm and 61,0 cm. These heights are similar to the N_o values of 60,6 cm (females) and 68,4 cm (males) estimated here. The one month old waterbuck shown in Fig. 56 had a shoulder height of 69,0 cm.

Growth in head plus body length with age (Fig. 57)

The theoretical von Bertalanfly growth curve for males is:

$$N_t = 209,76(1 - e^{-0,3718(t+2,118)}) \text{ cm.}$$

For females the equation is:

$$N_t = 198,34(1 - e^{-0,9070(t+0,741)}) \text{ cm.}$$

The asymptote is reached at four years in females and eight years in males. Hanks *et al.* (1969) gave length measurements for three neonates of 109,5 cm, 109,5 cm, and 107,0 cm, which are similar to N_o values of 97,1 cm for females and 114,3 cm for males found here. Sachs (1967) calculated a mean adult head plus body length of 193,7 cm for males and 186,7 cm for females, with ranges of 180,5 cm to 210,0 cm and 183,0 cm to 190,5 cm respectively.

Growth in chest girth with age (Fig. 58)

The theoretical von Bertalanfly equation for males is:

$$N_t = 146,42(1 - e^{-0,6790(t+0,739)}) \text{ cm.}$$

For females the equation is:

$$N_t = 132,29(1 - e^{-0,9047(t+0,515)}) \text{ cm.}$$

The asymptote is attained at four years in females and five years in males. Sachs (1967) gave a mean male chest girth of 141,1 cm with a range of 137,0 cm to 154,0 cm, and a mean female chest girth of 129,3 cm with a range of 127,0 cm to 132,0 cm. Spinage (1969a) recorded a maximum chest girth of 151 cm in males and 158 cm in females, compared with values of 160 cm and 142 cm in this study.

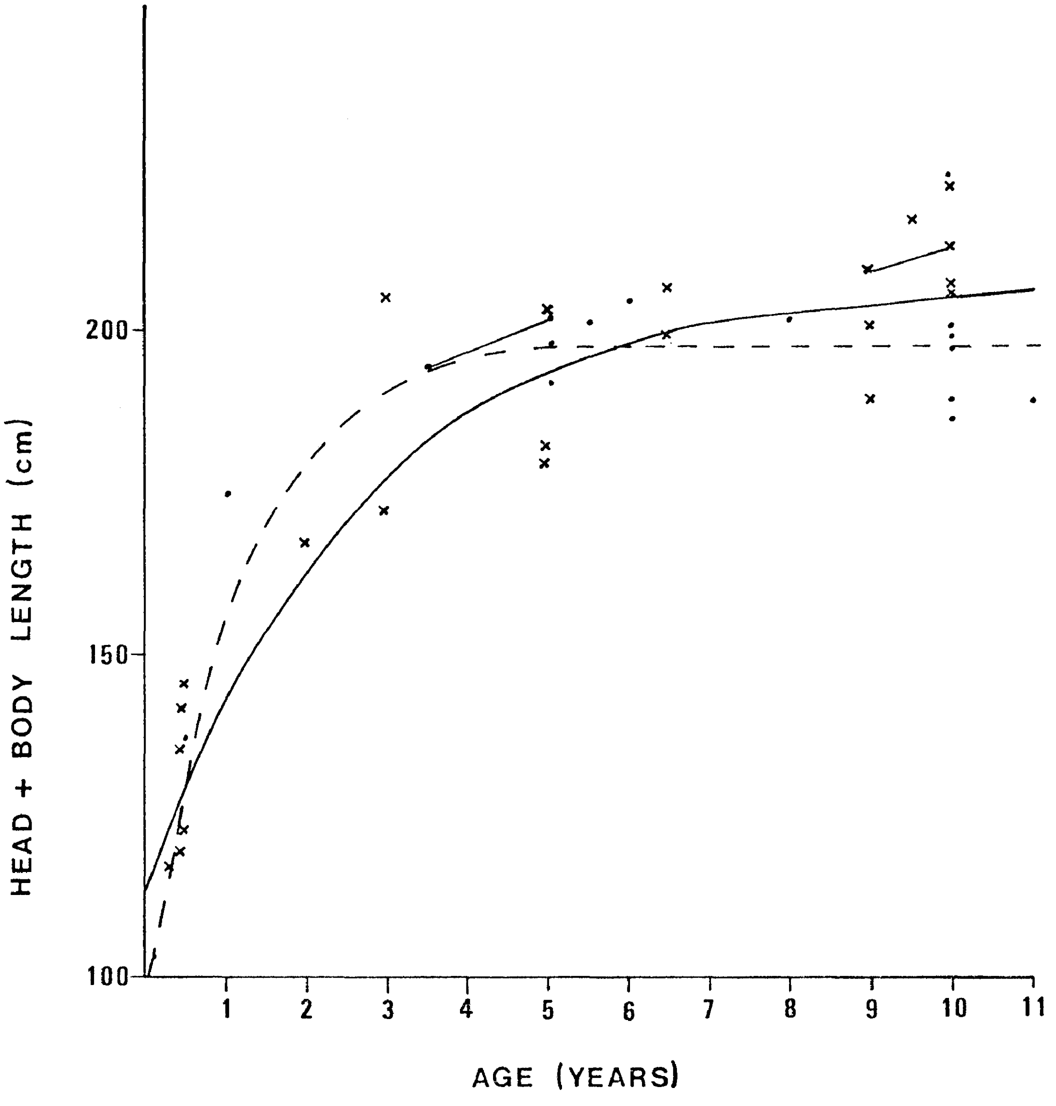


Figure 57. Theoretical von Bertalanfly growth in head plus body length curves for male (—x—) and female (– • –) waterbuck, together with measurements from individual animals; see text for equations. Joined data points refer to reimmobilised individuals.

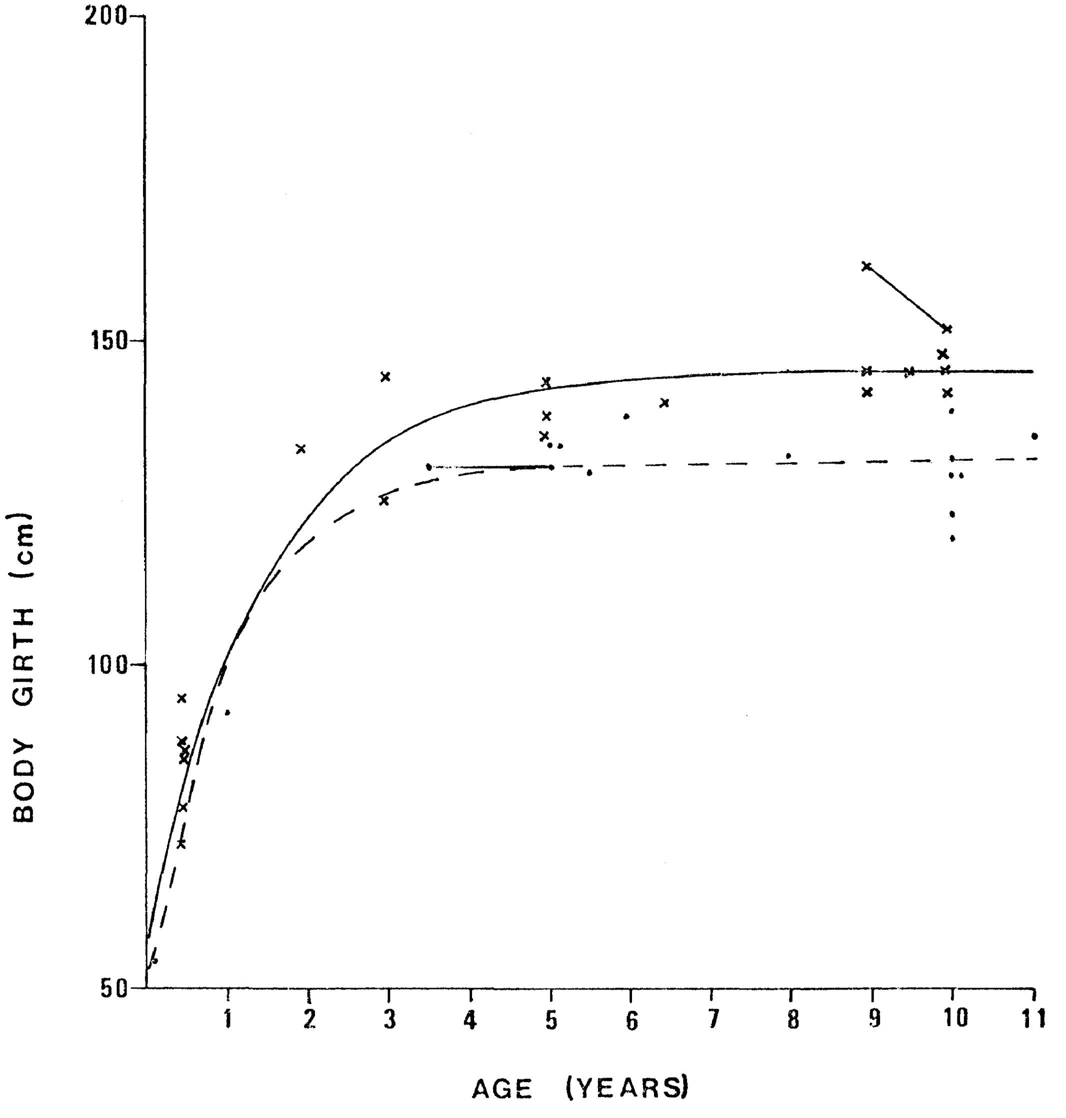


Figure 58. Theoretical von Bertalanfly growth in chest (body) girth curves for male (—x—) and female (—•—) waterbuck, together with measurements from individual animals; see text for equations. Joined data points refer to reimmobilised individuals.

Growth in horn length with age (Fig. 59)

The theoretical von Bertalanfly growth equation is:

$$N_t = 72,20(1 - e^{-0,400(t)}) \text{ cm.}$$

The asymptote is not reached until nine years but there is a wide range in length from five years on. Spinage (1967) found a wide spread in length from three years onwards and gave an asymptote of 78 cm fitted by eye to the mean value of the six year class. As an indication of the known variability in horn lengths he cited an eight year-old animal from Karamoja with a horn length of 57,5 cm. This horn length is equivalent to that of a four year-old animal in both Rwenzori National Park and UGR. He was also able to show from marking studies that horn tips wear down from as early an age as three years. Hanks *et al.* (1969) recorded lengths of 10 cm to 15 cm in one-year-olds, 28 cm in a 1,5 year-old, 31 cm in three 1,75 year-olds and 46 cm for a 2,5 year-old animal; all of which are within the range of values recorded here. Sachs (1967) gave a mean adult horn length of 66,3 cm for defassa waterbuck in Serengeti and a range of 59,2 cm to 75,0 cm. The marked animal shown in Fig. 59 to have constant horn lengths between ages nine years and 10 years is Male 2, whose tooth impressions have been mentioned above.

The goodness of curve fit given by the logistic equation was slightly better than that for the von Bertalanfly equation. The asymptote was 69,4 cm but otherwise the curves were very similar.

Growth in number of horn annuli with age (Fig. 60)

The von Bertalanfly growth equation is:

$$N_t = 26,85(1 - e^{-0,3650(t)}).$$

As with horn length, the asymptote is reached at nine years but there is much variation from five years on. The young marked male (23) shown in Fig. 60 whose rings were sampled on five occasions over two years, follows the theoretical curve well, if at slightly high values. Spinage (1967) also recorded an asymptote of 27 rings, reached at approximately eight years, but with much spread in number from four years of age on.

The logistic curve fitted to these data gave a slightly better

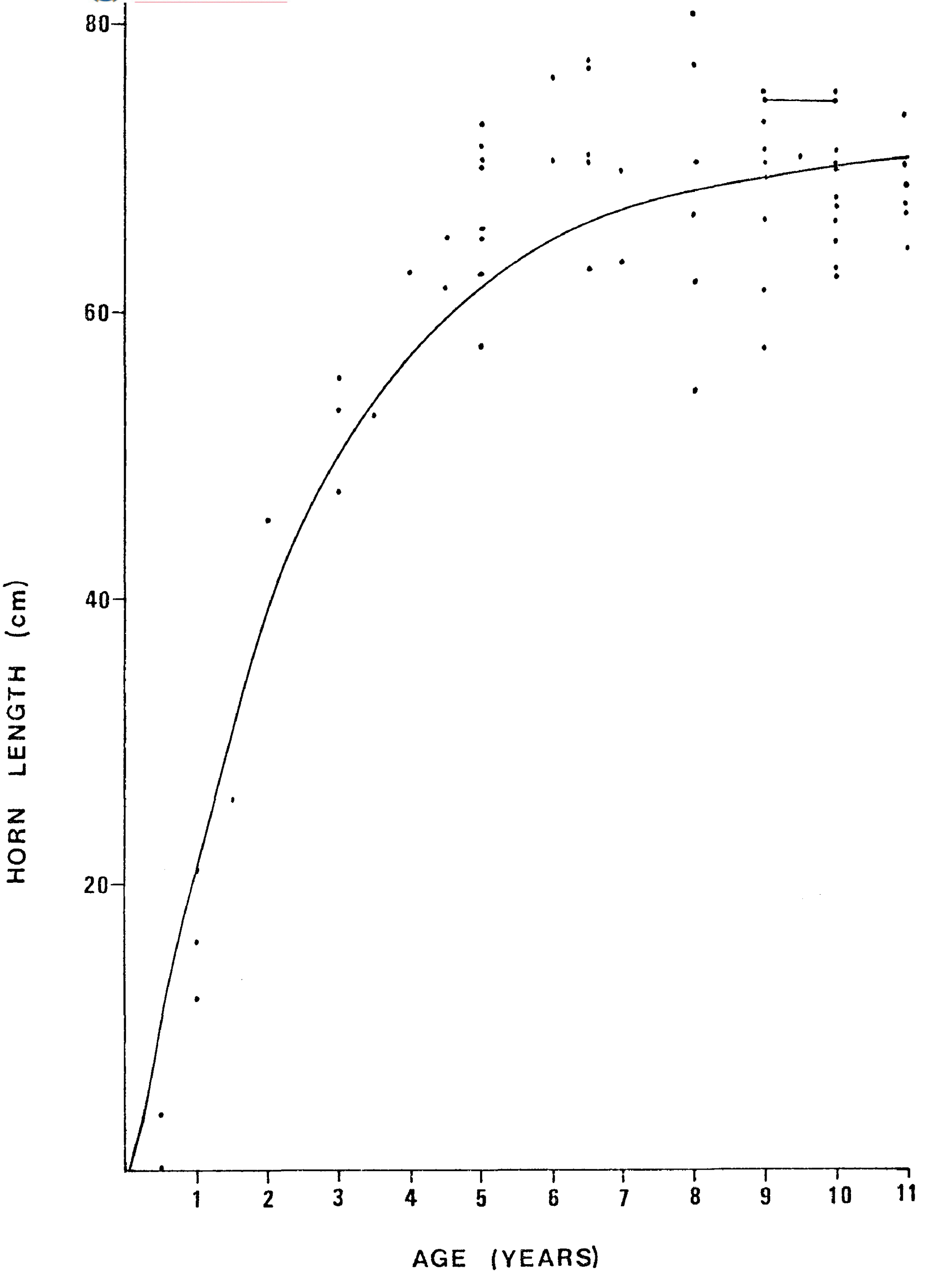


Figure 59. Theoretical von Bertalanfly growth in horn length curve for male waterbuck, together with measurements from individual animals; see text for equation. Joined data points refer to reimmobilised Male 2.

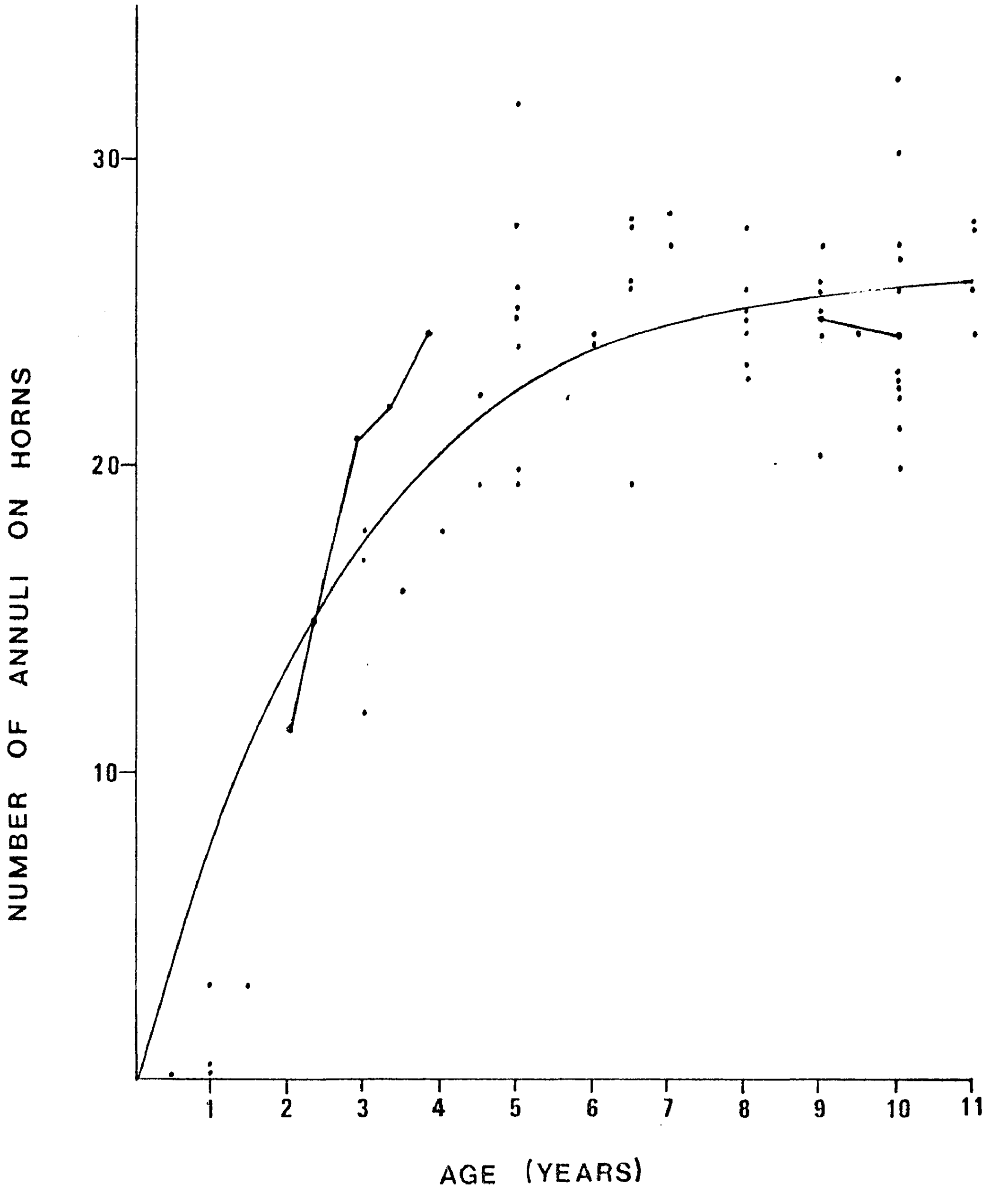


Figure 60. Theoretical von Bertalanfly growth in number of horn annuli curve for male waterbuck, together with measurements from individual animals; see text for equation. Joined data points refer to Sub-Adult Male 23 and Male 2.

fit but with the same asymptote.

Summary of growth curves

It is unfortunate that no growth equations have been published for waterbuck elsewhere and that the only detailed data given against age are for horn measurements, a parameter known to vary between areas. Information given by Spinage (1969a) allows one additional comparison to be made. He gave the mean estimated mass of four year-old males and females as 183 kg. This was calculated using an equation relating weight to neck girth and chest girth. For males the equation is:

$$\text{Mass (kg)} = -167{,}14 + (1{,}608 \;.\; \text{chest girth (cm)}) + (1{,}854 \;.\; \text{neck girth (cm)}).$$

Substituting values from Figs. 55 and 58 gives:

$$\text{Mass (kg)} = -167{,}14 + (1{,}608 \;.\; 140{,}6) + (1{,}854 \;.\; 68{,}7) = 186{,}3 \text{ kg}.$$

Substituting values from this study in the female equation gives:

$$\text{Mass (kg)} = -152{,}02 + (1{,}228 \;.\; 130{,}06) + (3{,}138 \;.\; 54{,}4) = 178{,}4 \text{ kg}.$$

Therefore the mean mass of four year-old animals in UGR is estimated as 182,4 kg, similar to Spinage's (1969a) value of 183 kg, suggesting similar body size at that age.

In general all comparative measurement data suggest that growth in size with age of UGR waterbuck is not dissimilar to that of waterbuck elsewhere. More detailed information from other areas would be necessary to confirm this, particularly for the fast growth phase in young animals.

The von Bertalanfly equation is considered, at best, to represent the growth processes of waterbuck in UGR only moderately well. However, it seems desirable that this equation should continue to be used unless a more precise general curve is described, since it allows easy comparison of growth processes. In general, its use is more beneficial when a large amount of data are available so that the precision of the constants generated can be used maximally; when this is not the case, by eye inspection can give as adequate an impression of growth as a mathematically fitted curve.

Field age classification

Waterbuck under one year old have previously been separated into two groups (Ansell 1965, Hanks *et al.* 1969, Herbert 1972). Animals whose withers are below the elbow and belly of an adult female are judged to be under one month of age and classed as infants. In UGR they also have a richer brown coat, as found by Herbert (1972) in the Sabi-Sand Game Reserve. Calves older than this but with the withers no higher than halfway between an adult female's elbow and shoulder are termed juveniles (Fig. 61). These size distinctions are based on shoulder height because it is the easiest body measurement to compare between individuals under field observation conditions. For females the asymptote in shoulder height has been shown to be reached at two years of age; because of this only two additional classes are recognised, yearlings and adults (Fig. 61). When the withers are above the halfway point on an adult female's back but distinctly below her withers, then the younger female is classed as a yearling. All other older females, that is two years old and above, are grouped together as adults. It has been possible to be definite about the absolute ages encompassed in these classes because births in UGR are centred on the late summer months, which allows yearly cohorts to be followed (see next chapter). The same is true for male field age classes, but here horn development is the main criterion.

The sexes are indistinguishable in the infant and juvenile classes until horns begin to develop in the late juvenile stage, as described by Spinage (1967). Four additional male classes can be distinguished; yearlings, two years, three years, and adults (Fig. 62). Yearlings and two year-old males are recognised from horn length alone, but in order to separate a three year-old male from an adult the number of annuli have to be counted. One year-old and two year-old males can also be classified purely on body size criteria because of the seasonality of births. Table 29 shows the number of annuli recorded from a sample of one years and two years classified by body size; records are shown separately for the first and second halves of the year. The field age classification system is simplified by assuming all animals are born in January; thus males between 1,0

Figure 61. A photograph of a juvenile waterbuck (left), a yearling female waterbuck (right) and an adult female waterbuck (centre), in the Umfolozi Game Reserve.

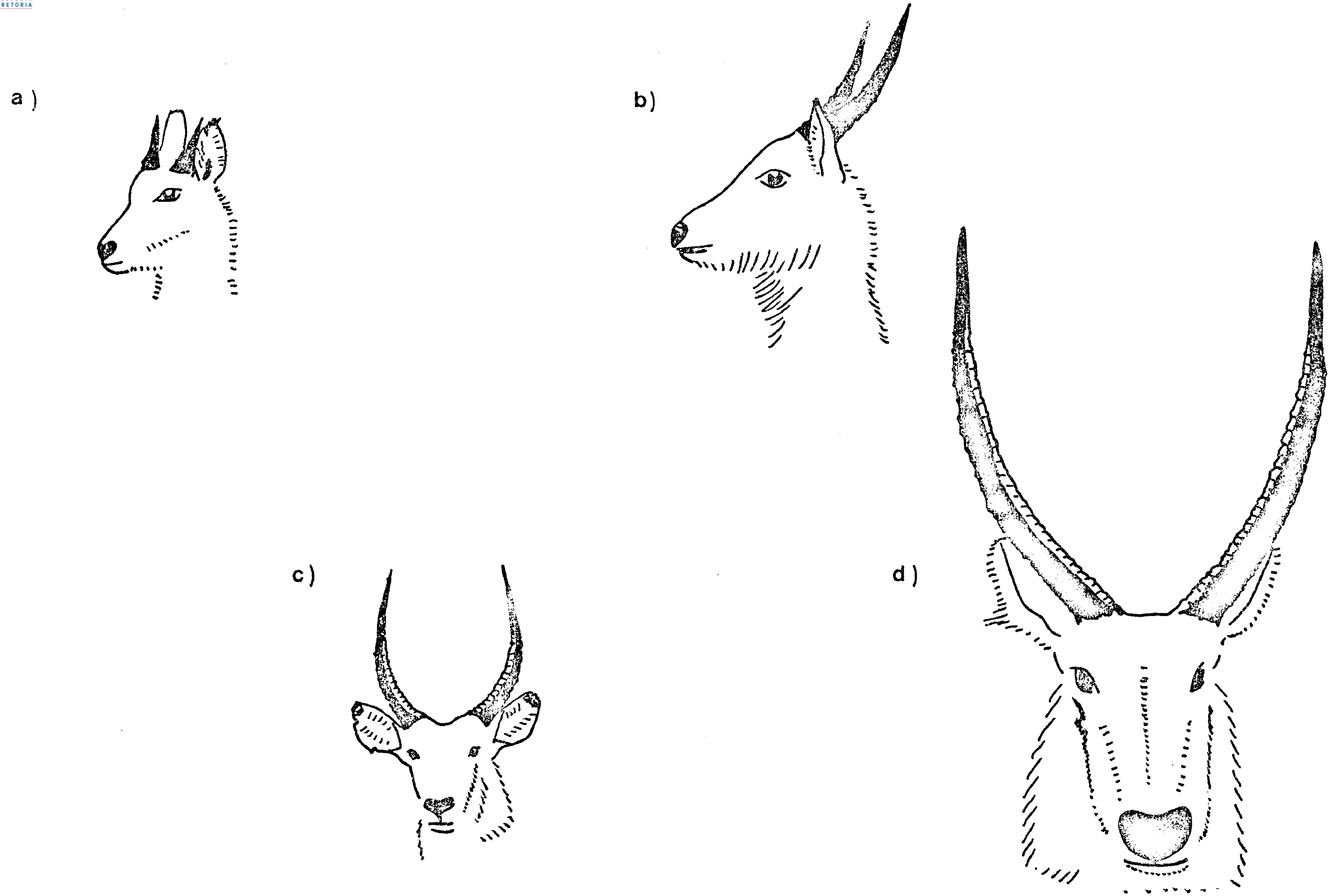


Figure 62. Line drawings of the four male waterbuck age classes taken from photographs: a) yearling, b) two year, c) three year and d) adult.

Table 29. The number of annuli on horns of sub-adult male waterbuck field classified to one or two years of age by body size.

Age (years)	Number of annuli on horns: January to June – Mean	Range	n	July to December – Mean	Range	n
1	0,5	0-1	4	5,6	3-9	13
2	7,0	6-9	4	12,4	6-19	24

and 1,5 years have a mean of 0,5 rings, from 1,5 to 2,0 years the mean is 5,6 rings, from 2,0 to 2,5 years the mean is 7,4 rings and from 2,5 to 3,0 years it is 12,4 rings. These results agree closely with those given by the theoretical von Bertalanfly equation, where age determination was based on tooth replacement and attrition.

CONCLUSION

Although cementum lines in the teeth of Umfolozi waterbuck were clearly visible in stained decalcified sections and a basic annual pattern has been established, difficulty in interpretation and hence counting of lines made this method too variable for determining the age of individuals. It is possible that known age material may have allowed more precise use of cementum lines, but this is not necessarily so. Since the age by wear method agrees with mean age predictions from cementum line counts and with much narrower confidence limits, ages based on the wear method are used in all further data analyses. The validity of wear criteria has been further verified by the use of tooth impressions obtained from two reimmobilised animals.

The comparison of growth curves for Umfolozi waterbuck with measurement data for waterbuck elsewhere suggests similar growth rates and asymptotes, although more detailed information is necessary to confirm this, especially for the younger age classes. All waterbuck observed in the field were classified as follows. Animals less than one year were classed as either infants or juveniles with sex undetermined. Females were further split into yearlings and adults. Males were classed as yearlings, two-year-olds, three-year-olds and adults; the three-year-olds not always being differentiated from adults owing to the necessity of counting annuli, which is difficult under field conditions.

CHAPTER 5

POPULATION STRUCTURE

INTRODUCTION

Knowledge of population structure in terms of sex and age of individuals is vital to an understanding of population dynamics. A detailed age-specific mortality schedule is necessary to calculate many statistics which have importance in this field; they include the reproductive value of each age class, the population's rate of increase, mean life expectancy at birth, mean generation length, and the percentage of the population that dies each year (Caughley 1966). In this chapter the goal is to describe mortality of Umfolozi waterbuck in order to identify those areas of mortality critical in influencing the instantaneous rate of increase (r) of the population. The mortality schedule will be given in the convenient format of a life table. In this way the age-specific reasons for the decline in density discussed in Chapter 3 can be investigated.

Data needed for this analysis come from two main areas. First, field age classification of individuals allows recruitment to the sub-adult segment of the population to be followed. Second, a sample of skulls from animals dying in the reserve form the basis of an age-specific mortality schedule for animals of one year and older. Animals under one year cannot be included as the fragility of their skulls results in gross under-representation in the skull sample. An additional estimate of population age structure comes from tooth impressions taken from immobilised animals. Details of group size and group structure are given later in Chapter 7, where they are discussed in relation to movement and behaviour.

METHODS

Population structure from field observations

Monthly samples of waterbuck separated into the field age classes given in the last chapter came from two sources; a record of all animals observed in the main study area and the maximum number seen density estimate (maximum number estimate). The majority of sightings making up all records come from observation procedures which involve coverage of the whole study area, either on foot (the ground census) or by Landrover (King's census), and are therefore representative of the whole population. The maximum number estimate also covers the whole population as it is a single density figure for the main study area broken down by sex and age. Details of these methods have already been given in Chapter 3.

The skull sample

All skulls referred to below are from individuals of estimated age one year and above. During 1976 and 1977, 59 such skulls were recovered from waterbuck carcasses in UGR. Over this period a number of skulls were also collected where the date of death was estimated as between 1974 and 1975 based on the degree of weathering. In addition some skulls of animals dying during 1974-1975 were already available having been collected by NPB staff, making a total of 36 for this earlier period. Skulls were assigned to year classes using tooth wear criteria as described in Chapter 4.

Tooth impressions

During 1976 and 1977, 23 waterbuck aged two years and above were immobilised and tooth impressions taken. Immobilisation procedures and the method of taking tooth impressions are given in Chapters 7 and 4 respectively. Only individuals aged two years and above could be considered for producing an estimate of age structure as those younger than this were selected against during darting from a helicopter.

RESULTS AND DISCUSSION

Population structure from field observations

The monthly population structures of the main study area waterbuck population are given in Tables 30 and 31, based on records of all animals observed and the maximum number estimate. These tables form the basis of the data analyses given below.

Sex ratios

The sex ratio of animals aged one year and older expressed as the number of females per male is shown monthly in Fig. 63 based on all sighting records. The male to female raio over the whole period

Table 30. Age structure of the study area waterbuck population based on field age classification and records of all animals seen.

Month	Adult males	3 yr males	2 yr males	1 yr males	Adult females	1 yr females	Juven-iles	In-fants	Sample size
1976									
Feb	17	0	0	0	45	0	3	-*	66
Mar	33	0	2	6	130	14	8	-*	193
Apr	53	0	29	21	139	16	20	-*	278
May	61	2	5	26	128	11	48	-*	281
Jun	31	0	14	18	82	4	36	0	185
Jul	56	2	12	17	170	27	44	3	331
Aug	56	3	4	14	101	8	33	0	219
Sep	44	1	13	12	73	10	20	0	173
Oct	74	2	28	83	330	11	35	0	572
Nov	87	2	26	60	325	11	51	0	562
Dec	52	3	22	33	355	7	27	2	499
1977									
Jan	59	0	30	17	267	18	2	5	398
Feb	62	2	43	13	193	4	33	6	356
Mar	59	2	23	9	168	10	22	9	302
Apr	22	1	2	0	52	1	15	0	77
May	49	4	10	13	83	7	28	2	196
Jun	34	1	8	3	75	10	25	2	158
Jul	24	1	9	5	71	5	22	0	137
Aug	12	0	0	1	65	0	7	0	85
Sep	37	2	1	3	125	6	20	0	174
Oct	107	1	28	2	546	5	51	0	740
Nov	42	1	9	5	203	7	16	0	283
Dec	43	0	5	6	184	2	10	0	250
1978									
Jan	12	1	0	1	55	5	0	0	74
Mar	18	7	4	3	42	2	1	3	80
									6 369

* Infants were not separated from juveniles until June 1976.

Table 31. Age structure of the study area waterbuck population based on field age classification and the maximum number seen density estimate.

Month	Adult males	3 yr males	2 yr males	1 yr males	Adult females	1 yr females	Juven-iles	In-fants
1976								
May	22	2	7	8	68	9	18	0
Jul	25	2	7	8	54	9	16	1
Aug	20	2	2	7	32	6	8	0
Sep	15	1	4	3	22	6	7	0
Oct	14	2	9	8	59	7	9	0
Nov	17	2	6	7	65	3	10	0
Dec	14	3	9	8	63	3	8	1
1977								
Jan	16	2	6	5	63	7	1	4
Mar	22	3	7	4	45	5	4	8
Apr	15	0	2	0	33	1	8	0
May	16	2	5	4	32	5	9	1
Jun	14	1	7	1	37	3	9	0
Jul	15	1	4	2	28	1	8	0
Sep	13	2	1	2	29	3	3	0
Oct	21	0	7	2	61	4	14	0
Nov	18	0	4	3	63	2	10	0
Dec	15	0	6	4	54	3	7	0

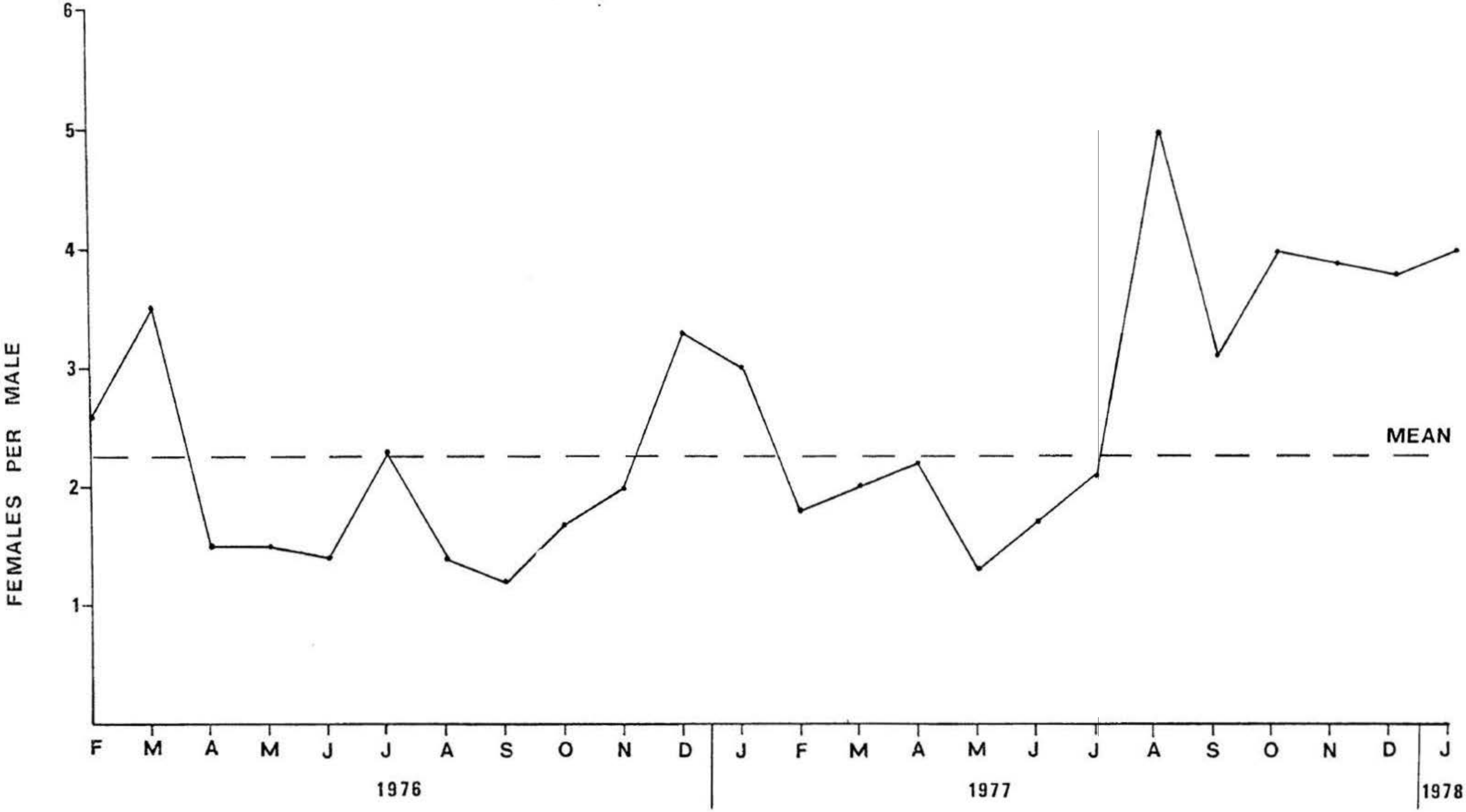


Figure 63. The sex ratio of waterbuck aged one year and older based on all sighting records during the study period.

was 1:2,24 (n=6 020). Similar data from the maximum number estimate are given in Fig. 64; here the overall raio was estimated as 1:1,82. Both sets of results show a similar variation in the proportion of females by month, with higher values during summer months, when the overall population density was higher (see Chapter 3). A regression of females per male from all sightings on the maximum number density estimate is positive and significant (Y=0,88+0,02x, n=17, r=0,48, $0,01 < P < 0,05$). The likely reason for this, a movement of females away from the study area during winter, is discussed in Chapter 7.

The male to female ratios calculated here are within the range of sex ratios given for common and defassa waterbuck elsewhere. Bourliere and Verschuren (1960) gave ratios between 1:2,3 and 1:4,6 for Zairean populations. Dasmann and Mossman (1962a) calculated ratios of 1:3,23, 1:0,92, 1:1,41, 1:2,50 and 1:2,66 for five populations in Rhodesia. Estimates for populations in Zambia include ratios of 1:0,9 (Dowsett 1966), 1:1,2 (deVos and Dowsett 1966) and 1:1 (Hanks *et al.* 1969). Foster and Kearney (1967) gave a ratio of 1:1,82 for Nairobi National Park Kenya, while Kutilek's (1974) data suggest one of 1:3,32 for Lake Nakuru National Park, Kenya. Spinage (1970) lists ratios between 1:0,5 and 1:4,3 for different subpopulations in Uganda. Herbert (1972) gave a ratio of 1:1,0 for 1967 and 1:1,7 for 1968 for waterbuck in the Sabi-Sand Reserve. A previous estimate for UGR waterbuck comes from Mentis (1970) who calculated a ratio of 1:1,5 from NPB records of animals shot during the anti-nagana campaign.

No obvious relationship is seen when these sex ratios are compared with waterbuck density in the same areas (see Chapter 3). Spinage (1970) concluded that in Uganda waterbuck density was independent of the sex ratio. However, he recorded that within a population females did tend to outnumber males more at high densities because of different movement patterns between the sexes, as has been found with Umfolozi waterbuck.

The sex ratio of one year-old waterbuck is considered to be 1:1 in UGR. The maximum number estimate produced a male to female (one year) ratio over the whole period of 1:0,97. During 1977 all sighting records show a ratio of 1:1,0. However, during 1976 the ratio was 1:0,41, resulting in a total period ratio of 1:0,54 (n=572, χ^2=50,6, $P < 0,005$). It is probable that this significant departure from 1:1 results from either immigration of one year males during 1976 or over-representative sampling caused by their movement patterns.

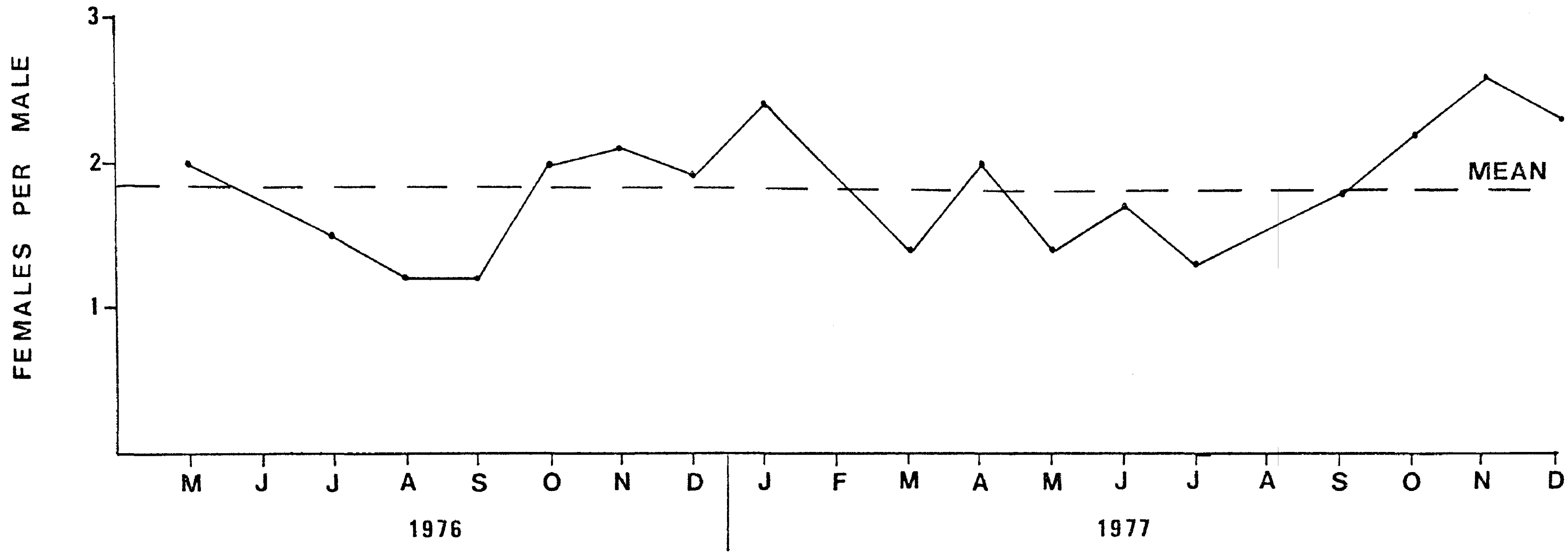


Figure 64. The sex ratio of waterbuck aged one year and older based on the maximum number estimate in the main study area.

Umfolozi waterbuck are likely similar to Uganda waterbuck, and indeed the majority of mammals, in having a 1:1 sex ratio at birth (Spinage 1969b, Caughley 1977). This means that the observed adult sex ratio results from a higher rate of male mortality beginning after one year of age.

Seasonality of births

The frequency of occurrence of infants in the UGR waterbuck population indicates that calving occurs between December and July, but with a definite peak during February and March (Fig. 65). The lack of sightings during April 1976 is probably because of the small sample size for that month (Table 30). Given that the gestation period in both defassa and common waterbuck is approximately eight months (Kenneth and Richie 1953, Dekeyser 1955, Spector 1956), this means that conceptions occur during the winter months with a peak during June and July.

Post-mortem examinations were carried out on only two adult female carcasses, both of which resulted from death during immobilisation on 6 June 1976. Each was pregnant; Female 14 was 10 years old and carrying a 1,0 g foetus, Female 16 was 5,5 years old and had a 0,1 g foetus. These two foetuses were calculated to be approximately four and six weeks old respectively, using the relationship between gestation period and foetal weight given by Spinage (1969b), based on the method of Huggett and Widdas (1951). This indicates that the conceptions occurred during April and May, with expected birth dates in December and January, which agrees with the observed seasonality of calving.

Not all records of waterbuck calving in other areas have shown them to be seasonal, but when seasonality is indicated it follows the same pattern as found here of births occurring during wet months. Spinage (1969b) calculated conception dates and expected birth dates for 72 foetuses taken from a female shot sample in Uganda, using the method described above. Births were predicted to occur throughout the year but with two peaks that coincided with the two wet seasons and a distinct decline over the June-July dry season. His observations of newborn calves supported this pattern. Elliott (1977) found births to occur throughout the year in Kenya. In Zambia, Ansell (1960) recorded births between May and August and mating observations

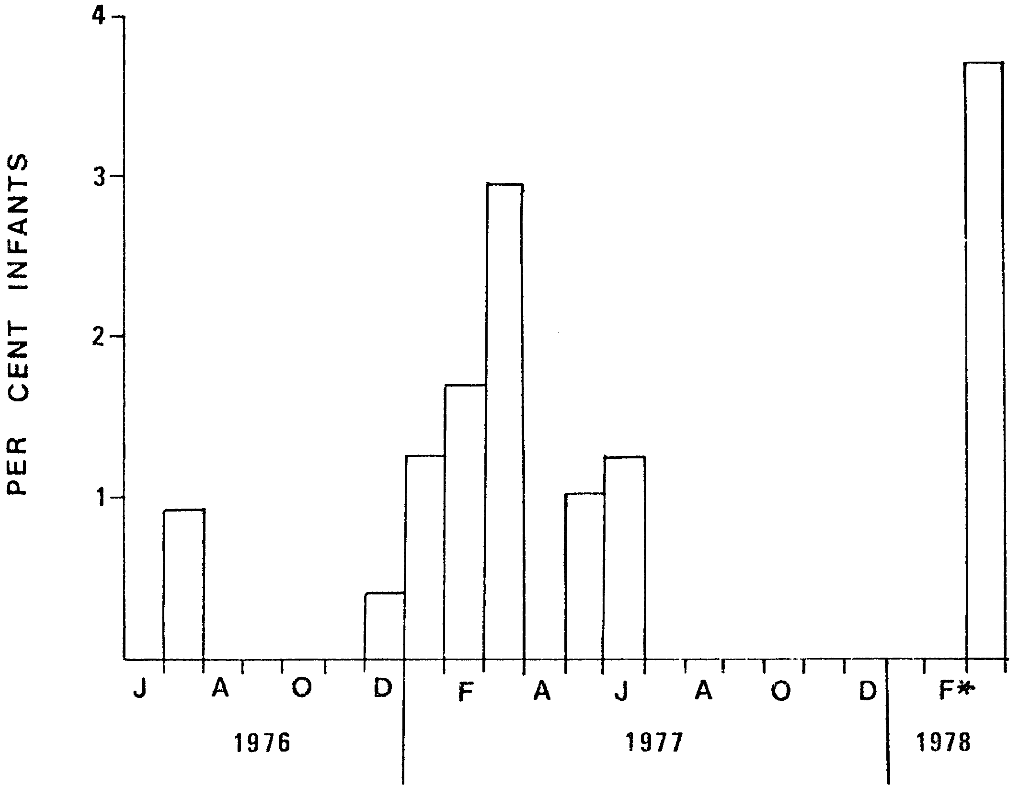


Figure 65. Seasonality of waterbuck births in the Umfolozi Game Reserve as shown by percentage infants in the population, based on all sighting records during the study period; "*" denotes no sample taken.

suggested births during February and April. He concluded that births occurred year round, but his sample was small and the results inconclusive. Hanks *et al.* (1969) found a definite calving season in Kafue National Park, Zambia, centred on the height of the rains. In both the 1965-1966 and 1966-1967 seasons a birth pulse was seen in January, with a spread of births between November and April during the earlier season, and between November and June during the latter. Over one year of observations in Rhodesia, Dasmann and Mossman (1962b) recorded neonates only between February and April. For the Kruger National Park Pienaar (1963) reported that calving occurred throughout the year except for the dry winter months and Fairall (1968) described a similar long birth season but with an increase from mid-January to mid-March. Herbert (1972) believed calving to occur through the year with no peak in the Sabi-Sand Reserve, as did Child and von Richter (1969) for Botswana.

Umfolozi waterbuck fit into a general pattern of waterbuck showing some degree of seasonality of births which are centred on the one or two annual wet seasons. It is possible that the records of no seasonality result from inadequate sampling.

Spinage (1969b) reviewed some of the proximate factors that could cause seasonality of births in Uganda waterbuck and suggested temperature as a possible factor since low mean maximum temperatures correlated with periods when conception was lowest. In order to define accurately causal relations, an in depth study would have to be carried out which examined all possible factors, including photoperiod, rainfall, nutrition, lunar variations and temperature. Sadlier (1969) gives a good review of the problems involved in such work. Whatever the cause of seasonality of births, the result in UGR is for late gestation, births and early lactation to occur during wet months when grass quality is maximal (see Chapter 9). This is expected to favour the condition of the mother and therefore the young calf.

Recruitment to the sub-adult population

Field age classification allowed the survival of three year classes of waterbuck to be followed. These were individuals under one year, which include infants and juveniles and will be termed calves; one year-old males and females, and two year-old males.

Three year-old males are not included as it has already been described how they cannot always be classified separately from adults under field conditions.

The survival of calves from the 1976 and 1977 birth seasons are shown in Figs. 66 and 67 based on all sighting records and the maximum number estimate. For the three sets of results covering a complete year the number of calves per 100 adult females reached a peak in May before declining as calf mortality began to excede births. The highest fraction of calves calculated from the maximum number estimate is lower than that from all sightings, but calf survival at year's end is higher, being approximately 19 calves per 100 females in 1976 and 14 per 100 in 1977. The same figures from all sighting records are 12 calves per 100 females for each season. Spinage (1970) gave the number of calves per 100 females as a yearly mean for each of four years for waterbuck in Uganda. Discounting the first year's results which he believed invalid, the numbers were 47,6, 52,6 and 43,5 calves per 100 females. Equivalent results from this study for 1976 and 1977 are 17,6 and 13,5 from all sighting records and 21,2 and 19,3 from the maximum number estimate. Even taking into account that the Uganda population was virtually continuously breeding, this comparison suggests either low fertility, low calf survival or both in the Umfolozi population. Similarly low numbers of calves were reported by Elliott (1977) working with a declining population of waterbuck in a newly fenced area in Kenya; she recorded between nine and 20 calves per 100 females in a main study area.

For all sighting records the highest number of calves per 100 females represents 13,7 per cent of the total population in 1976 and 13,6 per cent in 1977. The same results from the maximum number estimate are 19,5 per cent for both years; for both methods these percentages are well below 10 per cent by the end of the year. Dasmann and Mossman (1962a) gave percentages of calves for three areas of Rhodesia as 22 per cent, 32 per cent and 37 per cent. Hanks *et al.* (1969) described a local population consisting of 27,5 per cent young of the year in Zambia. De Vos and Dowsett (1966) observed 15,3 per cent calves between July and October in the Luangwa Game Reserve, Zambia. Herbert (1972) recorded only 7,0 per cent calves in the Sabi-Sand Reserve but believed this an underestimate owing to sighting difficulties. Therefore even the maximum percentage of calves found in UGR compares poorly with records from other areas.

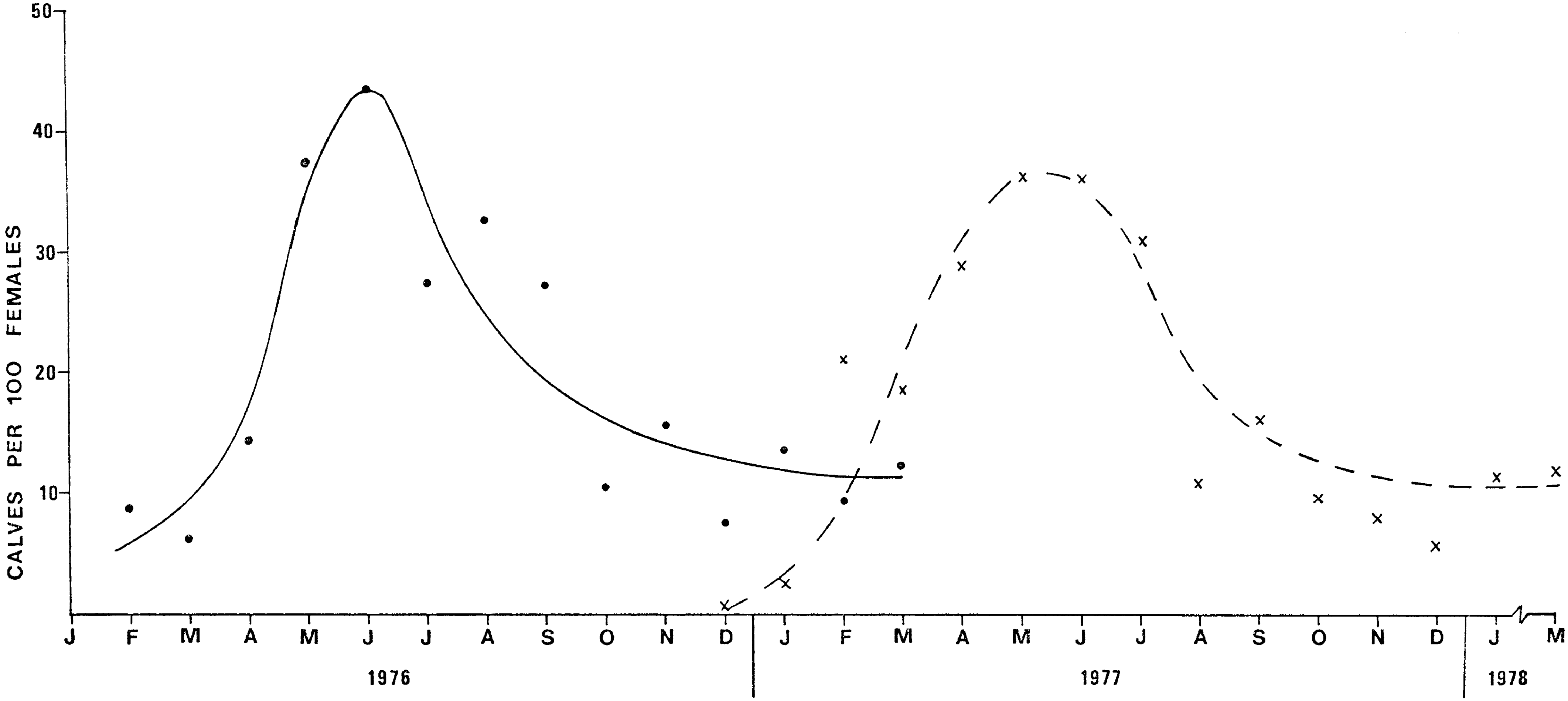


Figure 66. Changes in the proportions of the 1976 (—•—) and 1977 (– x –) year groups of waterbuck calves in the Umfolozi Game Reserve, based on all sighting records during the study period.

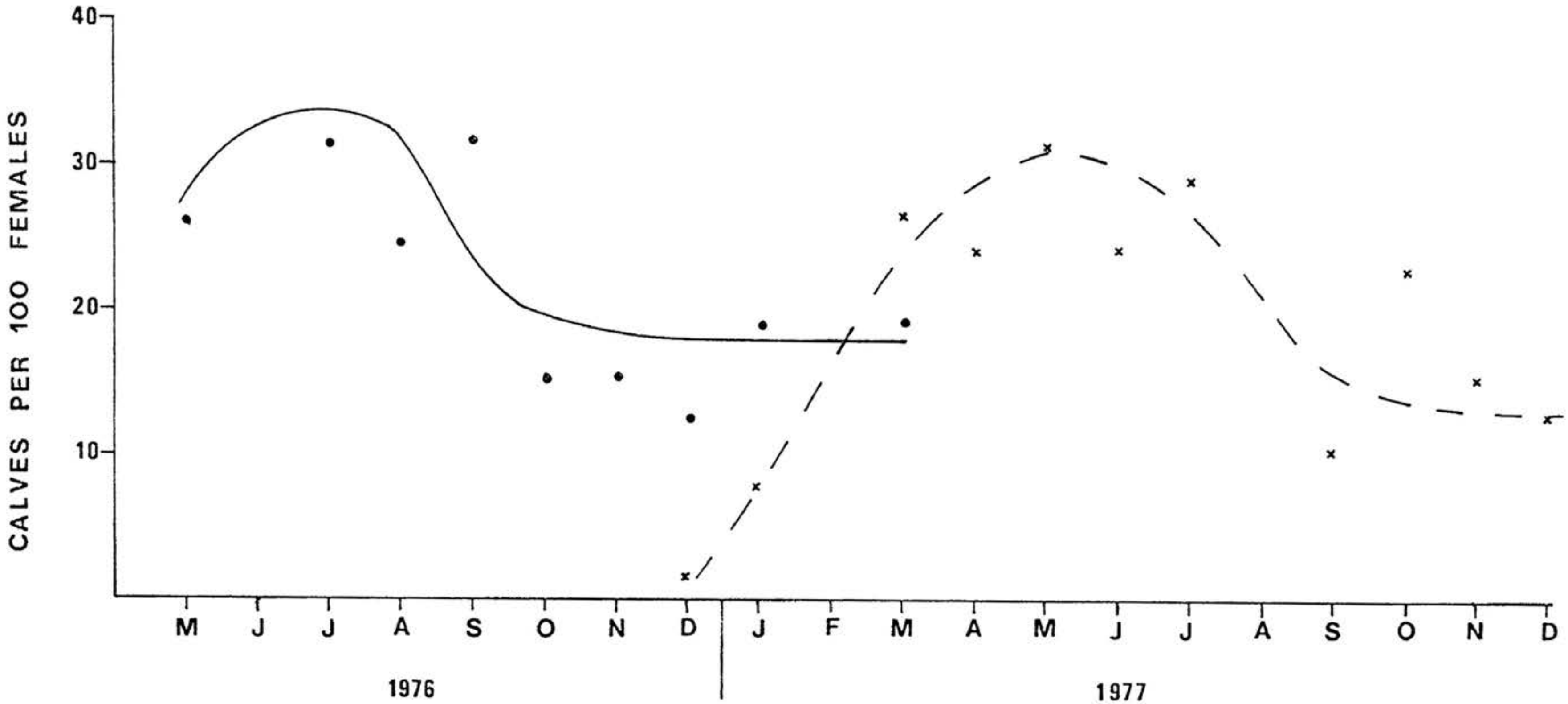


Figure 67. Changes in the proportions of the 1976 (—•—) and 1977 (—x—) year groups of waterbuck calves in the Umfolozi Game Reserve, based on the maximum number estimate in the main study area.

Calf mortality in UGR can be more precisely defined by using the method of Richards and Waloff (1954) to predict the number of calves entering the population each year. This method has been subsequently used by Sinclair (1974a) for buffalo in Serengeti. Knowing this fertility value and also the number of calves per 100 females surviving to one year of age means that first year mortality can be calculated.

The logarithm to base 10 ($\log_{10}$) of the number of calves per 100 females is plotted against time in Figs. 68 and 69 for the months when this proportion is declining after a maximum value. This analysis is shown for results from both age structure sampling methods for 1976 and 1977. For each graph a regression of log proportion calves is calculated and projected back to the month when the first young of the season was observed, which was January 1976 for the 1976 calving season and late December 1976 for the 1977 season. The log proportions read off for these months are the log proportions of adult females calving. Results from all sighting records produce fertility estimates for 1976 and 1977 of $\log_{10}$ 2,01 or 102,3 per cent and $\log_{10}$ 1,97 or 93,3 per cent. Equivalent results from the maximum number estimate are $\log_{10}$ 1,81 or 64,6 per cent and $\log_{10}$ 1,76 or 57,5 per cent. First year per cent survival estimates are obtained by dividing the number of calves per 100 females that survive after one year by the appropriate fertility estimate and multiplying by 100. Per cent mortality then equals 1 - per cent survival.

Using records of all sightings in 1976:

Calves per 100 females surviving to 1 year	= 11,8
Calves per 100 females born in 1976	=102,3
Calf mortality	= 88,5%

Using records of all sightings in 1977:

Calves per 100 females surviving to 1 year	= 11,5
Calves per 100 females born in 1977	= 93,3
Calf mortality	= 87,7%

Using the maximum number estimate in 1976:

Calves per 100 females surviving to 1 year	= 19,0
Calves per 100 females born in 1976	= 64,6
Calf mortality	= 71,6%

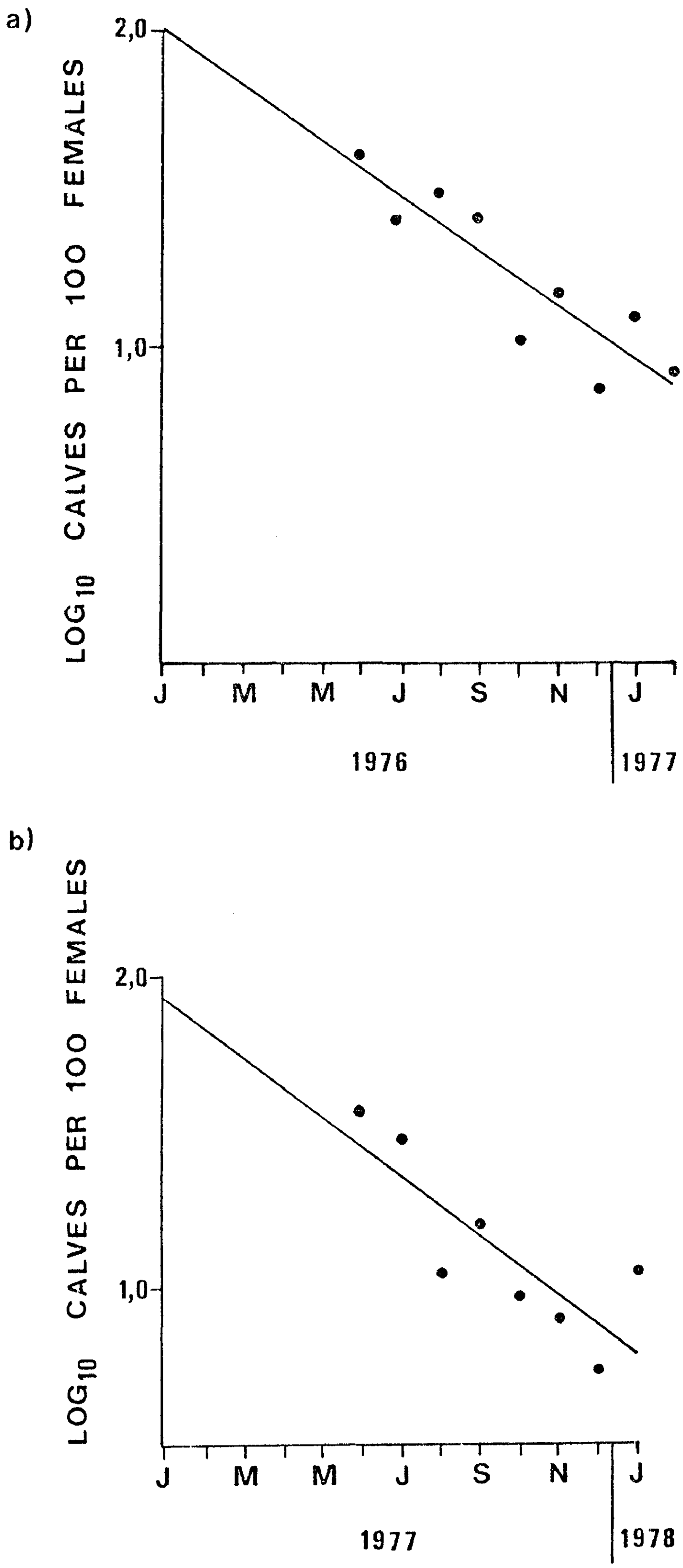


Figure 68. Fertility estimation for Umfolozi waterbuck using all sighting records during a) 1976 and b) 1977. See text for explanation of method.

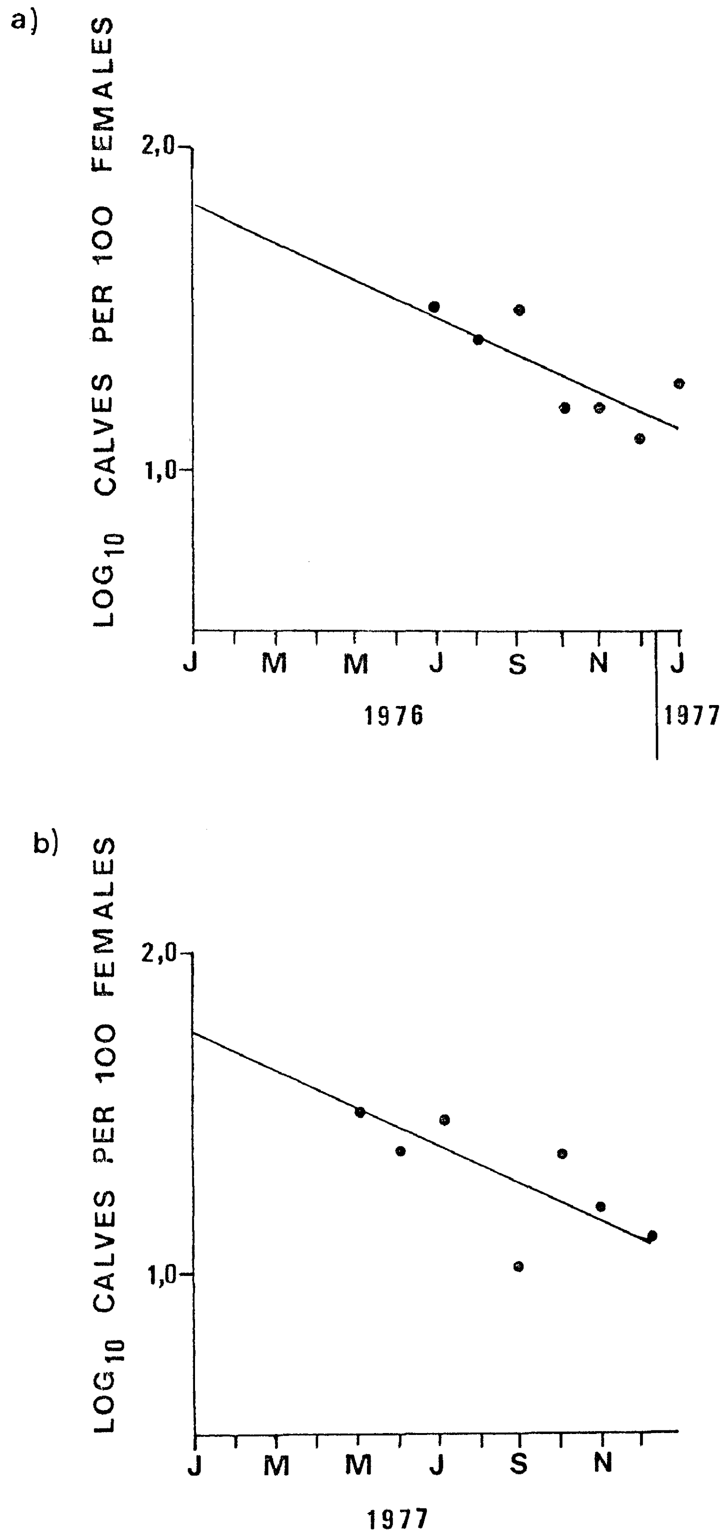


Figure 69. Fertility estimation for Umfolozi waterbuck using the maximum number estimate in the main study area during a) 1976 and b) 1977. See text for explanation of method.

Using the maximum number estimate in 1977:

Calves per 100 females surviving to 1 year	= 14,5
Calves per 100 females born in 1977	= 57,5
Calf mortality	= 74,8%

Both methods show constant poor calf survival for each year. Combining all four estimates produces a mean first year mortality figure of 80,7 per cent. Spinage (1970) working with a stable density waterbuck population calculated first year mortality to be approximately 50 per cent by using three independent methods. Elliott (1977) working with a declining waterbuck population calculated calf mortality from two sets of observation data and gave estimates of 73,2 per cent and 80,4 per cent. The importance of first year mortality in affecting the rate of increase of the UGR waterbuck population is explored below by the construction of life tables.

The survival of one year-old males and females and two year-old males is given in Table 32 for 1976 and 1977, as shown by both sampling methods. Results from the maximum number estimate are the most consistent and indicate no mortality of two year-old males, but a drop in one-year-olds equivalent to about four per cent of the adult (one year +) population each year. Since the maximum number seen density estimate actually declined each year this represents 35 to 40 per cent mortality of one-year-olds. Records of all sightings do not concur with this. A decline of one-year-olds is indicated for only one year and two year-old males are shown to decline throughout each year. It is considered unlikely that these results approximate acutal survival rates, rather they suggest that either movement of young animals occurred, or that the habitat utilization pattern of sub-adults caused variability in sampling efficiency through the year; two processes already suggested as the cause of anomalous sub-adult sex ratios. It is probable that both processes did occur; the latter is supported by the finding in Chapter 8 that sub-adult males show the most varied habitat associations of all age-sex classes.

The results for survival of one-year-olds and two-year-olds are therefore equivocal. Those of the maximum number estimate are possibly less subject to error and may reflect survival the best by indicating considerably reduced mortality in two-year-olds as compared to one-year-olds.

Table 32. Survival of one year-old males and females and two year-old male waterbuck in the main study area.

	Per cent of one year + population comprised of two sub-adult groups			
	All sighting records		Maximum number estimate	
	One-year-olds	Two year-old males	One-year-olds	Two year-old males
Begin 1976	12,6	12,0	14,7	6,0
End 1976	13,5	7,0	11,0	9,0
Begin 1977	7,3	9,8	12,1	6,1
End 1977	2,3	3,5	8,6	7,3
Begin 1978	7,3	2,7	-	-

The skull sample

The sex ratio of skulls

The skull sample for 1976-1977 had a ratio of females to males of 1:1,68, the same figure for the 1974-1975 sample was 1:8,0. The preponderance of male skulls in the older sample suggests that they may be sturdier to weathering and scavenger attack than female skulls.

Age-specific mortality and life tables

As was mentioned in the introduction to this chapter, the most convenient format in which to present an age-specific mortality schedule is the life table. There are a number of ways a life table can be constructed since any one column can be used to calculate all others, no new information being required. In this study the ages at death of 70 males and 25 females have been recorded for animals dying in UGR between 1974 and 1977. Caughley (1966) considered a sample of 50 ages at death or 150 ages of living animals to be minimal for life table construction. It is therefore not possible to construct a valid separate female life table, but a contingency table shows that this is not important since there is no significant difference in the age distributions of male and female skulls (Table 33).

By convention a life table is presented as a cohort of animals born simultaneously (the kl_x column) that are progressively reduced by age-specific mortality (the kd_x column). A population must fulfil two criteria for a life table to be valid; its density must be stable in time or have a uniform known rate of change and the age distribution must be stationary (Caughley 1977). It is doubtful if both of these assumptions are often completely fulfilled by wildlife results, but even so life tables constructed from such data still give a valid interpretation of an overall mortality pattern (Caughley and Birch 1971, Spinage 1972).

Caughley (1977) described how the normal method of life table formation with r equal to zero is only a special case of construction using any known r value. For age at death data the frequencies of ages at death (f'_x) are multiplied by a correction factor e^{rx}. When the population is stable e^{rx} reduces to unity. The universality of application of this correction factor for age at death data will be questioned below, but initially it appears that independently

Table 33. Contingency table comparing the age distributions of male and female waterbuck skulls collected in the Umfolozi Game Reserve.

	Age (years)											
	1	2	3	4	5	6	7	8	9	10	11	Total
Male												
Observed	4	0	3	4	8	8	6	9	9	13	6	70
Expected	4,4	0	2,2	3,0	7,4	7,4	5,2	8,1	8,9	17,0	6,7	
Female												
Observed	2	0	0	0	2	2	1	2	3	10	3	25
Expected	1,6	0	0,8	1,0	2,6	2,6	1,8	2,9	3,1	6,0	2,3	
Total	6	0	3	4	10	10	7	11	12	23	9	95
χ^2	0,14	0	1,1	1,3	0,2	0,2	0,5	0,4	0,1	3,6	0,3	

Total χ^2 = 7,93, df = 10, P>0,5.

obtained $\bar{r}$ values (see Chapter 3) can be used to construct a valid life table for a declining population.

It still remains to be seen if the age structure of the Umfolozi waterbuck population has remained stationary. Since it appears that the population has been declining for some time (see Chapter 3) a stationary age distribution could be expected, particularly if the age-specific cause of this decline was the same throughout. Because the year of death of all skulls was recorded, the constancy of the age distribution can be examined with a contingency table. Table 34 indicates no significant difference ($P > 0,25$) in age structure between animals dying prior to 1976 and animals dying during and after 1976.

The waterbuck population has therefore been shown to fulfil both criteria necessary for valid life table construction. Two life tables have been calculated, one assuming r equals zero and the other with r equal to -0,10 (Tables 35 and 36). The -0,10 figure was decided on from a consideration of four $\bar{r}$ estimates. Values of $\bar{r}$ from the three density methods in the main study area were -0,14, -0,15 and -0,29, although none of the trends in density which these rates described were significant (see Chapter 3). The regression line through the annual NPB helicopter counts for waterbuck (Fig. 23) is given by y=1 083,3-128,2x, which produces an $\bar{r}$ value = $\log_e N_t / \log_e N_0 . t$ = 5,75/(6,99.6) = -0,137. It is argued in Chapter 3 that the decline shown by the helicopter counts is too steep since it is probable that recent counts of waterbuck are greater underestimates than former ones, therefore a figure of -0,10 has been used as a compromise.

Survivorship ($1000l_x$) and rate of mortality ($1000q_x$) curves are shown in Figs. 70 and 71. A $\log_{10}$ scale is used for the $1000l_x$ curves since it is more important to compare rates of change than declines in absolute numbers. The $1000q_x$ curve is plotted on an arithmetic scale since mortality is already expressed as a rate ($q_x = d_x/l_x$). In each table a first year mortality of 80,7 per cent has been used, as calculated above from observed calf survival.

The corrected and non-corrected survivorship curves are similar in overall shape, but juvenile mortality is emphasised in the corrected curve, where there is also a slightly steeper rate of decline in numbers after five years of age. These characteristics are shown

Table 34. Contingency table comparing the age distribution of the pre-1976 waterbuck skull sample with the 1976-1977 skull sample from the Umfolozi Game Reserve.

	Age (years)											
	1	2	3	4	5	6	7	8	9	10	11	Total
Pre-1976												
Observed	0	0	0	2	3	4	3	6	7	6	5	36
Expected	2,6	0	1,1	1,5	3,8	3,8	2,7	4,2	4,5	8,7	3,4	
1976-1977												
Observed	6	0	3	2	7	6	4	5	5	17	4	59
Expected	3,7	0	1,9	2,5	6,2	6,2	4,3	6,8	7,5	14,3	5,6	
Total	6	0	3	4	10	10	7	11	12	23	9	95
χ^2	3,73	0	1,74	0,26	0,27	0,11	0,05	1,25	2,22	1,34	1,21	

Total χ^2 = 12,18, df = 10, P>0,25.

Table 35. Life table for Umfolozi male and female waterbuck.

Age (years)	Frequency of ages at death, f'_x	$1000d_x$ [1]	$1000l_x$ [2]	$1000q_x$ [3]
0	(397)*	807	1000	807
1	6	12	193	62
2	0	0	181	0
3	3	6	181	33
4	4	8	175	46
5	10	20	167	120
6	10	20	147	136
7	7	14	127	110
8	11	22	113	195
9	12	24	91	263
10	23	47	67	701
11	9	18	20	900

1. $d_x = f'_x / \Sigma f'_x$

2. $l_x = 1 - \sum_{0}^{x-1} d_x$

3. $q_x = d_x / l_x$

* First year mortality of 80,7 per cent from calf survival: see text.

Table 36. Life table for Umfolozi male and female waterbuck, assuming $r = -0{,}10$.*

Age (years)	f'_x	Correction factor $e^{-0,10x}$	Corrected frequency $f'_x.e^{-0,10x}$	$1000d_x$	$1000l_x$	$1000q_x$
0	(397)	1,00	397	894	1000	894
1	6	0,90	5,4	12	106	113
2	0	0,82	0	0	94	0
3	3	0,74	2,2	5	94	53
4	4	0,67	2,7	6	89	67
5	10	0,61	6,1	14	83	169
6	10	0,55	5,5	12	69	174
7	7	0,50	3,5	8	57	140
8	11	0,45	5,0	11	49	225
9	12	0,41	5,0	11	38	290
10	23	0,37	8,5	19	27	704
11	9	0,33	3,0	7	8	875

* Notation as for Table 35.

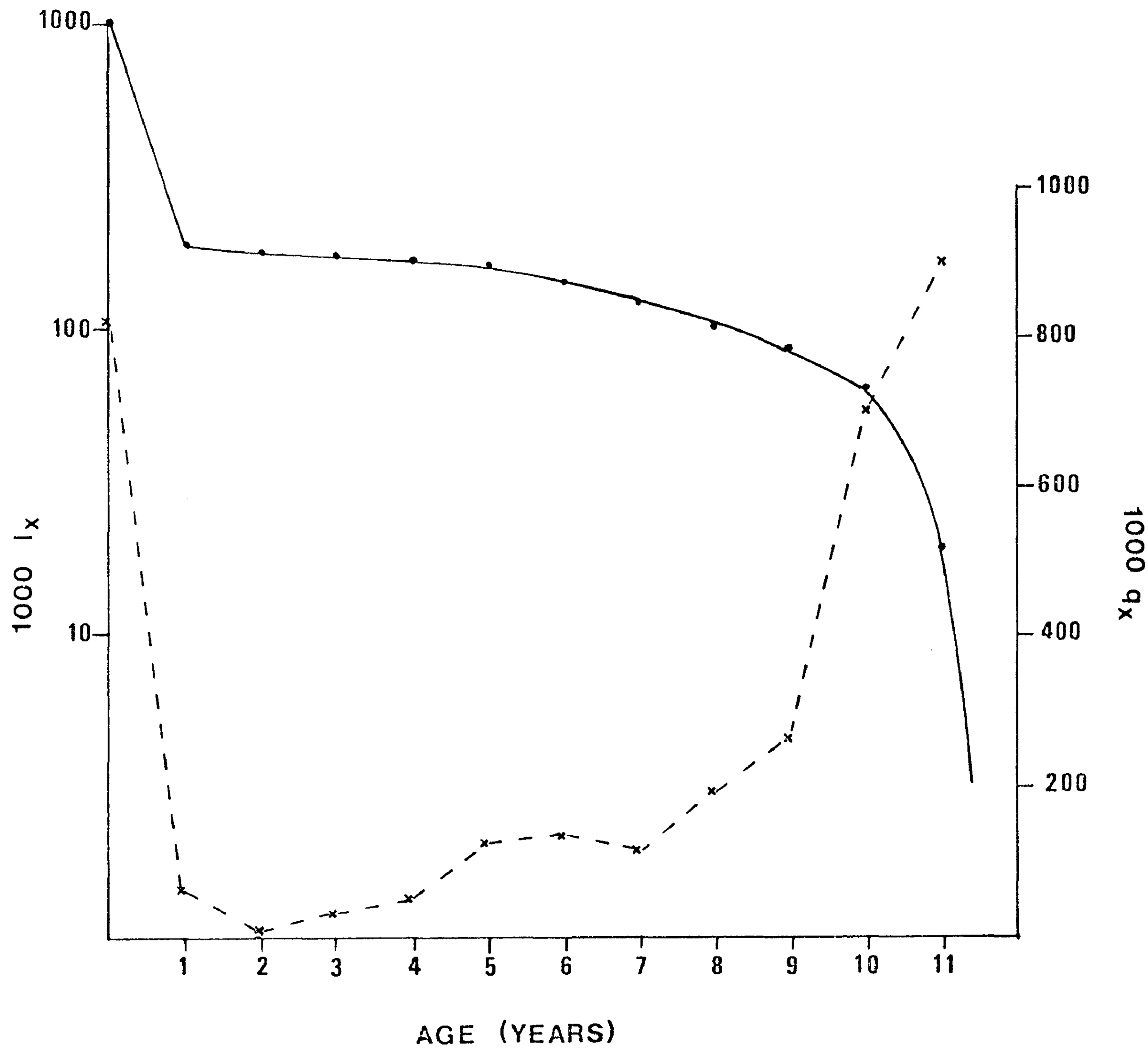


Figure 70. Survivorship ($1000l_x$) and rate of mortality ($1000q_x$) curves from the uncorrected frequency of ages at death schedule for Umfolozi waterbuck.

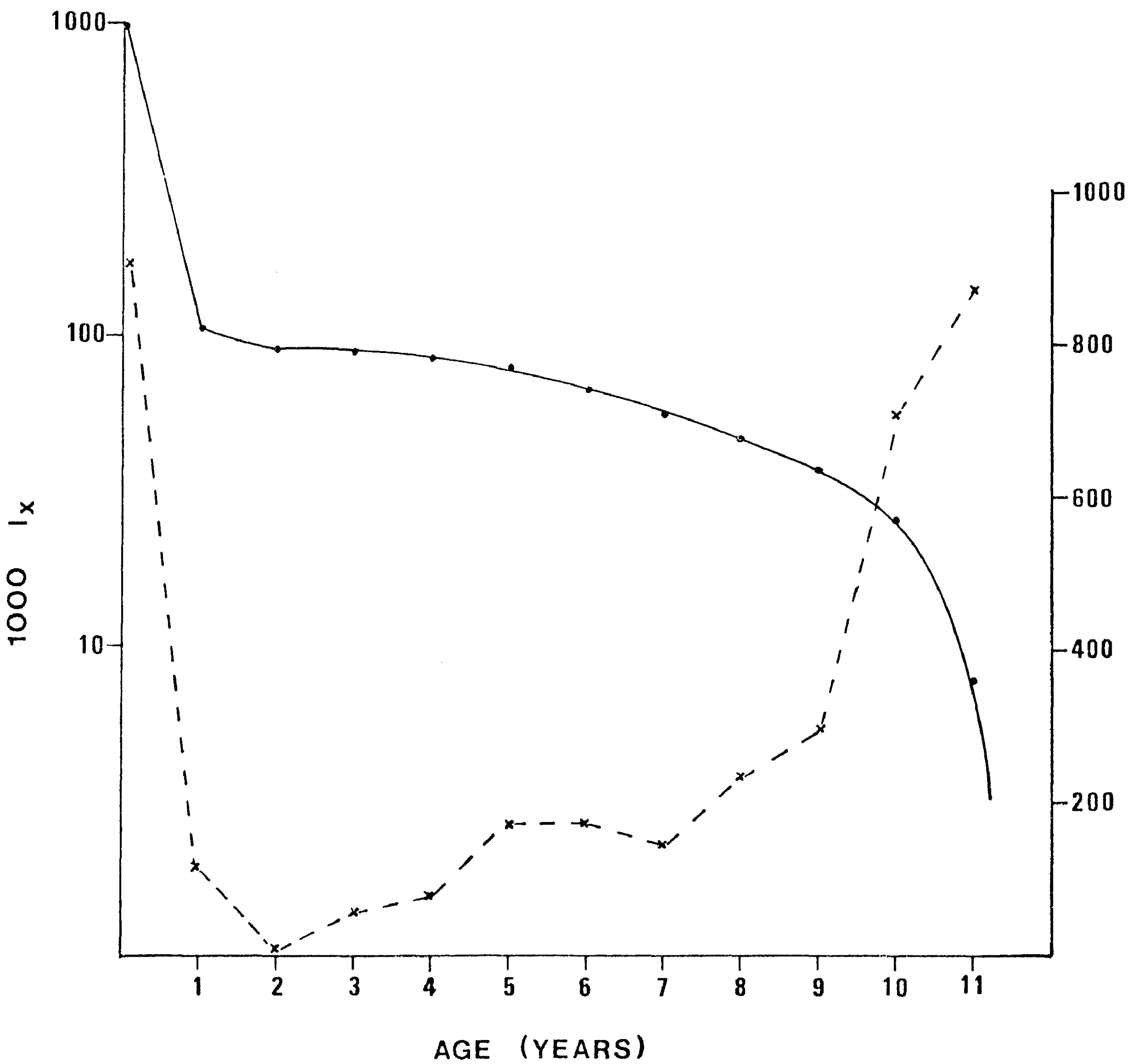


Figure 71. Survivorship ($1000l_x$) and rate of mortality ($1000q_x$) curves from the corrected frequency of ages at death schedule for Umfolozi waterbuck.

more clearly by the $1000q_x$ curves. Both life tables describe a population with a slow turnover rate and a preponderance of old animals, typical of either stable or declining density (Caughley 1977). Spinage (1970 and 1972) gave survivorship and rate of mortality curves for Uganda waterbuck, based on ages at death from 99 male skulls and 33 female skulls. The curves are similar to those given here except that a 50 per cent first year mortality figure had been independently calculated and incorporated into the table; also adult mortality rates began to increase at an earlier age, particularly for females. Therefore the UGR population shows an adult mortality schedule more beneficial to the production of young but is declining whereas the Uganda population is stable. Since fertility has been shown to be high in UGR waterbuck this comparison emphasises the very important role calf mortality plays in determining the population's rate of increase. Similar conclusions regarding the importance of juvenile mortality in affecting animal numbers have been made by a number of workers. Watson (1969, *In*: Watson 1970) described the critical role that juvenile mortality played in affecting the rate of increase of Serengeti wildebeest and suggested that as a population regulating mechanism it may be very sensitive to environmental change. Sinclair (1973) found mortality of young to potentially be that most important in causing density fluctuations of Serengeti buffalo, and Hanks and McIntosh (1973) showed the importance of juvenile mortality in controlling population growth in elephant. Recent review papers where this general conclusion has been supported are Caughley (1976), Eberhardt (1977) and Hanks (1978).

A fertility table (m_x schedule) is required before the role of calf mortality in affecting the rate of increase of the Umfolozi waterbuck population can be examined further. The symbol m_x represents the mean number of female offspring produced per female aged x years. Twins have never been recorded intra-utero (Brand 1963, Spinage 1969) and a 1:1 sex ratio at birth is assumed (see above). Dasmann and Mossman (1962b) suggested that most female waterbuck first give birth at two years of age. From the evidence of two primiparous females Spinage (1969b) showed that conception could take place at the first oestrus. He also confirmed that no conceptions occurred before one year, but found only two of 12 females aged two years to have corpora albicantia; adult ovary weight was reached by three years. These results suggest zero m_x values for the zero to one and one to two year classes, a reduced m_x value for two-year-olds and likely adult m_x values from three years on. With the lack of more detailed information a value of 50 per cent conception amongst one-year-olds is assumed which results in an m_x figure of 0,25 for two-year-olds. From the few data above this value is probably too high rather than too low. An estimate of mean adult fertility has already been calculated above by the method of Richards and Waloff (1954), which gives an m_x value of 0,41 for females aged two years and older. This, however, is an underestimate for animals of three years and above because of the non-maximal figure assigned to the two year class. With a value of 0,25 for two-year-olds the m_x figure for animals three years and older becomes 0,43.

The m_x column is given in Tables 37 and 38 together with the kl_x columns for each life table. From the above explanation on the use of an e^{rx} correction factor it would seem that only the corrected life table should be considered further. This is not so as will become clear below, and therefore similar analyses are conducted with both tables. Two statistics are available for describing the rate of change in numbers of a population from life table data. These are the net reproductive rate (R_o), which is the multiplication rate per generation, and the instantaneous rate of increase (r_s), both calculated from prevailing schedules of survival and fecundity (Caughley and Birch 1971). The following equations, as given by Andrewartha and Birch (1954), are used to obtain estimates of these two statistics from the uncorrected life table (Table 37):

$$R_o = \Sigma l_x . m_x = 0,514$$

$$\text{Generation time} = G = \frac{\Sigma l_x m_x . x}{R_o} = \frac{2,879}{0,514} = 5,60 \text{ yr}$$

$$r_s = \frac{\log_e R_o}{G} = \frac{-0,67}{5,60} = -0,119$$

The same calculations for the corrected life table (Table 38) are:

$$R_o = 0,245$$

$$G = \frac{1,319}{0,245} = 5,38 \text{ yr}$$

$$r_s = \frac{-1,41}{5,38} = -0,26$$

Table 37. Survivorship (l_x) and fertility (m_x) schedules necessary for calculating the instantaneous rate of increase of the Umfolozi waterbuck population.

Age (years)	l_x	m_x	$l_x.m_x$	$l_x.m_x.x$
0	1,000	0	0	0
1	0,193	0	0	0
2	0,181	0,25	0,045	0,090
3	0,181	0,43	0,078	0,234
4	0,175	0,43	0,075	0,300
5	0,167	0,43	0,072	0,360
6	0,147	0,43	0,063	0,378
7	0,127	0,43	0,055	0,385
8	0,113	0,43	0,049	0,392
9	0,091	0,43	0,039	0,351
10	0,067	0,43	0,029	0,290
11	0,020	0,43	0,009	0,099

Table 38. Corrected survivorship (l_x) and fertility (m_x) schedules for Umfolozi waterbuck.

Age (years)	l_x	m_x	$l_x.m_x$	$l_x.m_x.x$
0	1,000	0	0	0
1	0,106	0	0	0
2	0,094	0,25	0,024	0,048
3	0,094	0,43	0,040	0,120
4	0,089	0,43	0,038	0,152
5	0,083	0,43	0,036	0,179
6	0,069	0,43	0,030	0,180
7	0,057	0,43	0,025	0,175
8	0,049	0,43	0,021	0,168
9	0,038	0,43	0,016	0,144
10	0,027	0,43	0,012	0,120
11	0,008	0,43	0,003	0,033

The uncorrected life table produces an r_s estimate similar to the believed $\bar{r}$ value of -0,10, whereas the corrected life table gives an r_s value of -0,26, equal to a finite loss rate (λ) of 23 per cent per year ($\lambda = e^{-r}$). While it is agreed that a single sample standing age distribution (kl_x) estimate together with a fertility schedule cannot be used to validly calculate r_s (Caughley 1977), it is believed that for a population with a known stationary age distribution, the value of r_s calculated from a kd_x based life table will reflect the rate of increase of that population. In this instance of a declining population with a stationary age structure the use of a correction factor that emphasises early mortality must result in the observed exaggerated loss rate.

The uncorrected life table represents the valid starting point for an examination of the effect of juvenile mortality on r_s. Thus a present 80,7 per cent first year mortality equates with an instantaneous rate of increase of -0,119, which is a finite loss rate of 11 per cent per year, or an approximate halving of the population each generation time of five years. Four other life tables have been constructed based on the uncorrected f'_x column but with theoretical first year mortality values of 70 per cent, 60 per cent, 50 per cent and 40 per cent (Tables 39 to 42). They represent population age structures which would result if the present juvenile mortality was quickly reduced to these lower values.

With 70 per cent juvenile mortality (Table 39):

$$R_o = 0,786$$

$$G = \frac{4,363}{0,786} = 5,55 \text{ yr}$$

$$r_s = \frac{-0,24}{5,55} = -0,043$$

With 60 per cent juvenile mortality (Table 40):

$$R_o = 1,052$$

$$G = \frac{5,863}{1,052} = 5,57 \text{ yr}$$

$$r_s = \frac{0,0507}{5,57} = 0,009$$

With 50 per cent juvenile mortality (Table 41):

Table 39. Life table and fertility (m_x) schedule for Umfolozi waterbuck, with 70 per cent first year mortality.*

Age (years)	f'_x	$1000d_x$	l_x	$1000q_x$	m_x	$l_x.m_x$	$l_x.m_x.x$
0	(222)	700	1,000	700	0	0	0
1	6	19	0,300	63	0	0	0
2	0	0	0,281	0	0,25	0,070	0,140
3	3	10	0,281	36	0,43	0,121	0,363
4	4	13	0,271	48	0,43	0,117	0,468
5	10	32	0,258	124	0,43	0,111	0,555
6	10	32	0,226	142	0,43	0,097	0,582
7	7	22	0,194	113	0,43	0,083	0,581
8	11	35	0,172	203	0,43	0,074	0,592
9	12	38	0,137	277	0,43	0,059	0,531
10	23	73	0,099	737	0,43	0,043	0,430
11	9	29	0,026	1 115	0,43	0,011	0,121

* Notation as in Table 35.

Table 40. Life table and fertility (m_x) schedule for Umfolozi waterbuck, with 60 per cent first year mortality.*

Age (years)	f'_x	$1000d_x$	l_x	$1000q_x$	m_x	$l_x.m_x$	$l_x.m_x.x$
0	(143)	601	1,000	601	0	0	0
1	6	25	0,399	63	0	0	0
2	0	0	0,374	0	0,25	0,094	0,188
3	3	13	0,374	35	0,43	0,161	0,483
4	4	17	0,361	47	0,43	0,155	0,620
5	10	42	0,344	122	0,43	0,148	0,740
6	10	42	0,302	139	0,43	0,130	0,780
7	7	29	0,260	112	0,43	0,112	0,784
8	11	46	0,231	199	0,43	0,099	0,792
9	12	50	0,185	270	0,43	0,080	0,720
10	23	97	0,135	719	0,43	0,058	0,580
11	9	38	0,038	1 000	0,43	0,016	0,176

* Notation as in Table 35.

Table 41. Life table and fertility (m_x) schedule for Umfolozi waterbuck, with 50 per cent first year mortality.*

Age (years)	f'_x	$1000d_x$	l_x	$1000q_x$	m_x	$l_x.m_x$	$l_x.m_x.x$
0	(95)	500	1,000	500	0	0	0
1	6	32	0,500	64	0	0	0
2	0	0	0,468	0	0,25	0,117	0,234
3	3	16	0,468	34	0,43	0,201	0,603
4	4	21	0,452	46	0,43	0,194	0,776
5	10	53	0,431	123	0,43	0,185	0,925
6	10	53	0,378	140	0,43	0,163	0,978
7	7	37	0,325	114	0,43	0,140	0,980
8	11	58	0,288	201	0,43	0,124	0,992
9	12	63	0,230	274	0,43	0,099	0,891
10	23	121	0,167	725	0,43	0,072	0,720
11	9	47	0,046	1 021	0,43	0,020	0,220

* Notation as in Table 35.

Table 42. Life table and fertility (m_x) schedule for Umfolozi waterbuck, with 40 per cent first year mortality.*

Age (years)	f'_x	$1000d_x$	l_x	$1000q_x$	m_x	$l_x.m_x$	$l_x.m_x.x$
0	(63)	399	1,000	399	0	0	0
1	6	38	0,601	63	0	0	0
2	0	0	0,563	0	0,25	0,141	0,282
3	3	19	0,563	34	0,43	0,242	0,726
4	4	25	0,544	46	0,43	0,234	0,936
5	10	63	0,519	121	0,43	0,223	1,115
6	10	63	0,456	138	0,43	0,196	1,176
7	7	44	0,393	112	0,43	0,169	1,183
8	11	70	0,349	201	0,43	0,150	1,200
9	12	76	0,279	272	0,43	0,120	1,080
10	23	146	0,203	719	0,43	0,087	0,870
11	9	57	0,057	1 000	0,43	0,025	0,275

* Notation as in Table 35.

$$R_o = 1{,}315$$

$$G = \frac{7{,}319}{1{,}315} = 5{,}57 \text{ yr}$$

$$r_s = \frac{0{,}2737}{5{,}57} = 0{,}049$$

With 40 per cent juvenile mortality (Table 42):

$$R_o = 1{,}587$$

$$G = \frac{8{,}843}{1{,}587} = 5{,}57 \text{ yr}$$

$$r_s = \frac{0{,}4619}{5{,}57} = 0{,}083$$

The relationship between r_s and juvenile mortality given by these results is shown in Fig. 72; they predict a stable population when juvenile mortality is reduced to approximately 60 per cent. A similar curvilinear relationship between r_s and calf mortality was produced by Attwell (1977) for wildebeest in UGR; there a 50 per cent mortality figure was suggested for zero growth.

Age structure from immobilised animals

The age structure of 23 animals aged two years and above which were immobilised during 1976 and 1977 is given in Fig. 73. As also indicated by the skull sample, no significant difference is seen in age distributions of males and females ($\chi^2 = 9{,}49$, df = 9, $P > 0{,}25$). The age structure indicated is equivalent to that predicted by the life table analyses above; the population is dominated by older animals, which suggests that recruitment to the adult segment has been poor for a number of years.

CONCLUSION

The results presented in this chapter suggest that a high mortality of young waterbuck is the proximate cause of the decline of this species in UGR. Juvenile mortality would have to be reduced to at least 60 per cent before the population could be expected to stabilise. The 60 per cent figure translates into a survival of 32 juveniles per 100 females at year's end, which is between two and three times that observed during the study. It is realised that these results come from a crude analysis which relies on a number of generalisations. They do, however, serve as a basis from which any management action can be both planned and monitored.

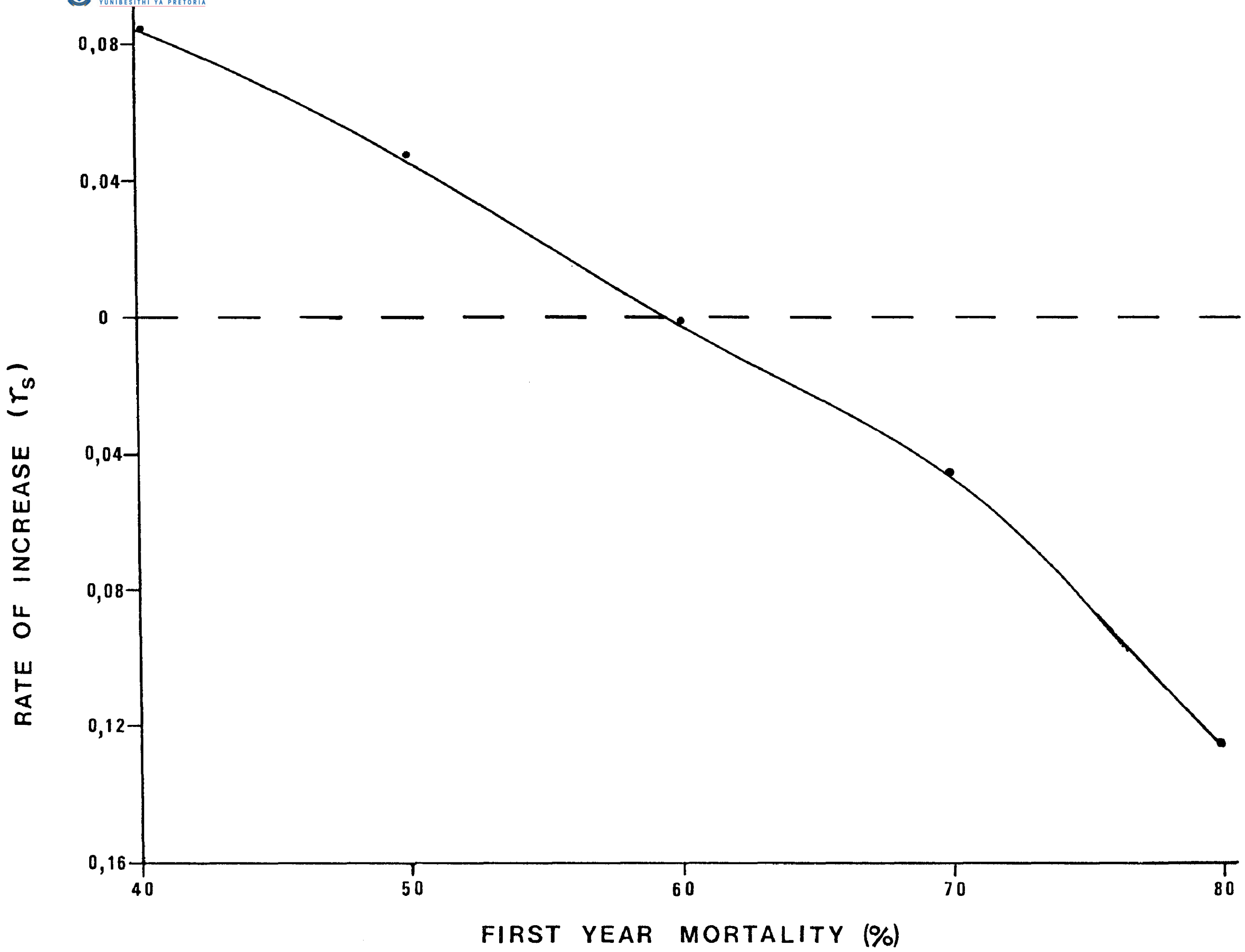


Figure 72. The relationship between r_s and calf mortality for Umfolozi waterbuck.

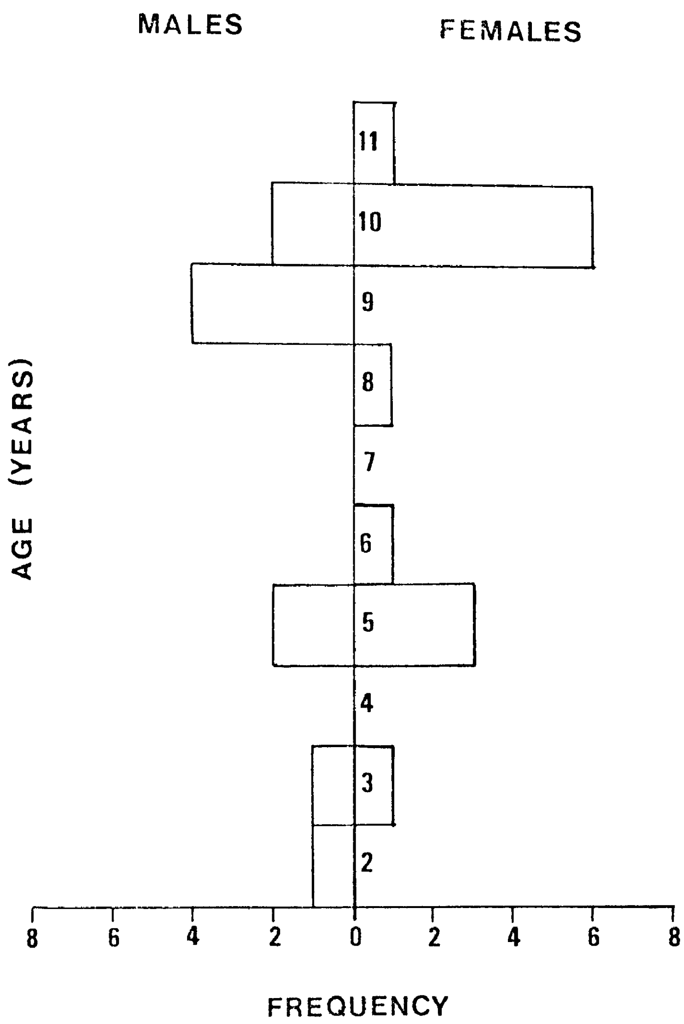


Figure 73. Age distributions from tooth impressions of 23 adult (2 yr +) waterbuck immobilised in the main study area during 1976 and 1977.

CHAPTER 6

MORTALITY AND CONDITION

INTRODUCTION

An investigation of mortality factors and indices of physiological condition are two areas vital to an understanding of the functional aspects of population dynamics. The results presented in this chapter plus those from life table analyses will together allow an assessment of overall population condition as envisaged by Hanks (1978). This synthesis and resulting conclusions regarding population regulation in Umfolozi waterbuck will be made in Chapter 10. Supplementary data from behavioural observations, habitat utilization, competition and feeding ecology will also provide a background for defining population condition.

Results to be presented here come from three main areas: an analysis of mortality records in terms of broad mortality categories, an investigation of cause of death from post-mortem examinations and a study of condition using immobilised animals.

Before giving the methods used it is useful to review briefly the subject of condition estimation in ungulates. Criteria for condition assessment are usually closely linked to the chances of an individual animal living or dying (Hanks 1978). The majority of condition estimates using carcasses are based on the observation that animals in relatively good condition show high total body fat reserves when compared to those in poor condition where these reserves have been mobilised. It is time consuming and tedious to obtain these data by dissecting or rendering out all body fat and consequently this has not often been attempted (Ledger and Smith 1964, Ledger, Sachs and Smith 1967). Fortunately it has been found practical to measure indices of total fat instead, of which the kidney fat index (KFI) and bone marrow fat (BMF) content are the commoner two (Riney 1955). The KFI has been used in many condition studies of which three recent ones are Smith (1970) for 10 species of ungulate in East Africa, Sinclair and Duncan (1972) for wildebeest, kongoni (*Acelaphus buselaphus cokei*) and buffalo, and Brooks, Hanks and Ludbrook (1977) for impala, buffalo and eland. In seven of the 10 species examined by Smith (1970), including waterbuck, KFI and total body fat were significantly correlated.

Various methods have been used to estimate the fat content of bone marrow, but actual extraction of fat is preferable to methods based on colour or consistancy of the marrow (Franzmann and Anreson 1976). Brooks *et al.* (1977) found in eight species that per cent fat content of the bone marrow approximated to per cent dry mass minus seven.

Assessing condition in live wild ungulates presents greater problems. If animals cannot be hand restrained or drug immobilised then a visual system based on key signs of body deterioration represents a convenient, albeit crude, method (Riney 1960). Even when animals can be handled, quantification of body growth through weighing or linear measurements is still useful for gauging condition (Smith 1970).

Haematology and blood chemistry have recently been used as potential indices of physiological condition in a number of wild ungulate studies. The parameters quantified in this recent work include many of those used for human clinical tests and in veterinary studies. Seal, Verme, Ozoga and Erickson (1972) alone carried out 27 assays including haematology, chemicals and hormones. In many cases the importance of blood assays is diminished because details of demography, habitat utilization and feeding are not given. Under these circumstances the figures lose value even as baseline information. Differences in blood values also occur between age and sex classes (Pedersen and Pedersen 1975), but these are not often taken into account. A further complication is that parameter values can be affected by drug immobilisation and by excitability during hand restraint and drug immobilisation. Blood chemical levels are usually lower in tranquilised animals than in samples taken after a head shot (Seal, Ozoga, Erickson and Verme 1972, Drevemo, Grootenhuis and Karstad 1974). This is probably because blood pressure falls in a sedated animal which results in haemodilution. Excitability can significantly alter haematology and blood chemicals (Seal, Ozoga, Erickson and Verme 1972). Franzmann (1972) found that packed cell volume (PCV) and serum cholesterol were both positively related to excitability in bighorn sheep (*Ovis canadensis canadensis*). Haematology is probably mainly altered because of splenic contraction mobilising blood cell reservoirs (Gartner, Ryley and Beattie 1965).

Even with these problems, haematology and blood chemistry could contribute much to the understanding of animal-environment relations.

The physiological rationales behind the use of a few main blood chemicals that have been suggested to be potential indicators of condition and which were assayed in this study are given below.

Blood urea nitrogen

The α-amino groups of amino acids which result from protein breakdown are ultimately excreted as urea, which is synthesised in the liver and transported in the blood to the kidneys (Harper 1975). Blood urea nitrogen (BUN) is therefore a good indicator of the amount of protein in the diet. Two situations could occur which would cause a rise in BUN unrelated to diet. The first is dehydration or any other pathologic condition affecting kidney function. The second is during periods of inanition when muscle protein may be catabolised to provide energy (de Calesta, Nagy and Bailey 1977).

Serum total protein

Serum total protein consists primarily of albumin and globulin which perform several functions including maintainance of osmotic balance, buffering the blood, transporting insoluble substances and acting as a reserve of body protein (Harper 1975). There is a direct relationship between the amount and type of protein in the diet and the formation of serum proteins since protein in the diet serves as a precursor to the serum proteins. There is evidence that this parameter may be insensitive to nutritional deprivation because normal values are maintained except under extreme deprivations (LeResche, Seal, Karns and Franzmann 1974).

Serum albumin

Albumin levels can be lowered following inadequate protein intake or as a result of chronic liver disease. If albumin and total protein are both measured an estimate of serum globulin can be made by subtraction. Globulin levels may be elevated with infectious disease or decreased with malnutrition and starvation (Harper 1975).

Total lipids

Total lipids refer to chylomicrons and low density lipoproteins in the serum, which include triglycerides, cholesterol and phospholipids. Of these triglycerides compose approximately 43 per cent and cholesterol and cholesterol ester 32 per cent (Harper 1975).

Chylomicrons and very low density lipoproteins (VLDL) are produced from fat via the intestine whereas triglycerides are hepatic in origin. It is likely that VLDL are primarily vehicles for transporting triglycerides (Olson and Vester 1960), which can vary two-fold depending on nutritional state. They are further reduced during starvation because of transport problems related to impaired ability of the liver to secrete VLDL (Topping and Mayes 1972). Total lipids should reflect an overall picture of energy balance.

Serum cholesterol

Cholesterol is mainly synthesised in the liver and is transported in the blood in the form of low density lipoproteins. Its functions are not entirely understood; it is important as a precursor of steroid hormones but these and their degradation products are of minor significance in the total amount of cholesterol metabolised (McDonald, Edwards and Greenhalgh 1973). Cholesterol levels do reflect the prevailing diet as its synthesis is affected by total caloric intake and specifically increased with diets high in carbohydrate and saturated fatty acids (Harper 1975).

Free fatty acids

These are the most metabolically active of the serum lipids and may be taken up by many organs to provide an energy source when insufficient glucose is available. Free fatty acid (FFA) concentration in serum is determined by the relative rates of lipolysis and re-esterification in adipose tissue. For ruminants FFA levels remain low and constant under normal feeding conditions but rise during fasting to supply between 25 to 50 per cent of energy requirements (Harper 1975).

Blood analyses in wildlife studies

Apart from FFA all the above chemicals have been employed previously to help assess condition in ungulates. Bjarghov, Fjellheim, Hove, Jacobsen, Skjenneberg and Try (1976) found significantly higher levels of BUN, total protein, albumin, cholesterol and total lipids in reindeer (*Rangifer tarandus tarandus*) calves fed a supplemented diet as compared with animals on a normal winter diet. They also showed that PCV, serum inorganic phosphorus, magnesium and the enzyme alkaline phosphatase were all elevated with a high plane of nutrition. Seal *et al.* (1972a) reported significant seasonal variation in the levels of BUN, total protein, albumin, potassium, haemoglobin, PCV, red cell count (RCC), inorganic phosphorus and fibrinogen during a study on white-tailed deer (*Odocoileus virginianus*). Coblentz (1975) documented a significant decline in serum cholesterol in white-tailed deer as winter progressed which he ascribed to a decline in the nutrient content of their diet. Kirkpatrick, Buckland, Abler, Scanlon, Whelan and Burkhard (1975) working with penned white-tailed deer fawns were able to show that BUN reflected recent protein intake only, there being little carry through in values from one month to the next when the plane of nutrition was altered. Franzmann (1972) working with bighorn sheep also considered that BUN adequately reflected protein intake and suggested that PCV may be the best blood parameter for assessing overall physiological condition. LeResche *et al.* (1974) reviewed blood data for moose (*Alces alces*) and concluded that BUN was the chemical best correlated with nutritional-seasonal differences, followed by cholesterol, total protein and glucose; that latter was thought surprising since it is known that glucose is rapidly elevated in handling stress. Wilson (1975) found that KFI was significantly related to animal weight, serum total protein, serum albumin and PCV for sable (*Hippotragus niger*).

This survey of the physiological background behind a few blood chemicals and the use of blood data in some recent wildlife studies has been very brief. It has, however, demonstrated the problems involved in using blood data for condition assessment and will form a background for considering results to be given here and results to be mentioned from studies of other ungulates.

METHODS

Mortality records

Since 1970 records have been routinely kept by NPB staff of animals found dead in UGR. Information from these records was summarised for the years 1970 to 1977 for all ungulate species. Most death records come from game guards on routine patrols; cause of death, age and sex of animal is recorded. Cause is defined as either from a particular predator, poaching, "natural causes" (poor condition and disease), other non-predatory causes such as fighting, or unknown where the animal has usually been heavily scavenged. Age is given as juvenile, immature or adult, corresponding approximately to the juvenile plus infant, yearling and adult groups used in this study; although some yearlings were seen classified as juveniles for the first few months of the year.

During 1976 and 1977 a separate record was kept of all animals found dead in the main study area.

Carcass examination

The majority of carcass finds were so consumed by scavengers that often only the skull remained. During the study period 15 water-buck carcasses were examined from which tissue samples could be taken. For these, details were noted for inclusion in the mortality record as described above and the following procedure was carried out where possible.

Body condition was classified as poor, moderate or good using the system of Riney (1960) and body measurements were taken as described in Chapter 4.

Tick infestation was recorded as low, moderate, heavy or severe using the criteria applied to immobilised animals which are described below. A sample of ticks was collected in 70 per cent alcohol for identification.

A blood or serum sample was taken from the heart and a blood slide made. Subsequent procedures for processing and analysing blood samples and slides are as given below for immobilised animals.

The kidneys were removed along with the fat immediately around them. Kidneys and fat were weighed separately to the nearest 1,0 g and the KFI calculated as weight of perinephric fat/kidney weight.100. Small samples of kidney and other organs were fixed in 10 per cent formalin for later histological examination.

Bone marrow samples were taken from the three long bones of a forelimb or hindlimb. Up to 10 g of marrow was removed from the central region of the bone and weighed to the nearest 0,1 g. Samples were oven dried to constant weight at 100 °C and the per cent dry weight calculated. Fat was extracted with Petroleum Ether by reflux action and a Soxhlet apparatus for eight hours, after which the residue was dried and weighed. The amount of fat extracted was calculated by subtraction and expressed as a percentage of the original fresh weight. This process is as given by Brooks *et al.* (1977).

Immobilised animals

Immobilisation procedures and details of data collection not connected with condition assessment are given elsewhere. Twenty-eight animals were examined during May and June 1976 and four during July 1977.

Body condition and ticks

Body condition was rated on a three point scale as described for carcasses.

Tick infestation was qualitatively assessed as either absent, low, moderate, high or severe. This scale was based on the progression of infestations of engorged adult ticks seen on live animals during field observations. A low infestation consisted of a few ticks on the head, mainly around the bases of the ears. If the clusters around the ears were large a moderate infestation was recorded. Infestations were listed as heavy when large numbers of ticks were attached to the head with others on the neck and perhaps other parts of the body. Severe infestations were characterised by patches of contiguous engorged ticks on the head and neck plus others attached elsewhere. The eyes could be partially closed by ticks on the eyelids, blood would streak the neck from ticks ruptured during attempted grooming and hair loss from the head and neck could be marked. Figure 74 shows a two year-old male with a heavy infestation.

Tick samples were taken and on the four animals examined during 1977 thorough collections were made from the ears, neck, brisket, belly, tail, feet and anus. All ticks were preserved in 70 per cent alcohol for identification.

Excitement

The possible effects of varying degrees of excitement on blood parameters have been mentioned in the introduction to this chapter. Quantification of this complicating factor was made by taking rectal temperatures at the beginning and end of the immobilisation period with a mercury bulb thermometer. Franzmann (1972) found a highly significant ($P < 0,001$) association between excitement and rectal temperature in bighorn sheep.

Blood sampling and field laboratory procedures

A blood sample was taken as soon as possible after immobilisation

Figure 74. A two year-old male waterbuck in the Umfolozi Game Reserve with a heavy tick infestation. Photograph by A.R. Lewis, March 1978.

from each of the 28 waterbuck handled in 1976. Between 10 and 20 ml of blood was slowly removed from the jugular vein using a disposable syringe with a 4,0 cm 18 gauge needle. Approximately 2 ml of blood was placed in a 5 ml container treated with the anticoagulant lithium heparin. Two drops of blood were used to make two slides using a standard technique (Giles 1971). The remainder of the blood was put into two 10 ml blood vials.

In 1977 two 5 to 10 ml blood samples were taken from each animal. The first was taken as soon as possible after immobilisation and the second towards the end of the immobilisation period. This was done in order to examine the effects of the duration of drug immobilisation on blood chemicals and haematology. Blood slides were prepared and blood samples stored as described for the 1976 sampling.

Blood slides were fixed in 100 per cent methanol for two minutes within six hours of preparation, and then stored for staining. Between two and 12 hours after collection a sample of heparinised blood was transferred to a capillary tube and the PCV read after spinning in a haematocrit centrifuge for ten minutes at 8 000 r/min. In 1977 two further analyses were carried out in the field on whole blood samples. First, haemoglobin concentration was determined using the method given below and second, erythrocyte cell counts were made using a Brite-Line manual haemocytometer.

Fresh blood samples were allowed to clot at ambient shade temperatures for a number of hours after which the clot was rimmed and serum removed using a disposable syringe. The serum obtained from each animal was split between two 5 ml containers and frozen for later analysis.

Blood slides: permanent laboratory phase

Blood slides were stained with giemsa stain prepared as described by Merk (1974), and viewed with a Zeiss binocular microscope at x 1 000 magnification. At least 100 fields were examined for the presence of blood parasites and signs of anaemia such as anisocytosis and the presence of chromatin in erythrocytes. One slide from each animal sampled in 1976 was sent for expert examination of blood parasites.

Blood chemistry

For the 1976 samples one bottle of serum per animal was thawed and analysed for BUN, total protein, albumin, total lipids and cholesterol.

The actual number of tests carried out was slightly below the maximum possible owing to accidental loss of some serum. In 1977 the serum samples were anlysed for BUN, total protein, albumin, cholesterol, phosphorus and free fatty acids. As already mentioned, haemoglobin was assayed using whole blood. All these tests, apart from FFA, were carried out with the Unitest System (Bio-Dynamics, Indianapolis, USA), using prescribed colorimetric methods and a Biodynamics Unimeter. Free fatty acids were measured by the method of Procos, de Villers and van der Walt (in press) using a Beckman model 25 spectrophotometer.

Viral studies

One bottle per animal of frozen serum from the 1976 sampling was sent for viral studies. Another project involved taking nasal and rectal swabs from all waterbuck immobilised during 1976. The swabs were sealed in culture medium and frozen before being dispatched.

Field observations and condition

The only routine field monitoring connected with condition was for tick infestation. It has been described above how severity of infestation was seen to progress on waterbuck in a uniform manner. This was observed during 1976, as was an apparent seasonality of infestation. To quantify this latter observation all animals observed well at close range with x 7 binoculars or from farther away with a x 30 telescope, were classified as having severe infestations or not. This simpler system was used because severe infestations were very distinct and therefore allowed certain quick classification. Monitoring was run for one year from December 1976 to November 1977.

RESULTS AND DISCUSSION

Adult mortality records

Since the majority of death records refer to adults and since there is also a particular interest in calf mortality arising from the results of the last chapter, these two areas are analysed separately. Adult refers here to animals over one year old; that is death records of adults plus immatures. The numbers of immature and juvenile carcasses found were very low.

The proportionate numbers of deaths attributed to the various causes have remained fairly constant over the period 1970 to 1977 with no obvious trends visible (Fig. 75). Death from lion and unknown cause predominate except for 1970 when the sample size was small. No reliance can be placed on the general increase in the number of waterbuck deaths reported annually since 1970. The number reported is a large underestimate of the actual numbers dying and fluctuations could be caused by such factors as the personnel involved, the number of game guard patrols per month, or even the arrival of a biologist in the reserve.

Predation

On a few occasions game deaths were seen to be attributed to lion on flimsy or non-existant evidence, which may have caused an over-estimation of lion predation. Having acknowledged this source of error the records show that 75,2 per cent of all predator kills were by lion. Other predators recorded as killing adult waterbuck in UGR were hyaena, leopard, cheetah, crocodile (*Crocodylus niloticus*) and feral dogs. Similar percentages from the Kruger National Park and the Sabi-Sand Reserve are 80,4 per cent and 62,6 per cent respectively (Pienaar 1969, Herbert 1972). Spinage (1970) noted that lion infrequently took waterbuck in the Rwenzori National Park and Hanks *et al.* (1969), although finding high mortality from lion, recorded that little meat was ever eaten from the kills. Such evidence of unpalatability was never seen in UGR and has not been reported in any other recent publications. Verheyen (1955) and Hanks *et al.* (1969) found that more male waterbuck were taken by lions than females which was perhaps due to lone territorial males being more susceptible to predation. During 1976 and 1977 25 waterbuck of known sex were killed by lion in UGR, and of these 13 were females and 12 males. This may still indicate some selectivity for males when the adult sex ratio is taken into account. Elliott (1977) found that male and female waterbuck were preyed upon to the same extent by lion in Kenya.

Since the main known cause of adult waterbuck mortality in UGR is lion predation, this factor has been explored in more detail. Pienaar (1969) calculated lion preference indices for prey species as per cent in kill/per cent in the prey population. This index relies on two estimates subject to much error because of the differential sturdiness of carcass remains to scavengers and from the difficulties

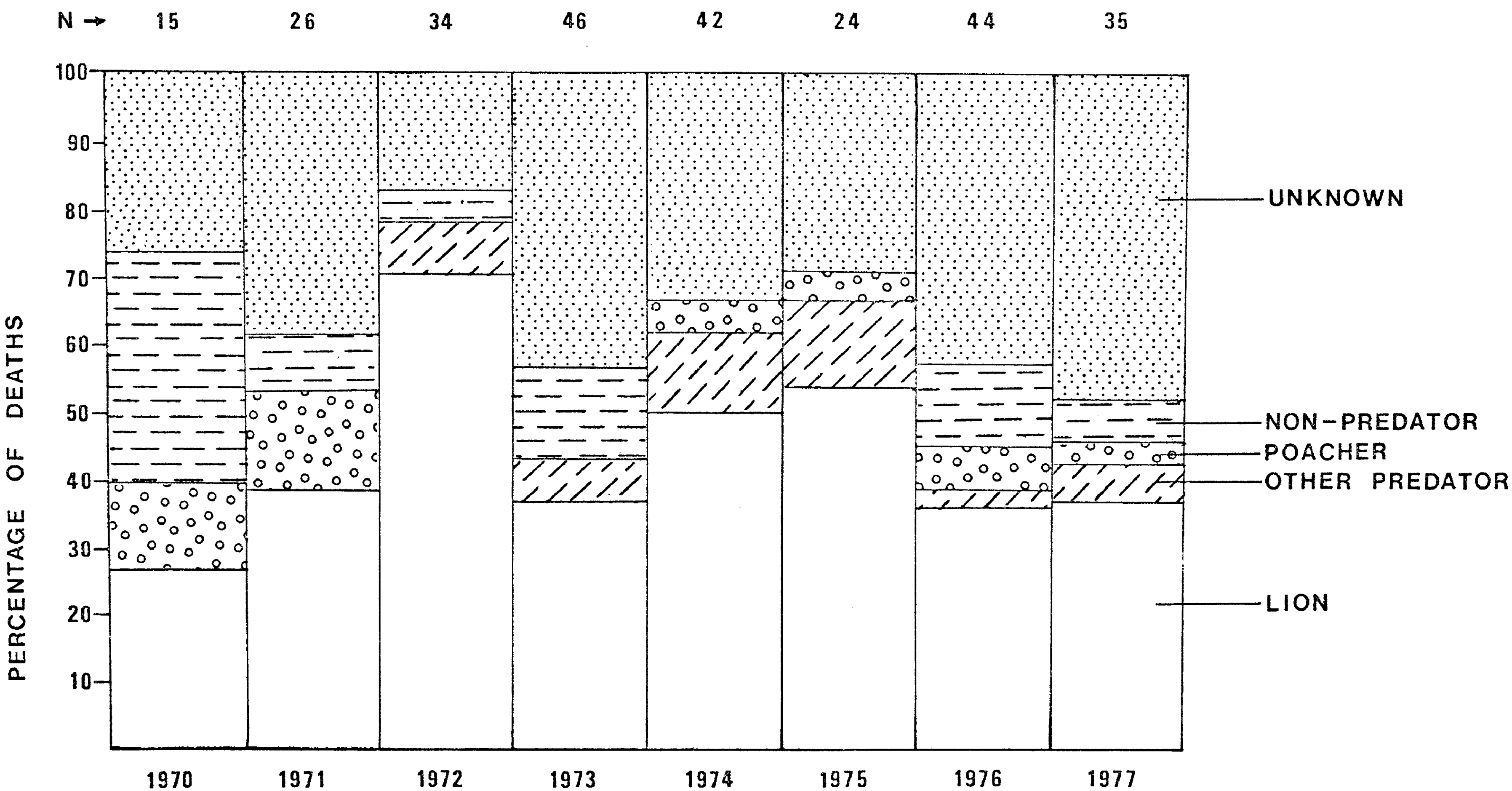


Figure 75. Summary of waterbuck mortality records in the Umfolozi Game Reserve from 1970 to 1977; N refers to the number of deaths reported.

in censusing game populations. It will be shown below that consistant bias can arise and give a false picture of lion preferences.

The lion preference indices for 1970 to 1976 calculated from death records over all UGR plus the uncorrected helicopter counts are shown in Fig. 76 and Table 43. Results are only given for the eight main grazers, as in any year these account for over 95 per cent of lion kills, usually over 98 per cent. These data suggest a number of trends. For example, waterbuck, nyala, wildebeest and kudu are consistantly preferred and there appears to be a switch in preference between nyala and waterbuck over the first four years. However, it is likely that these results are artifacts of sampling error and cannot be used as even an approximation of true lion preferences. The reason is that, as shown in Chapter 3, the helicopter count represents varying degrees of underestimation for the species censused.

Preference indices have been calculated for two additional sets of results for both 1976 and 1977. The first analysis uses carcass records for all UGR and the corrected 1976 helicopter estimates; the second is based on death records from the main study area and the mean 1976-1977 density estimates for that area (see Chapter 3). All these results are given in Table 44. They indicate the same trends for each year when compared with the indices calculated from the uncorrected helicopter census, with wildebeest and zebra now the preferred prey species and the importance of both nyala and waterbuck diminished (Fig. 77). The reason for these differences lies mainly with density estimates of ungulates other than the four just mentioned. The study area density estimates and to a somewhat lesser extent the corrected helicopter estimates give higher and more accurate abundance estimates for those species seen poorly from the helicopter, such as impala and nyala. When the uncorrected helicopter counts are used the denominators in the fractions for the preference indices of species seen well from the helicopter, such as zebra and wildebeest, are inflated resulting in artificially low lion preference indices. So although adult waterbuck are a preferred prey of lion in UGR they are probably less preferred than both wildebeest and zebra. Elliott (1977) reported that no predator was selectively killing waterbuck in the Solio area of Kenya and that warthog and eland were the preferred prey of lion.

Another way of viewing predator-prey relations of lion is just by examining the percentage of the kill made up of the various species

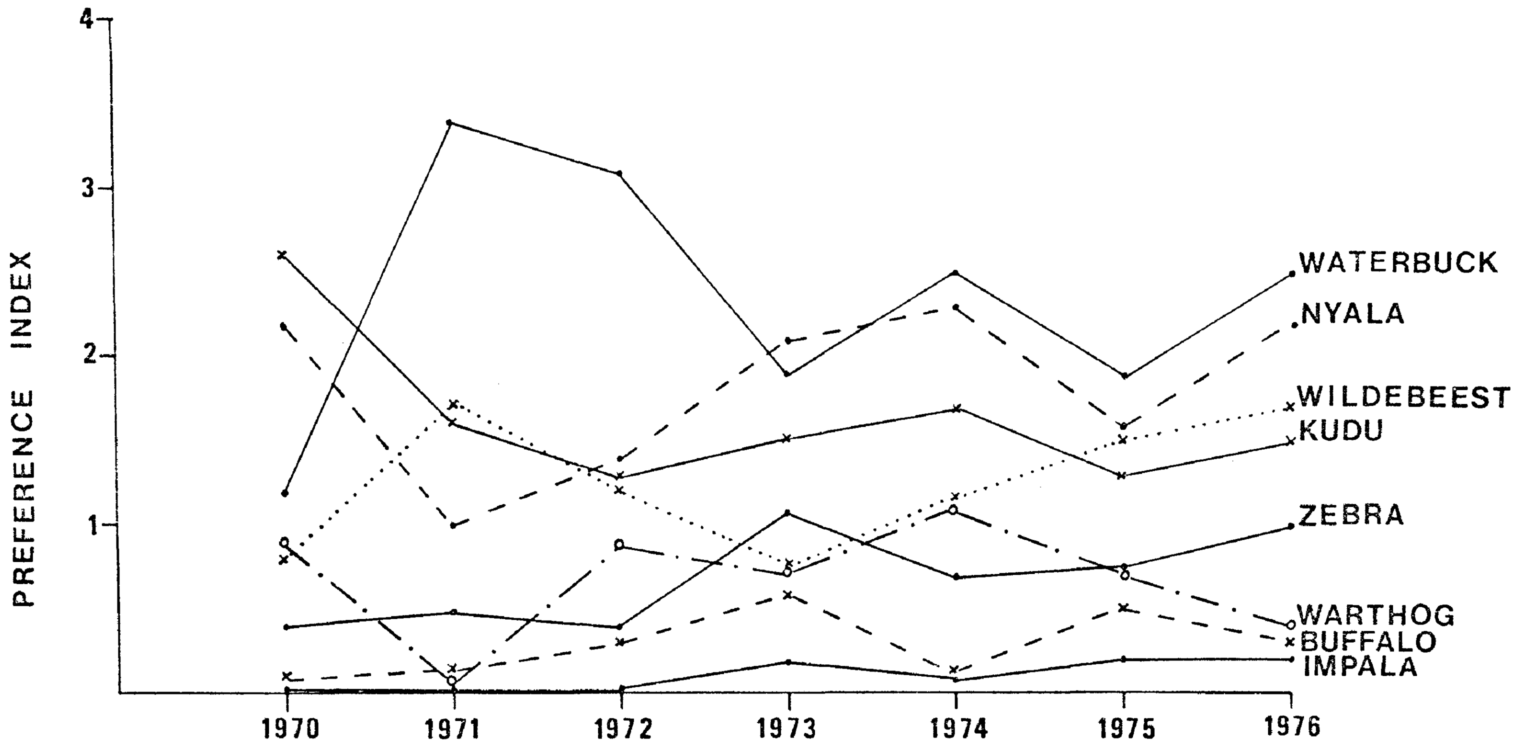


Figure 76. Lion preference indices for the eight main herbivore species making up the lion diet, calculated from uncorrected helicopter counts and death records over all the Umfolozi Game Reserve.

Table 43. Calculation of lion preference indices (PI)* for 1970 to 1976 using results over all the Umfolozi Game Reserve; the species considered in this table comprise over 95 per cent of lion kills.

	Waterbuck	Nyala	Kudu	Impala	Warthog	Wildebeest	Zebra	Buffalo
1970								
Per cent in prey	10,2	12,2	7,8	11,6	15,5	31,2	7,6	3,9
Per cent in kill	11,8	26,5	20,6	0	14,7	23,5	2,9	0
PI	1,2	2,2	2,6	0	0,9	0,8	0,4	0
1971								
Per cent in prey	10,5	14,1	8,9	14,8	18,5	21,9	7,0	4,8
Per cent in kill	35,7	14,3	14,3	0	0	32,1	3,6	0
PI	3,4	1,0	1,6	0	0	1,7	0,5	0
1972								
Per cent in prey	9,8	11,6	8,0	16,6	13,8	21,2	9,6	9,5
Per cent in kill	30,0	16,0	10,0	0	13,0	26,0	3,8	2,4
PI	3,1	1,4	1,3	0	0,9	1,2	0,4	0,3
1973								
Per cent in prey	9,2	12,2	8,1	16,2	12,1	24,4	7,3	10,5
Per cent in kill	17,7	26,0	12,5	3,1	8,3	17,7	8,3	6,3
PI	1,9	2,1	1,5	0,2	0,7	0,7	1,1	0,6
1974								
Per cent in prey	6,5	12,6	8,3	24,3	11,5	16,7	8,0	11,7
Per cent in kill	16,0	29,0	14,5	2,3	12,2	19,1	5,3	1,5
PI	2,5	2,3	1,7	0,1	1,1	1,1	0,7	0,1
1975								
Per cent in prey	6,7	13,1	8,9	16,8	13,8	18,6	9,4	12,5
Per cent in kill	12,6	20,4	11,7	3,9	9,7	28,0	6,8	6,8
PI	1,9	1,6	1,3	0,2	0,7	1,5	0,7	0,5

continued

* PI = $\frac{\text{per cent in kill}}{\text{per cent in prey}}$, using uncorrected helicopter counts.

Table 43, continued.

	Waterbuck	Nyala	Kudu	Impala	Warthog	Wildebeest	Zebra	Buffalo
1976								
Per cent in prey	4,3	10,4	7,8	23,2	15,5	17,9	8,7	12,3
Per cent in kill	10,6	22,5	11,9	5,3	6,6	29,8	8,6	3,3
PI	2,5	2,2	1,5	0,2	0,4	1,7	1,0	0,3

Table 44. Calculation of lion preference indices (PI)* for 1976 and 1977 using results over all the Umfolozi Game Reserve (uncorrected and corrected helicopter count estimates) and for the main study area.

	Waterbuck	Nyala	Kudu	Impala	Warthog	Wildebeest	Zebra	Buffalo
1976								
Uncorrected UGR								
Per cent in prey	4,3	10,4	7,8	23,2	15,5	17,9	8,7	12,3
Per cent in kill	10,6	22,5	11,9	5,3	6,6	29,8	8,6	3,3
PI	2,5	2,2	1,5	0,2	0,4	1,7	1,0	0,3
Corrected UGR								
Per cent in prey	4,1	13,5	7,5	40,0	18,9	7,0	4,1	4,8
Per cent in kill	10,6	22,5	11,9	5,3	6,6	29,8	8,6	3,3
PI	2,6	1,7	1,6	0,1	0,4	4,3	2,1	0,7
Study area								
Per cent in prey	10,6	17,7	4,6	37,9	14,8	5,8	5,0	3,6
Per cent in kill	23,5	17,6	5,9	0	5,9	23,5	17,6	5,9
PI	2,2	1,0	1,3	0	0,4	4,1	3,5	1,6
1977								
Uncorrected UGR								
Per cent in prey	4,3	10,4	7,8	23,2	15,5	17,9	8,7	12,3
Per cent in kill	11,7	26,2	9,7	7,8	12,6	20,3	9,7	1,9
PI	2,7	2,5	1,2	0,3	0,8	1,1	1,1	0,2
Corrected UGR								
Per cent in prey	4,1	13,5	7,5	40,0	18,9	7,0	4,1	4,8
Per cent in kill	11,7	26,2	9,7	7,8	12,6	20,3	9,7	1,9
PI	2,9	1,9	1,3	0,2	0,7	2,9	2,4	0,4
Study area								
Per cent in prey	10,6	17,7	4,6	37,9	14,8	5,8	5,0	3,6
Per cent in kill	13,3	13,3	6,7	6,7	13,3	33,3	13,3	0
PI	1,3	0,8	1,5	0,2	0,9	5,7	2,7	0

* $PI = \frac{\text{per cent in kill}}{\text{per cent in prey}}$

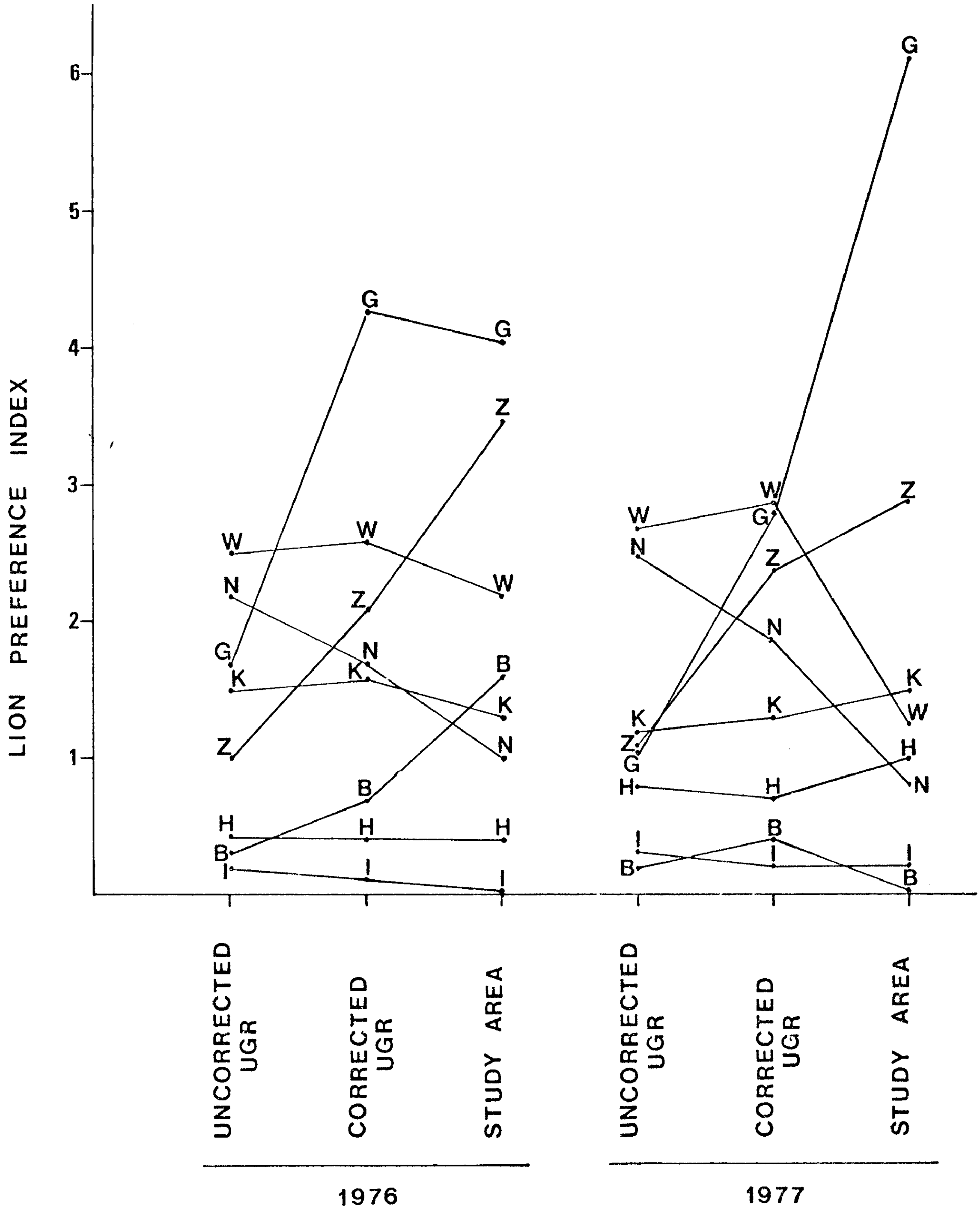


Figure 77. Comparison of lion preference indices in 1976 and 1977 using three sets of results each year; see text for details. W = waterbuck, N = nyala, G = wildebeest, K = kudu, Z = zebra, H = warthog, B = buffalo, and I = impala.

irrespective of their proportionate availability. From Table 43 it can be seen that waterbuck have steadily declined in importance in the lion diet from 35,7 per cent in 1971 to 10,6 per cent in 1976. This supports the belief that the waterbuck population has declined over this period but in no way implies a causal relationship between lion predation and the decline. Two species which have consistantly made up the highest percentages of the lion kill are wildebeest followed by nyala. Pienaar (1969) in the Kruger National Park and Hirst (1969) in a nearby reserve both recorded wildebeest as being the species making up the highest percentage of lion kills. Even so, when the availability of prey was considered, Pienaar (1969) found waterbuck to have the highest preference index. This finding may be correct but it should be treated with caution since Pienaar (1969) also calculated waterbuck to be the second highest preferred prey of cheetah, wild dog (*Lycaon pictus*) and leopard, which may indicate constant underestimation of the waterbuck population relative to other species rather than true preference by these four predators.

Poaching

Waterbuck are also a favoured prey of another predator in UGR, man. Between 1970 and 1977, 49 deaths of ungulates were recorded from poaching, of which 34,7 per cent were warthog, 30,6 per cent waterbuck, 22,4 per cent nyala and 12,2 per cent kudu. Poaching is mainly carried out with spears and dogs, which favours waterbuck as a prey item since they can be brought to bay in water (Hanks *et al.* 1969) or in thick bush and then speared. The relative ease with which they are taken is attested to by the following episode. During August 1976 three poachers plus six dogs ran within 100 m of my squaredavel chasing three yearling female waterbuck which were showing signs of exhaustion and moving slowly only 30 m ahead of their pursuers. On this occasion the hunt was disrupted and two dogs shot but the next week a collared male waterbuck (Male 8) was snared and the meat taken, 500 m from my house (Fig. 78); heavy-duty truck brake cable was used for the snare. The absolute numbers of animals poached is probably much greater than is indicated by the death record. The meat is obviously palatable to poachers as it was to most of the black staff in the reserve.

Figure 78. The remains of collared waterbuck Male 8, snared in the main study area during August 1976.

Non-predator deaths

Between 1970 and 1977, 28 adult waterbuck were recorded dead of non-predator causes (Fig. 79). Deaths were reported from fighting, from broken bones usually associated with falls, from drowning or being stuck in mud, during parturition, from poor condition and from unknown causes. Deaths of animals in poor condition only occurred in late winter and in one year four such deaths were reported after exceptionally cold wet weather. Deaths from unknown causes were observed during the late dry season and summer, while fighting mortality, including one female, was restricted to winter months which coincides with the believed peak in conceptions (see Chapter 5). Spinage (1970) believed death from fighting to be not uncommon in waterbuck and Herbert (1972) recorded a male dying from peritonitis as a result of a horn wound. Details of deaths from fighting and other non-predator causes will be discussed below after details of individual carcass examinations have been given.

Seasonality of adult deaths

Monthly frequencies of adult waterbuck deaths resulting from all causes are shown in Fig. 80 for the period 1970 to 1977. A peak in deaths occurs during winter months as was found for non-predator mortality analysed separately. The mean monthly number of deaths in winter (April to September) was 3,6 which is significantly more (t = 2,27, df = 94, $0{,}01 < P < 0{,}05$) than the mean number of 2,5 found in summer (October to March). The high value for March results from 14 deaths all recorded in 1973 in one area of UGR and attributed to lion and unknown causes. When this figure is omitted the significance of the winter peak in deaths is increased considerably (t = 3,17, df = 93, $0{,}001 < P < 0{,}005$). The overall pattern suggests that irrespective of the proximate cause of death, stress over the winter months probably plays an important role in increasing mortality of adults at that time.

Adult mortality and recruitment

Fifteen adult waterbuck were found dead in the main study area during 1976 and eight during 1977. These figures represent 16,3 per cent and 11,3 per cent of the one year + population as given by the maximum number seen estimates for each year (see Chapter 3). In

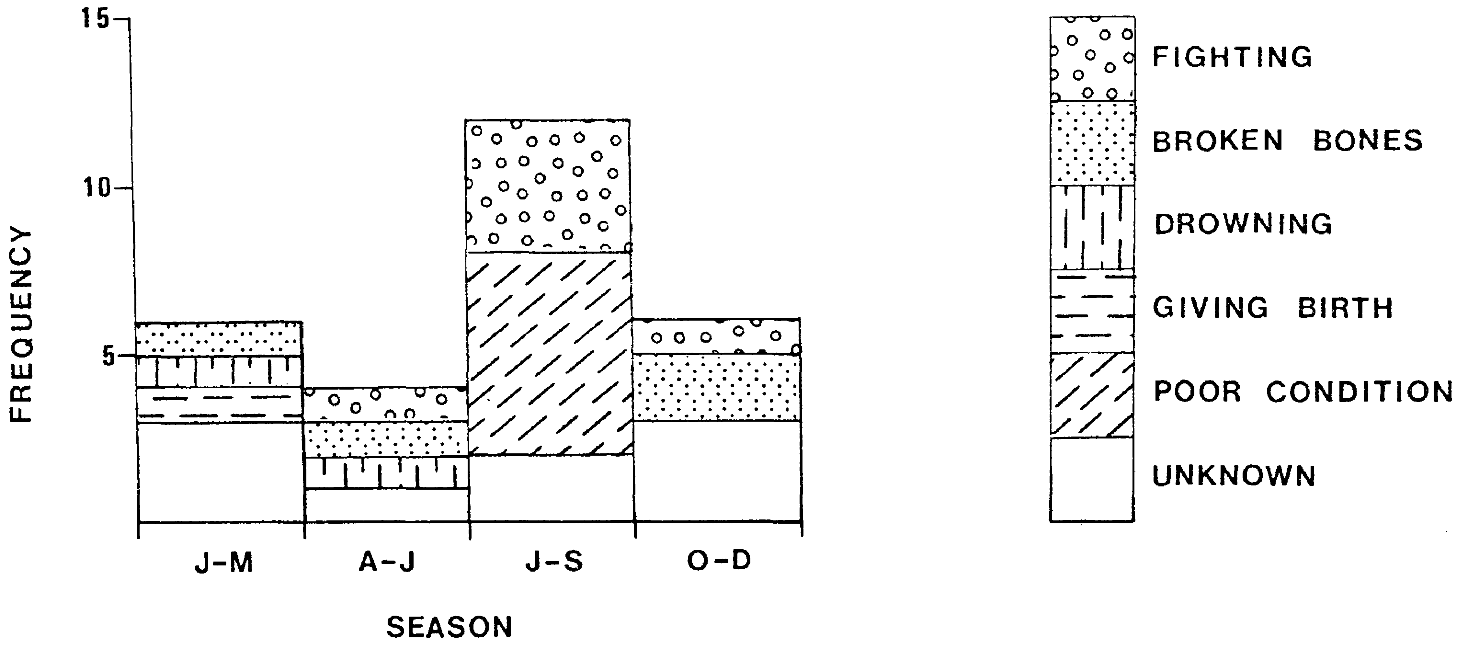


Figure 79. Details of 28 adult waterbuck deaths reported from non-predator causes between 1970 and 1977 in the Umfolozi Game Reserve.

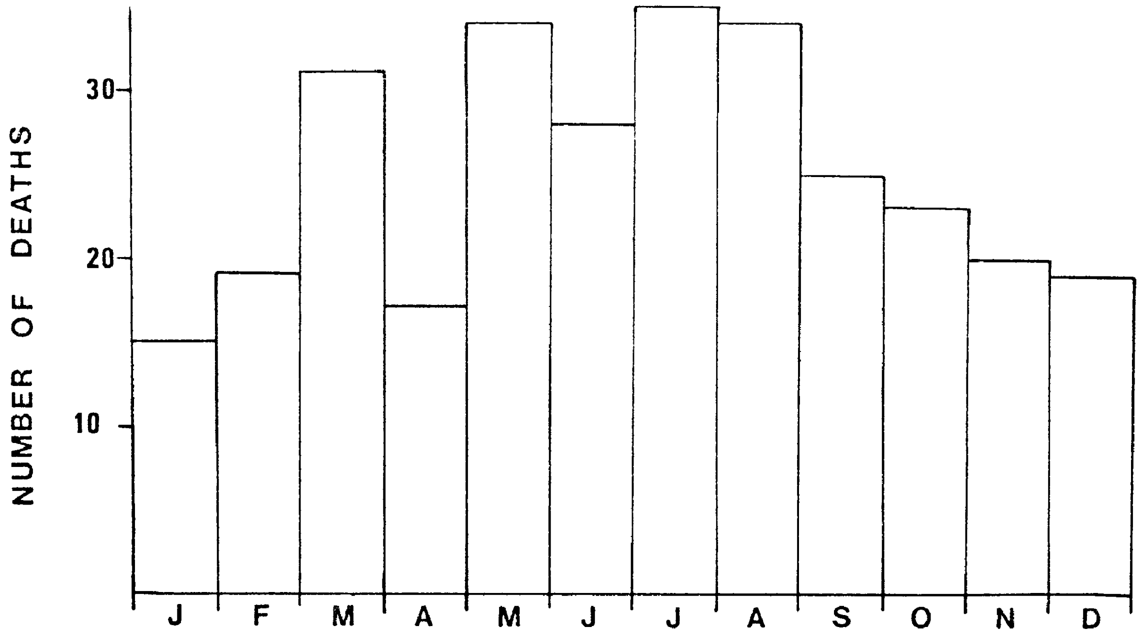


Figure 80. Monthly frequencies of adult waterbuck deaths in the Umfolozi Game Reserve from 1970 to 1977.

Chapter 5 recruitment to this segment of the population was calculated as 7,2 per cent at the end of both 1976 and 1977. This means that the population declined by an estimated 9,0 per cent in 1976 and 4,4 per cent in 1977. These figures support previous negative values for the rate of population increase as given by $\bar{r}$ and r_s estimates.

Juvenile mortality records

Only 35 records of juvenile waterbuck deaths were recorded in UGR from 1970 to 1977. This is no doubt owing to the often complete consumption of these carcasses by predators and scavengers. Of these, 14 were cause unknown, seven were non-predator deaths with animals in poor condition and frequently severely infested with ticks, five were cheetah kills, three were lion kills, two were leopard kills, one was a jackal kill and one had been poached. In the Kruger National Park, Pienaar (1969) found that cheetah, leopard and wild dog took mainly young waterbuck while lion killed mainly adults. In the Sabi-Sand Reserve Herbert (1972) reported that 70,1 per cent of waterbuck calves predated were taken by leopard and none by lion. Elliott (1977) believed that the high juvenile mortality of waterbuck which she recorded in Kenya was probably related ultimately to low rainfall and poor nutrition. In UGR the few data available make it difficult to point to a main cause of juvenile mortality. It is significant though that here 33 per cent of calf deaths of known cause have been attributed to non-predator factors, while a similar figure for the Sabi-Sand Reserve is three per cent (Herbert 1972). It is quite probable that these few non-predator deaths in UGR are indicative of a much higher mortality rate from such causes considering the speed with which these small carcasses are scavenged.

It is possible to follow this line of speculation further by examining the seasonality of deaths of both juvenile and immature carcass classes (Fig. 81). The majority of deaths of both calves and yearlings occur during the first three months of the year. The proportion of yearlings involved is probably higher than that indicated in Fig. 81 since as described above yearlings were sometimes classed as juveniles at this time in the UGR death record. This trend would not be very interesting if only young of the year were involved since many factors could cause high neonatal mortality. Because animals aged approximately one year are also included raises a number of questions. If predation were the main cause of mortality in young, why would a

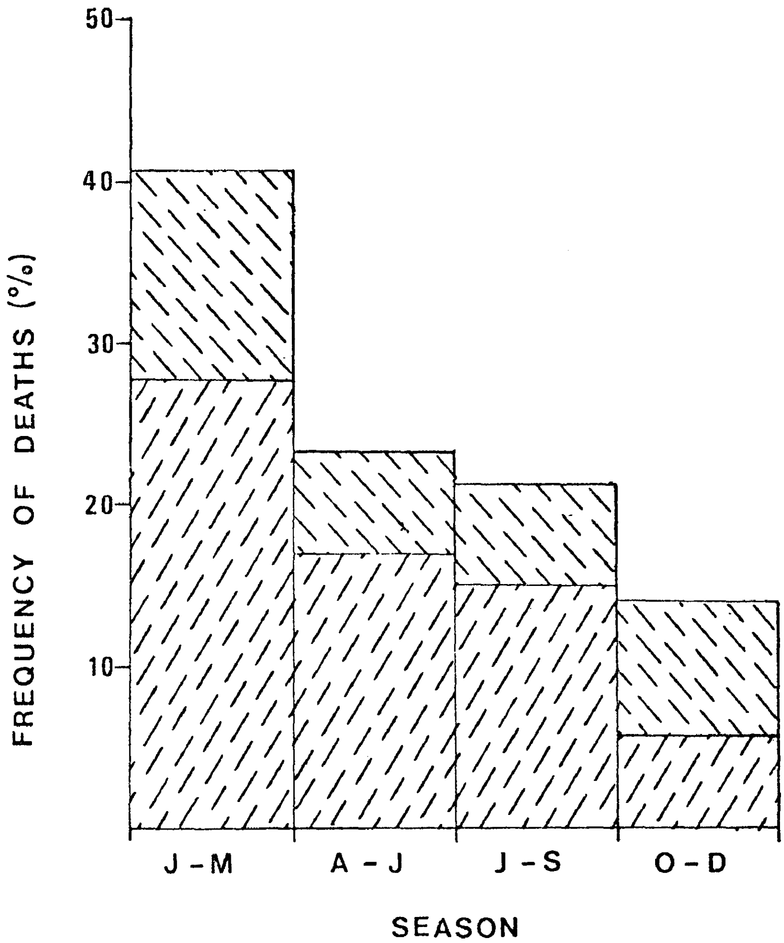


Figure 81. Seasonality of calf (/,/) and yearling waterbuck (\,\) deaths in the Umfolozi Game Reserve for the period 1970 to 1977.

peak occur during late summer that included yearlings? If poor condition were a prime factor a peak during winter would be expected as found for adults. These results suggest that the main cause of calf and yearling mortality operates seasonally during late summer and that the mortality factor responsible is different from a main one occurring in adults.

Figure 82 shows the results of noting when severe tick infestations occur on waterbuck. Severe infestations are virtually confined to the first three months of the year. This is also the period when all deaths of calves and yearlings with severe infestations have been recorded. Herbert (1972) observed high infestations of ticks on waterbuck in the Sabi-Sand Reserve from January to June. Table 45 shows that both adult male and female waterbuck are similarly affected at this extreme level of infestation, but Tables 46 and 47 indicate that yearlings and calves suffer significantly more often from severe infestations than adults ($P < 0{,}01$ and $P < 0{,}05$).

These results show that severe infestations of successfully engorging adult ticks fulfil the criteria of a possible main juvenile mortality factor causing a summer increase in deaths, in terms of both seasonality and age-specificity. Details of ticks involved and the possible pathology of infestation will be given below from examination of carcasses and immobilised animals. It will then be suggested that severe infestations of the brown ear tick *Rhipicephalus appendiculatus* are the probable main proximate cause of death in young waterbuck in UGR.

Immobilised animals

Body condition

Of the 26 adults examined during 1976 and 1977, two were classed as in poor condition, three as in moderate condition and 21 as in good condition. These results do not necessarily mean that waterbuck in UGR are generally in good condition. External appearance and body measurements can remain constant while body fat reserves are progressively depleted (Hanks, Cumming, Orpen, Parry and Warren 1976). Also animals were only sampled during the first half of winter whereas it is expected that nutrition would be most limiting during the end of the dry season and early wet season.

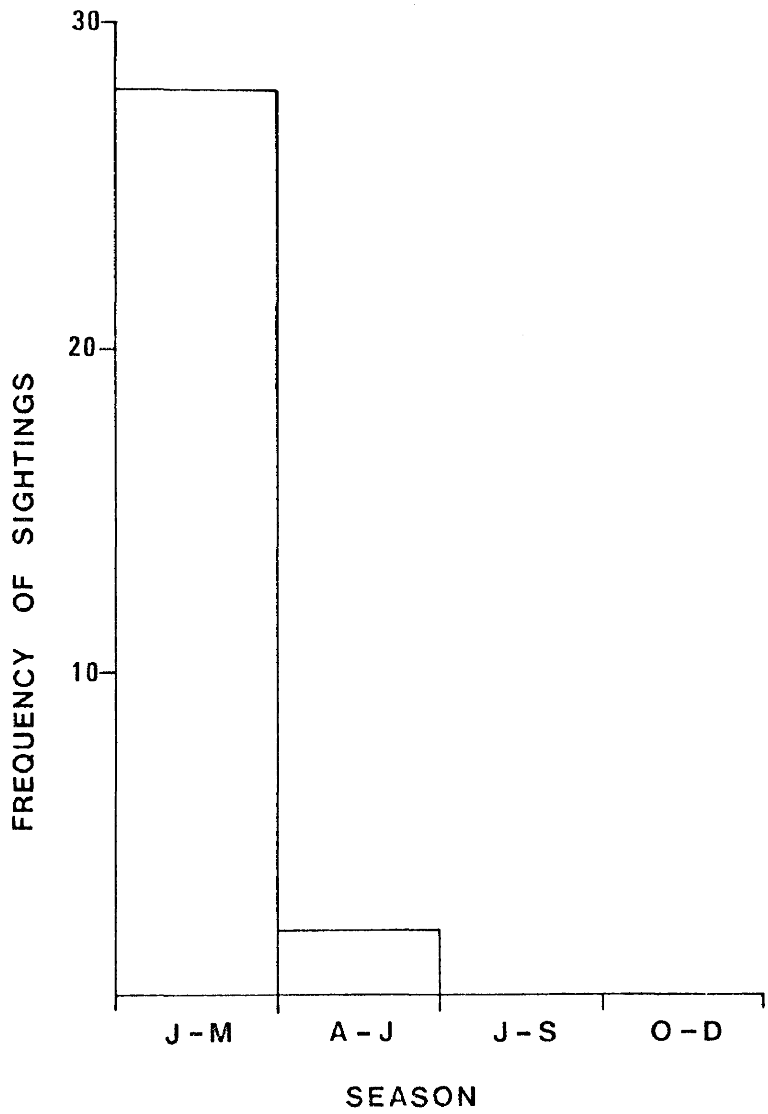


Figure 82. Seasonality of sightings of waterbuck with severe tick infestations in the Umfolozi Game Reserve.

Table 45. Contingency table comparing the frequency of occurrence of severe tick infestations on adult male and adult female waterbuck in the Umfolozi Game Reserve, for those months when severe infestations occurred.

	Ticks severe	Ticks not severe	Total
Adult males			
Observed	7	227	234
Expected	6,1	225,4	
Adult females			
Observed	11	436	447
Expected	11,9	437,6	
Total	18	663	681
χ^2	0,2	0,02	0,22

χ^2 = 0,22, df = 1, P$>$0,75.

Table 46. Contingency table comparing the frequency of occurrence of severe tick infestations on adult and one year-old waterbuck of both sexes in the Umfolozi Game Reserve, for those months when severe infestations occurred.

	Ticks severe	Ticks not severe	Total
One-years			
Observed	6	46	52
Expected	1,7	50,9	
Adults			
Observed	18	681	699
Expected	22,3	676,1	
Total	24	727	751
χ^2	11,7	0,5	12,2

χ^2 = 12,2, df = 1, P$<$0,005.

Table 47. Contingency table comparing the frequency of occurrence of severe tick infestations on adult waterbuck of both sexes and calves in the Umfolozi Game Reserve, for those months when severe infestations occurred.

	Ticks severe	Ticks not severe	Total
Calves			
Observed	6	91	97
Expected	2,9	92,6	
Adults			
Observed	18	681	699
Expected	21,1	679,4	
Total	24	772	796
χ^2	3,8	0,04	3,84

$\chi^2 = 3,84$, df = 1, $0,01 < P < 0,05$.

Tick infestations

Four species of tick were collected from immobilised waterbuck; the brown ear tick, the bont tick (*Amblyomma hebraeum*), the red-legged tick (*Rhipicephalus evertsi evertsi*) and an unidentified *Rhipicephalus* species. The attachment sites of ticks collected during the 1977 sampling are given in Table 48. The majority of ticks were brown ear ticks collected on the head and neck. These results are in agreement with the field observations of tick infestation reported above, where severe infestations of adult engorged ticks were confined to late summer and occurred mainly on the head and neck. *R. appendiculatus* always favours the head, particularly the ears and has a seasonal cycle in South Africa that results in maximum numbers of adults on animals during late summer with larvae and nymphs following through the winter (Mönnig and Veldman 1970, Londt, Horak and de Villiers (in press)).

Four animals were classed as having high infestations, 14 as moderate and 14 as low. Since severe infestations were caused by *R. appendiculatus*, their absence is to be expected during the immobilisation periods.

Herbert (1972) recorded the same three tick species on waterbuck in the Sabi-Sand Reserve, while Theiler (1962) lists 18 species collected from waterbuck. Baker and Keep (1970) collected *R. appendiculatus*, *R. evertsi*, *R. maculatus*, *R. muhlensi*, *R. simus* and *Boophilus decoloratus* from waterbuck in Zululand. Elliott (1977) found *R. appendiculatus* to be the most common tick on waterbuck in Kenya.

Haematology and blood chemistry

The effects of immobilisation and excitement on blood assays. Before examining mean values for blood parameters measured in the 1976 samples it is necessary to consider the effects of drugs and handling on these figures. The results of blood analyses carried out on samples taken at the beginning and end of the immobilisations in 1977 are given in Table 49. Apart from cholesterol all assays are lower in the second sample,significantly so for phosphorus and total protein ($P <$ 0,05). This suggests that the drugs do cause haemodilution and that this is increasing for some time after darting. When absolute values are considered, however, it is concluded that for interpretive purposes

Table 48. The attachment sites of ticks sampled from four adult waterbuck in the Umfolozi Game Reserve during July 1977.

	Rhipicephalus appendiculatus				*Amblyomma hebraeum*			*R. evertsi evertsi*		R. sp.
	M	F	N	L	M	F	N	M	F	M
Neck	6	5	55	22	0	0	0	0	0	0
Ear	63	30	278	25	0	0	0	0	0	0
Brisket	25	8	8	2	1	0	0	0	0	0
Belly	1	0	14	0	4	3	3	0	0	0
Feet	0	0	23	1	0	0	17	0	0	1
Tail	0	0	34	2	0	0	2	0	0	0
Anus	0	0	2	0	2	0	0	1	1	0

M = male; F = female; N = nymph; L = larvae.

Table 49. Comparison of the values of seven blood parameters in samples taken at the beginning and end of the immobilisation of four waterbuck during July 1977, using the Student's t test for paired variates.

	Packed cell volume (per cent)	Haemoglobin (g/dl)	Inorganic phosphate (mg/dl)	Total protein (g/dl)	Albumin (g/dl)	Blood urea nitrogen (mg/dl)	Cholesterol (g/dl)	Red cell count ($x10^6 mm^3$)
Beginning $\bar{x}$	31,3	10,8	6,1	7,3	2,6	13,2	193	9,14
End $\bar{x}$	30,5	10,5	5,3	6,9	2,5	12,8	194	8,76
Significance								
Sd	1,49	0,46	0,44	0,21	0,10	1,48	22,9	0,62
t	1,07	1,42	3,83	3,18	1,57	0,61	-0,11	1,15
	$P>0,4$	$P>0,2$	$0,01<P<0,05$	$P = 0,05$	$P>0,2$	$P>0,4$	$P>0,5$	$P>0,2$

$\bar{x}$ = mean value

Sd = standard deviation of difference

blood levels are stable once immobilisation has been effected. This is helpful since the time lapse between darting and taking blood varied considerably in 1976 (see Appendix 2). The question still remains as to how these depressed values relate to values from a resting animal. Lewis[1] (pers. comm.) experimented with this problem by taking blood samples from three drug immobilised blesbok and then shooting the animals a few days later and collecting blood believed to be representative of the resting animal. Although there was some trend for lowering of blood parameters in the immobilised samples he concluded that under these standardised conditions blood samples from a drug immobilised animal were similar to those of a resting one. It is possible that where a marked difference has been observed between samples from drugged and shot animals the cause lies partly in elevated values of the shot sample owing to prior excitement (Drevemo *et al.* 1974).

Figure 83 shows how rectal temperature, an index of excitement, climbed during the immobilisation period for virtually all individuals. As explained in Chapter 7, a more potent tranquiliser was administered in 1977 and Fig. 83 shows that the more sedated animals had lower rectal temperatures. The relationship between low tranquilisation and death will be explained below for two animals that died during immobilisation.

Even though rectal temperatures indicate an excited state for most animals when they are compared to resting values (Taylor, Spinage and Lyman 1969), the results suggest that the effects of drugs causing reduced blood pressure and haemodilution outweigh any tendancy for elevation of assays because of excitement. Therefore assays obtained may approximate to resting values as found by Lewis. Unfortunately this is definitely not so for juvenile waterbuck as these were not drugged but only hand restrained. These animals all had very high rectal temperatures (Fig. 83) and since no drugs were given blood values are expected to be elevated over resting values as found by Gartner *et al.* (1965) and Franzmann (1972).

<u>Blood assays.</u> Frequency histograms for all blood assays carried out in 1976 are shown in Figs. 84 and 85. Unfortunately virtually no data were found for waterbuck elsewhere with which to compare

1. Dr A.R. Lewis, Veterinarian, Natal Parks Board.

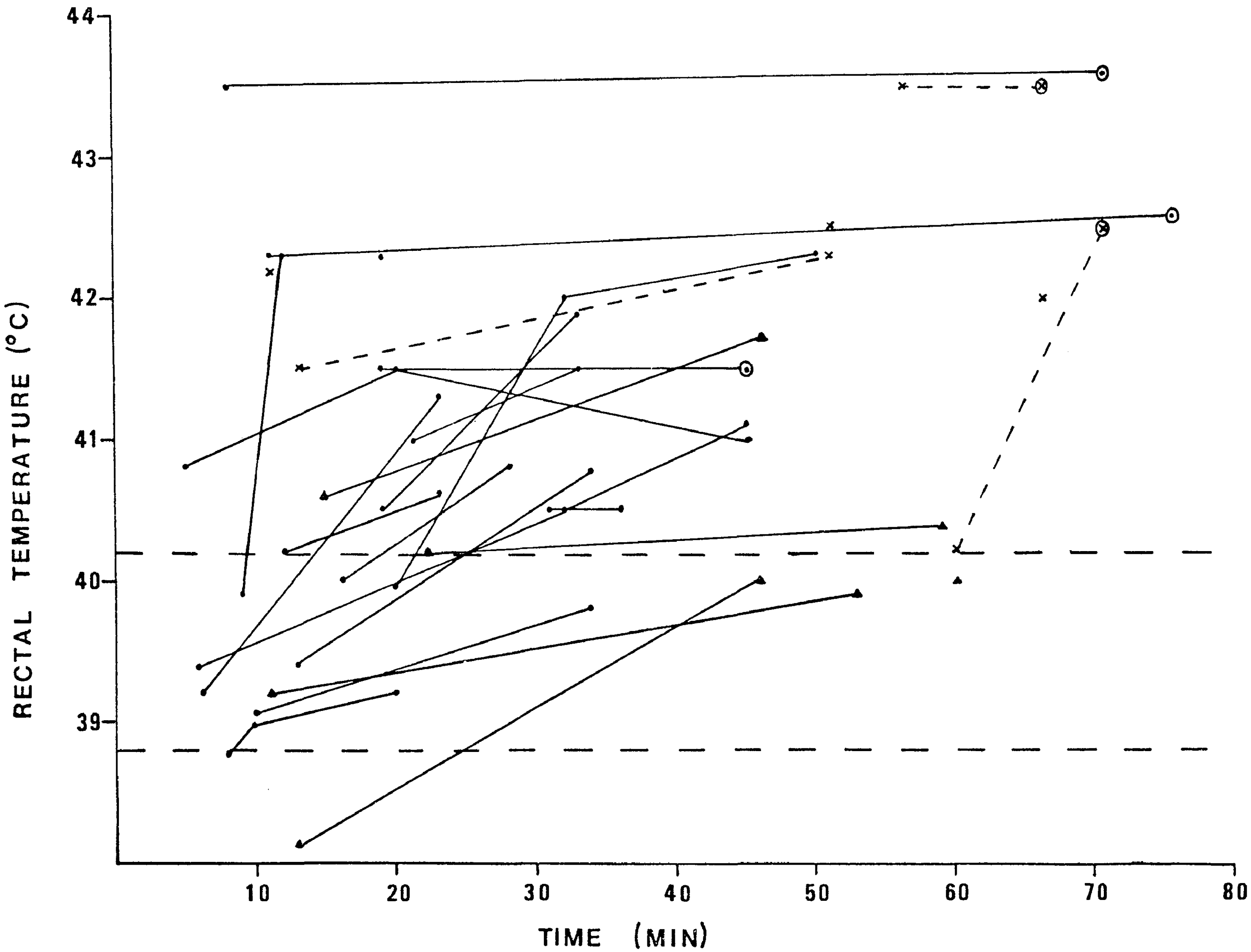


Figure 83. The relationship between waterbuck rectal temperature and time since darting (with minimal sedation (•) and with good sedation (▲)), or time since hand restrained (x). Circles around a symbol denote death; joined symbols refer to individuals. Horizontal dashed lines denote resting values for ambient temperatures of 25 °C and 40 °C (Taylor *et al.* 1969).

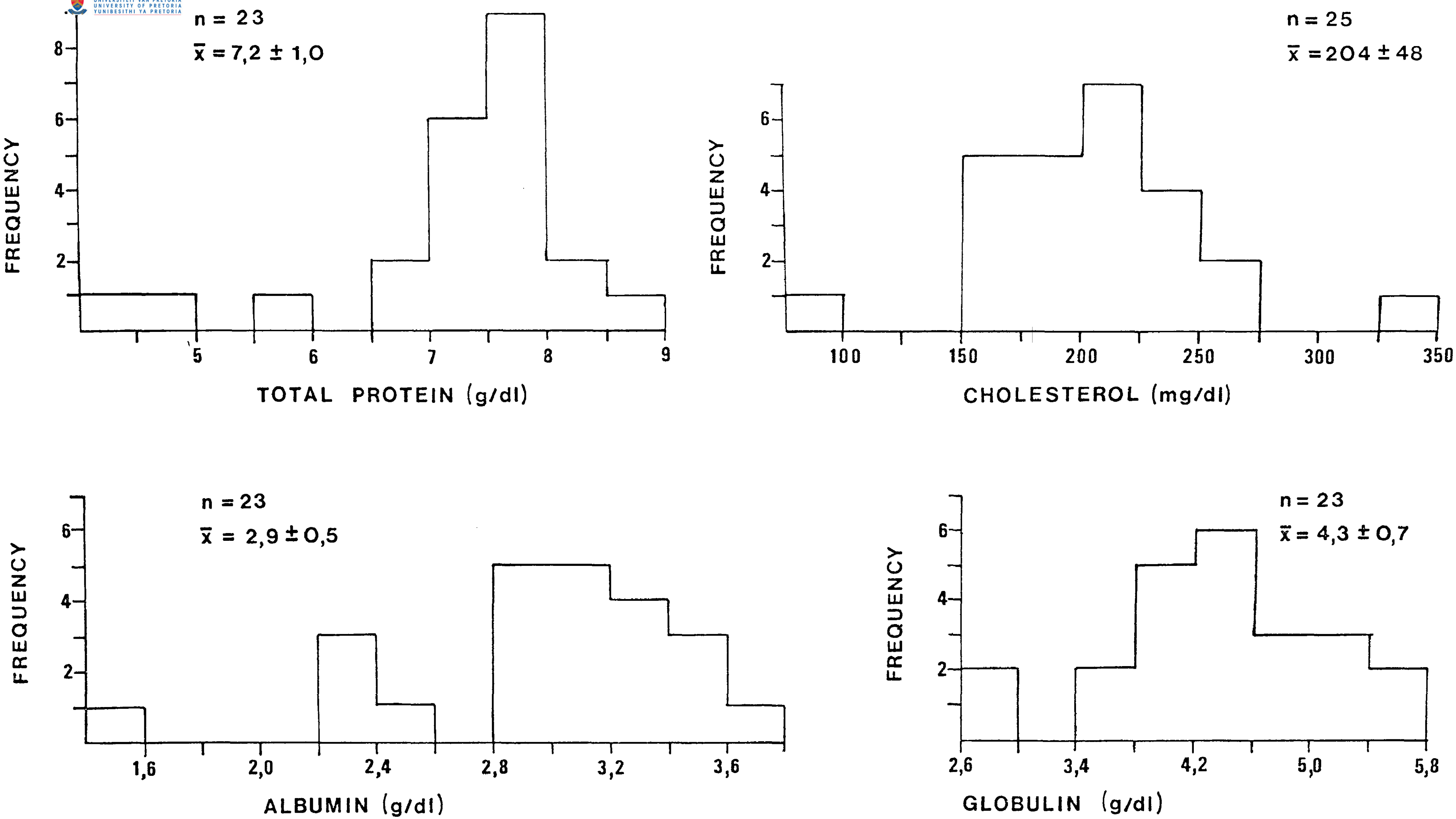


Figure 84. Waterbuck blood assays; frequency histograms for serum total protein, cholesterol, albumin and globulin from animals sampled during 1976; the sample size, mean and standard deviation are given.

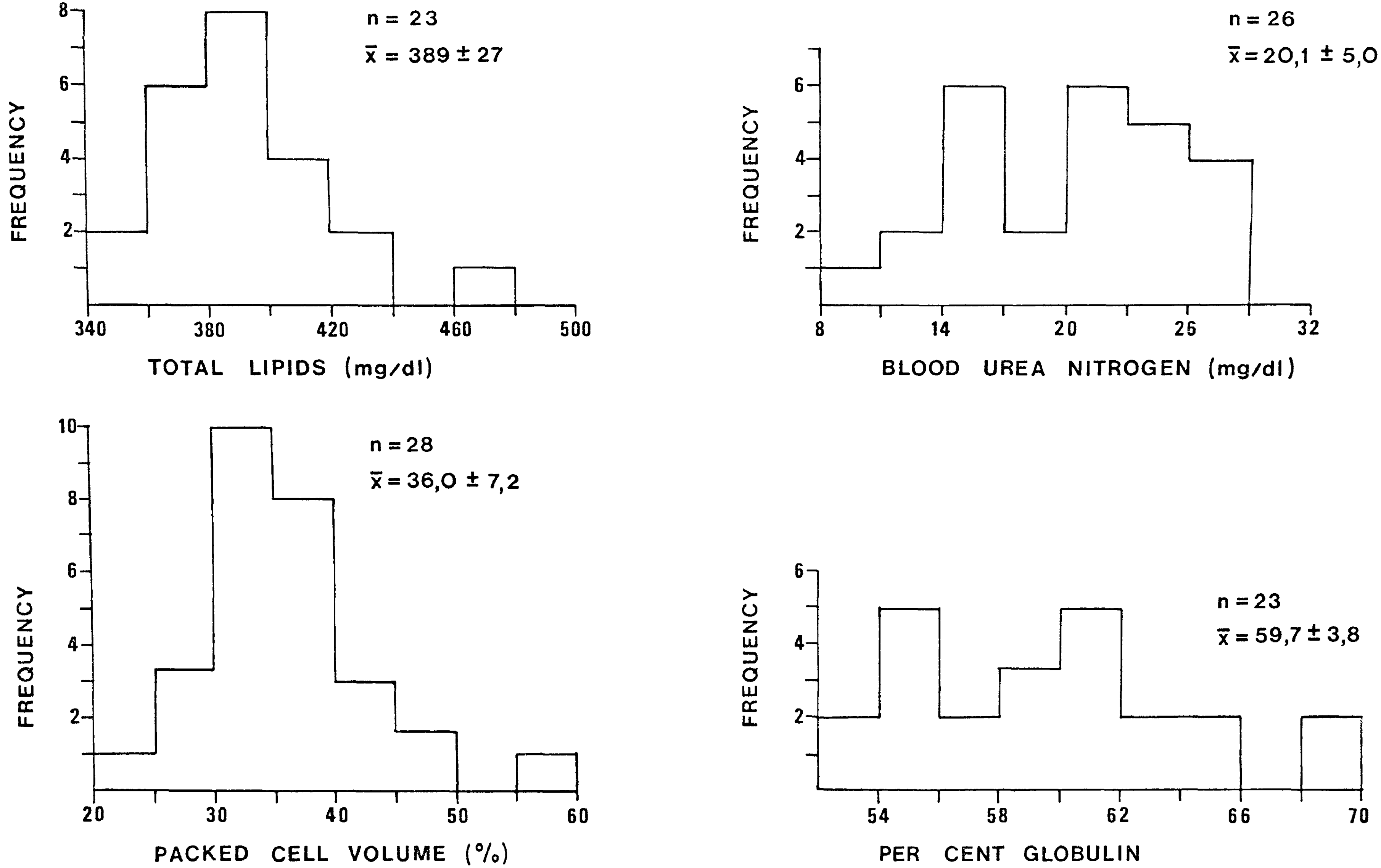


Figure 85. Waterbuck blood assays: frequency histograms for serum total lipids, blood urea nitrogen, packed cell volume and per cent globulin from animals sampled during 1976; sample size, mean and standard deviation are given.

these results. Values for other ungulates are given for comparison as are normal bovine levels taken from Cornelius and Keneko (1963) and Anon. (1977). This is done as a starting point in interpretation of waterbuck blood chemistry and haematology and agreement between waterbuck values and values for other species in no way implies normality for the waterbuck samples.

The mean total protein concentration of 7,2 g/dl is well within the ranges reported for other African ungulates (Cooper, Stuttaford and Carmichael 1975, Keep 1976, Kreulen[1] pers. comm.)., for North American ungulates (Franzmann 1972, Seal, Verme, Ozoga and Erickson 1972, LeResche *et al.* 1974, Pedersen and Pedersen 1975) and for normal bovine values which lie between 6 and 8 g/dl. De Smet (1978) gave a value of 6,7 g/dl total protein concentration for a common waterbuck serum sample.

The mean serum albumin figure of 2,9 g/dl is a little below the normal bovine range of 3,1 to 3,7 g/dl, but still above mean values reported for buffalo, wildebeest, lechwe and warthog in Botswana (Cooper *et al.* 1975) and for nyala, black rhino and white rhino in Zululand (Keep 1976).

Mean waterbuck globulin concentration was 4,3 g/dl, which results in a figure of 59,7 per cent globulin and an albumin:globulin ratio of 0,7:1. Cooper *et al.* (1975) measured species mean globulin levels ranging from 2,6 g/dl in springbok (*Antidorcas marsupialis*) to 5,8 g/dl in buffalo. Normal bovine values lie between 3,7 g/dl and 4,4 g/dl with an albumin:globulin ratio of 0,9:1.

The mean BUN value of 20,1 mg/dl is similar to that of wildebeest in Serengeti (Kreulen pers. comm.) but at the lower end of the normal bovine range of 20 to 30 mg/dl. Kirkpatrick *et al.* (1975) working with white-tailed deer fawns recorded means of 22,0 mg/dl and 25,2 mg/dl for animals on two high protein diets and values of 12,8 mg/dl and 9,3 mg/dl for animals on low protein diets. Franzmann (1972) suggested that values less than 15 mg/dl reflect inadequate protein intake in bighorn sheep and that values between 15 and 20 mg/dl represent a potential problem. In 1977 the mean waterbuck assay at first sampling was only 13,2 mg/dl suggesting that waterbuck undergo a swift decline in dietary protein as winter progresses. The 1977 winter was more prolonged than that in 1976 (see Chapter 2) and waterbuck were sampled six weeks later in 1977. No other parameters were markedly

1. Dr D.A. Kreulen, Haren, Holland.

lower in 1977 suggesting as found by other workers that BUN is the first measure to reflect a change in dietary intake.

Mean figures for serum cholesterol and total lipids are 204 mg/dl and 389 mg/dl, which are generally higher than have been reported for temperate species (Bjarghov *et al.* 1975, Coblentz 1975) or other African ungulates (Harthoorn 1975, Seal, Barton, Mather and Gray 1976, Seal and Shobert 1976, Jeffrey[1] pers. comm.). They are however similar to levels found in common reedbuck (*Redunca arundinum*) in Zululand (Lewis pers. comm.). One obviously haemolysed waterbuck sample gave a cholesterol reading of 350 mg/dl and was excluded from further calculations. Harthoorn (1975) and Lewis (pers. comm.) have both associated haemolysis with serum cholesterol values over 200 mg/dl. It is possible, but unlikely, that the high level for cholesterol results from general low level haemolysis to which this parameter appears particularly sensitive. More likely the normal range for cholesterol in waterbuck is higher than most herbivores, as for example it is in the gopher (*Geomyidae*) where a mean value of 262 mg/dl has been reported (Caroll 1963). Normal bovine cholesterol values lie between 80 and 120 mg/dl.

The mean packed cell volume of 36 per cent is in the centre of the bovine range of 27 to 43 per cent. Franzmann (1972) however, described PCV values of 40,4 per cent for low condition bighorn sheep and 50,5 per cent for good condition animals. Drevemo *et al.* (1974) recorded PCVs in nine ungulate species in Kenya and found species means to range from 25,0 per cent in buffalo to 44,9 per cent in Thompson's gazelle (*Gazella thomsoni*).

Results of three additional assays carried out in 1977, haemoglobin, phosphorus and a red cell count, are given in Table 49; all fall within the ranges of normal bovine values. No results have been presented for serum free fatty acids since it is believed that storage of frozen samples for one month prior to analysis caused elevated readings as found by Procos *et al.* (in press). Values for the four animals were between 1,92 and 2,43 mM/l. FFA appear to have little potential for use in free-ranging wildlife studies because of this sensitivity to serum storage.

The lack of comparable data for waterbuck elsewhere makes these results difficult to interpret. When such data become available

1. Mr R. Jeffrey, University of Natal, Pietermaritzburg.

and details of the collection method of samples and demography of the population are also given, the knowledge of habitat relations for both populations will be increased. Some more information can be extracted at this time by examining the interrelations between parameters. Waterbuck BUN assays suggest that as found in other studies this chemical reflects immediate dietary intake and that protein requirements are not met from mid-winter until summer. Figures 86 and 87 show the relationship between BUN and four other blood parameters. The comparison with total protein suggests that this chemical remains high except when very low BUN levels occur. Such buffering of total protein was mentioned by LeResche *et al.* (1974). Cholesterol shows a more linear relationship with BUN suggesting that it too changes quickly with quality of diet. Neither PCV nor total lipids show any relation to BUN but neither are they correlated to each other (Fig. 88). These results indicate that PCV and serum total lipids represent something other than immediate diet and therefore may reflect condition with respect to past events in the same way that KFI and BMF do.

This comparison has been very speculative but it serves to point out an area needful of controlled experimental research. The problem is to define the speed at which blood levels of various parameters change once the plane of nutrition changes and to find the extent to which fat reserves affect the attainment of new values. BUN is useful in reflecting lowered quality of diet but it does not fulfil the role of a physiological condition index in allowing assessment of the resilience of an animal to withstand a poor diet.

Blood assays, age and sex. Significant ($P<0,05$) differences occur between adult males, adult females and juveniles with respect to the levels of serum globulin, total lipids and PCV (Table 50). Juvenile values are lower than adult values for all blood chemicals except for cholesterol; PCV figures are equivalent. It has been described above that juvenile assays will be elevated over resting values because of handling stress. The finding of generally lower levels suggests that juveniles may be in considerably poorer condition than adults. This is again speculative and more data are required to settle the problem.

Blood assays and body condition. As was recorded above only two animals were classed as being in poor condition judging from

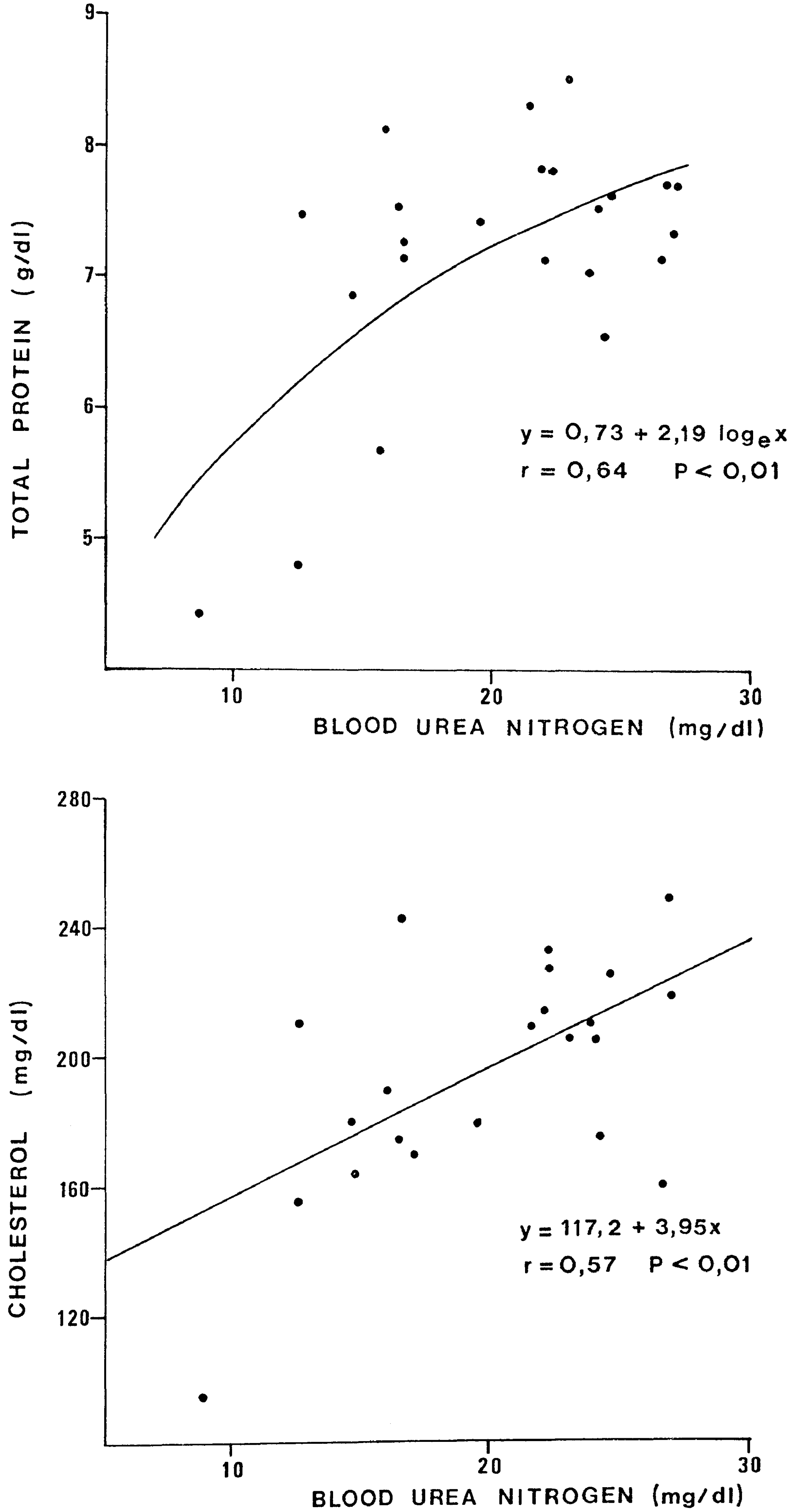
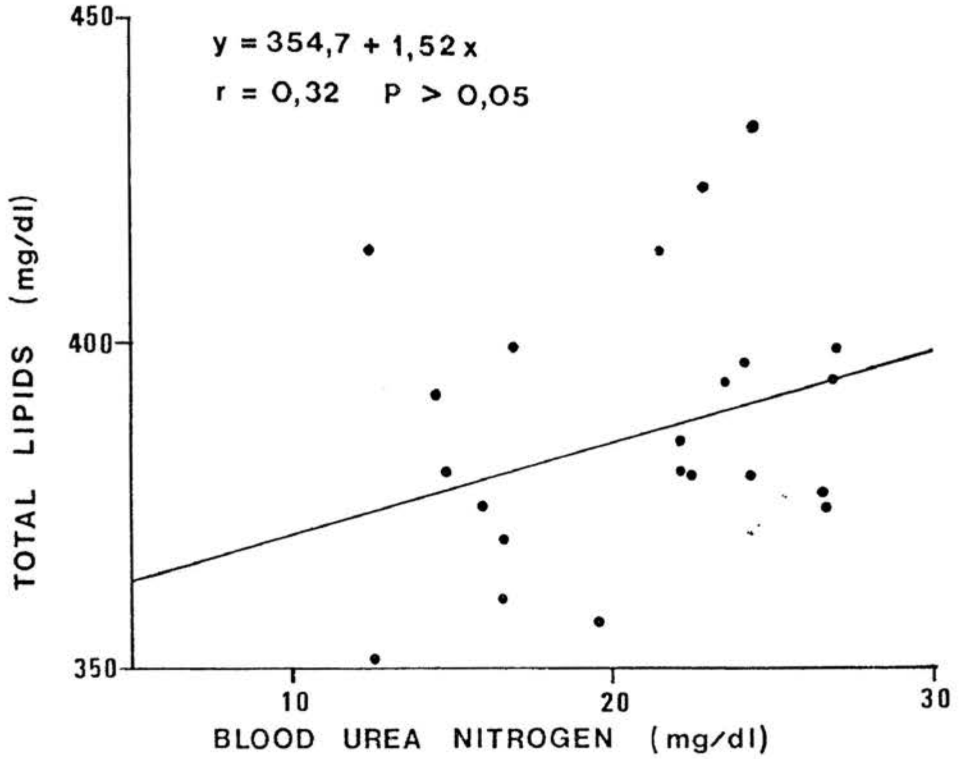


Figure 86. Waterbuck blood assays: relationships between serum total protein and blood urea nitrogen and between serum cholesterol and blood urea nitrogen for animals sampled during 1976.



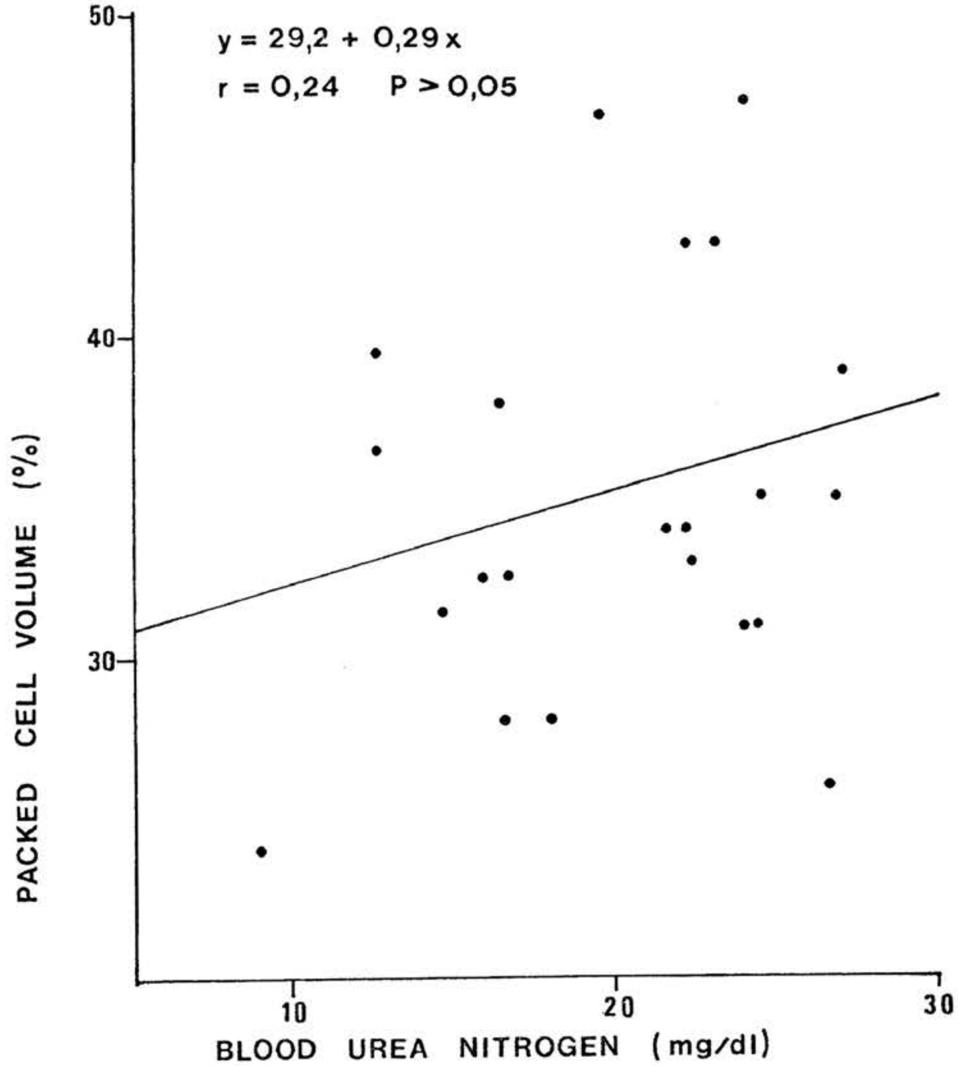


Figure 87. Waterbuck blood assays: relationships between serum total lipids and blood urea nitrogen and between packed cell volume and blood urea nitrogen for animals sampled during 1976.

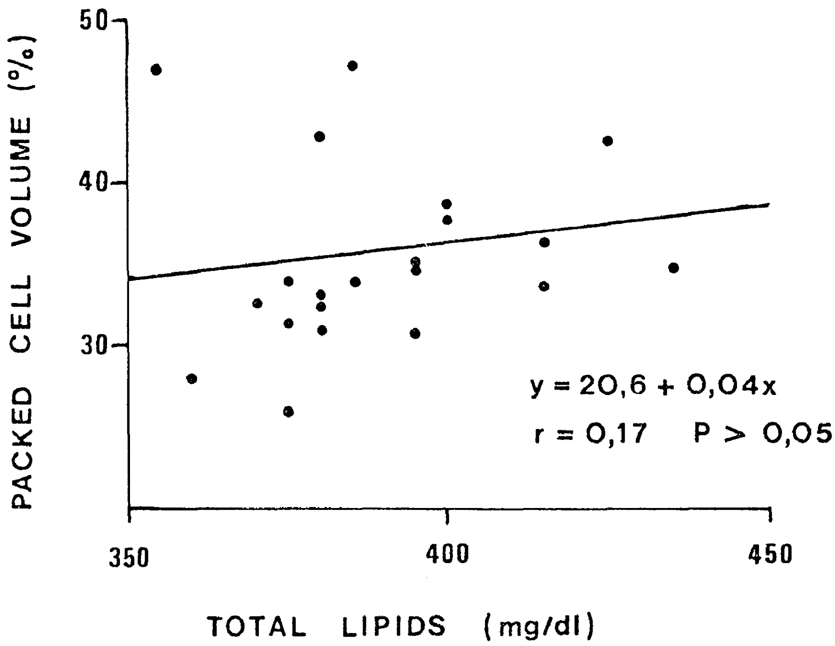


Figure 88. Waterbuck blood assays: relationship between packed cell volume and serum total lipids for animals sampled during 1976.

Table 50. Comparison of blood assays for adult male, adult female and juvenile waterbuck from the Umfolozi Game Reserve, using a one way analysis of variance.

Blood parameter		Adult male	Adult female	Juvenile	Significance
Cholesterol (mg/dl)	$\bar{x}$	196	192	200,0	NS
	n	9	12	2	
	s	26,1	40,8	80,7	
Total protein (g/dl)	$\bar{x}$	7,6	7,1	6,0	NS
	n	9	12	2	
	s	0,4	1,1	1,8	
Albumin (g/dl)	$\bar{x}$	2,9	2,9	2,7	NS
	n	9	12	2	
	s	0,3	0,6	0,7	
Globulin (g/dl)	$\bar{x}$	4,7	4,2	3,3	F = 4,18 P<0,05
	n	9	12	2	
	s	0,4	0,7	1,1	
Per cent globulin	$\bar{x}$	61,5	59,2	55,2	NS
	n	9	12	2	
	s	3,7	5,4	1,4	
Total lipids (mg/dl)	$\bar{x}$	382,2	400,4	355,0	F = 3,65 P<0,05
	n	9	12	2	
	s	17,0	28,6	21,2	
Blood urea nitrogen (mg/dl)	$\bar{x}$	21,3	21,7	17,7	NS
	n	9	12	5	
	s	4,9	5,4	3,4	
Packed cell volume (per cent)	$\bar{x}$	38	33	36	F = 3,82 P<0,05
	n	10	12	6	
	s	8,3	5,3	5,2	

$\bar{x}$ = mean; n = sample size; s = standard deviation of sample;
NS = P>0,05.

external appearances; both were adult females. One animal had low values for serum cholesterol, total protein, albumin, BUN and PCV; the readings were 95 mg/dl, 4,4 g/dl, 1,5 g/dl, 8,8 mg/dl and 24 per cent respectively. The other animal showed usual Umfolozi waterbuck values except for cholesterol and PCV which were low at 160 mg/dl and 26 per cent; no measurement of total lipids was made for this sample. These results support the conclusion already drawn that during times of poor condition many blood parameter values are lowered. The evidence from the second animal suggests that PCV and cholesterol may reflect physiological condition rather than immediate dietary intake. This is in agreement for above findings for PCV, but not for cholesterol which was more linearly related to BUN. The sample size for these observations is small and the results in need of confirmation.

Blood assays and tick infestation. The only significant ($P < 0,01$) difference between the three infestation classes is for increased percentage globulin with high tick loads (Table 51). This results from both reduced albumin and increased globulin and could reflect lowered feeding efficiency related to the irritative aspect of ticks or increased secondary infection resulting from tick sores. It is not surprising that no more marked relations were seen since severe infestations are virtually confined to late summer. The effects of these severe infestations can only be gauged in a winter sample in terms of mean population blood values, the significance of which are at present uncertain.

Blood assays and blood parasites. The only parasites observed in blood slides were *Theileria* sp. and *Babesia* sp. piroplasms seen in erythrocytes. The forms of these piroplasms are shown in Fig. 89 and their frequency of occurrence is given in Table 52. Piroplasms are somewhat more common in juveniles than adults, particularly *Babesia* sp. which occurred in three of six juveniles but in only one of 25 adults. *Theileria* sp. occurred in 60 per cent of adults but all at very low rates of less than 1/6 000 cells, and in four of six juveniles including erythrocyte infection rates of 1/3 000 and 1/1 000 cells. These results suggest a high incidence of low level *Theileria* sp. infection indicative of a carrier state as described by Wilson, Bartsch, Bigalke and Thomas (1974) for roan (*Hippotragus equinus*) and sable. Brockelsby and Vindler (1965) also recorded

Table 51. Comparison of values of blood parameters in samples taken from immobilised waterbuck during 1976 in relation to the degree of tick infestation, using a one way analysis of variance.

Blood parameter		Tick infestation Low	Moderate	High	Significance
Cholesterol (mg/dl)	$\overline{x}$	212	198	167	NS
	n	8	12	4	
	s	36,2	51,5	53,3	
Total protein (g/dl)	$\overline{x}$	7,1	7,4	6,9	NS
	n	7	12	4	
	s	1,1	0,8	1,7	
Albumin (g/dl)	$\overline{x}$	3,1	2,9	2,4	NS
	n	7	12	4	
	s	0,5	0,4	0,8	
Globulin (g/dl)	$\overline{x}$	3,9	4,5	4,5	NS
	n	7	12	4	
	s	0,7	0,6	1,1	
Per cent globulin	$\overline{x}$	55,6	60,2	64,5	$F = 7,40$ $P < 0,01$
	n	7	12	4	
	s	28,4	20,5	38,2	
Total lipids (mg/dl)	$\overline{x}$	391	382	409	NS
	n	7	12	4	
	s	28,4	20,5	38,2	
Blood urea nitrogen (mg/dl)	$\overline{x}$	20,7	19,7	20,2	NS
	n	9	13	4	
	s	4,5	4,8	7,9	
Packed cell volume (per cent)	$\overline{x}$	36	35	33	NS
	n	10	13	4	
	s	4,5	8,2	10,9	

$\overline{x}$ = mean; n = sample size; s = standard deviation of sample;
NS = $P > 0,05$.

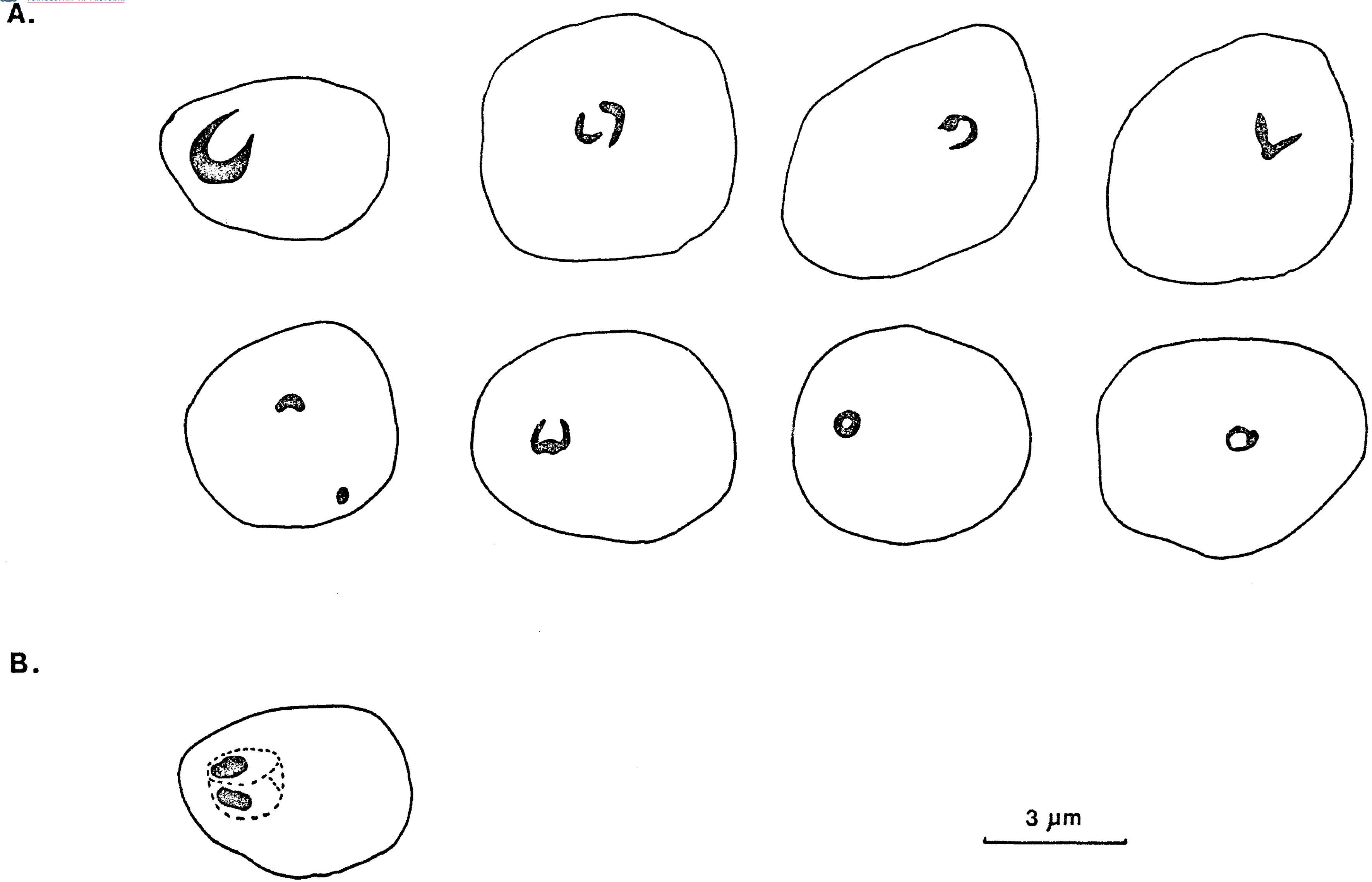


Figure 89. *Theileria* sp. (A) and *Babesia* sp. (B) piroplasms as viewed in the erythrocytes of Umfolozi waterbuck.

Table 52. Erythrocytic infection frequencies for two piroplasm types in Umfolozi waterbuck immobilised during 1976 and 1977.

Piroplasm	Frequency*	Adult male waterbuck	Adult female waterbuck	Juvenile waterbuck
Theileria sp.	absent	2	8	2
	rare	9	5	2
	not rare	0	0	1
	not uncommon	0	0	1
	common	0	0	0
Babesia sp.	absent	10	14	3
	rare	1	0	3
	not rare	0	0	0
	not uncommon	0	0	0
	common	0	0	0

* rare: 1/6 000 cells;
not rare: 1/6 000-1/3 000 cells;
not uncommon: 1/3 000-1/1 000 cells;
common: $<$ 1/1 000 cells.

Theileria sp. in waterbuck in East Africa as did Neitz (1931) and Keep (1970) in Zululand. That these are carrier levels is confirmed by there being no significant difference in blood assays from animals with piroplasms and those without (Table 53).

Virology

All nasal swabs sent for viral studies proved negative. Serum samples are still being tested but as yet no viruses have been isolated.

Carcass examination

Bone marrow

The regression of per cent fat content on per cent dry mass for waterbuck bone marrow is given by y = 1,04x - 7,63 (Fig. 90), which is very close to the general relationship of per cent fat = per cent dry mass - 7 suggested by Brooks *et al.* (1977). Waterbuck bone marrow fat content can probably be adequately calculated from dry mass using either equation.

The few data presented here (Table 54) suggest a sequence of bone marrow mobilisation beginning in the humerus and femur as described by Brooks *et al.* (1977) for four other species. Marrow should therefore be taken from these bones in preference to others as they are probably most sensitive to poor condition.

Animals aged one year and less exhibited generally lower fat content than adults, but this does not necessarily reflect poorer condition. Hanks *et al.* (1976) found bone marrow fat to be of little use as an index of condition in young impala since the marrow is still active in erythrocyte formation.

The sample size is too small to comment on any trends for change in BMF with season. Also any such trends are likely blurred because animals dying from all non-predatory causes have generally lower fat content than animals killed by predators, poachers or during immobilisation, irrespective of season. Elliott (1977) also noted that most waterbuck dying of non-predatory causes had low bone marrow fat content, as judged by visual inspection.

Individual carcass records

Details of carcass examinations where information other than

Table 53. Comparison of blood parameters from waterbuck with and without piroplasm infections.

		Cholesterol (mg/dl)	Total protein (g/dl)	Albumin (g/dl)	Globulin (g/dl)	Per cent globulin	Total lipids (mg/dl)	Blood urea nitrogen (mg/dl)	Packed cell volume (per cent)
Piroplasms	$\bar{x}$	204,4	7,4	3,0	4,3	59,0	383,1	20,3	36,7
present	n	12	11	11	11	11	11	13	15
Piroplasms	$\bar{x}$	203,1	7,2	3,1	3,9	60,3	295,1	19,1	32,9
absent	n	13	10	10	12	10	12	13	12
Significance		t=0,07	t=0,46	t=0,63	t=-0,02	t=0,51	t=-1,05	t=0,23	t=1,50
		$P > 0,1$	$P > 0,1$	$P > 0,1$	$P > 0,1$	$P > 0,1$	$P > 0,1$	$P > 0,1$	$P > 0,1$

$\bar{x}$ = mean; n = sample size.

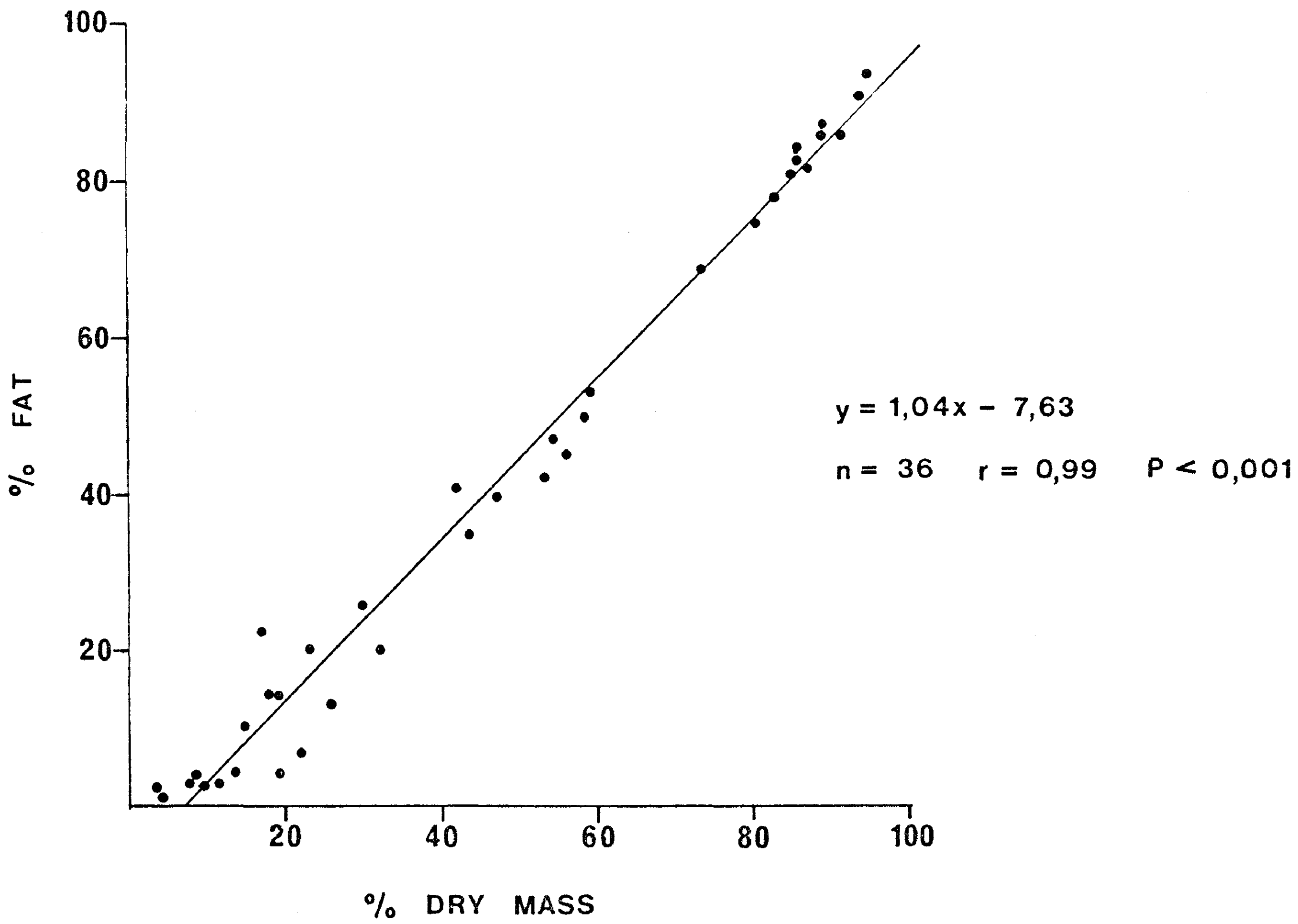


Figure 90. The relationship between per cent fat content and per cent dry mass in waterbuck bone marrow.

Table 54. Fat content of bone marrow obtained from 15 waterbuck carcasses in the Umfolozi Game Reserve during 1976 and 1977.

Carcass number	Sex*	Age (yr)	Date of death	Cause of death	Bone marrow fat (per cent)		
					Femur or humerus	Tibia or radius	Metatarsus or metacarpus
1	F	1,5	9/3/76	Non-predator	34,9	-	-
3	?	0,5	24/3/76	Lion predation	13,3	6,4	39,6
5	M	6,5	23/4/76	Non-predator	2,6	21,7	-
8	F	10,0	6/6/76	During drug immobilisation	83,2	82,1	85,5
9	F	6,0	6/6/76	During drug immobilisation	44,8	93,8	90,2
15	M	5,0	24/7/76	Territorial fighting	2,4	3,1	2,9
24	F	7,0	2/8/76	Poached	78,3	87,1	-
26	M	6,5	16/9/76	Territorial fighting	-	0,6	1,2
30	M	10,0	6/11/76	Non-predator	-	52,9	46,8
31	M	5,0	5/12/76	Poached	68,8	83,0	-
28	M	0,5	11/2/77	Non-predator	10,5	-	-
32	M	10,0	6/6/77	Cause unknown	-	-	41,5
33	M	1,0	29/7/77	Lion predation	3,7	9,7	19,9
34	F	5,0	14/10/77	Lion predation	50,0	81,5	75,0
40	F	1,0	24/3/77	Non-predator	11,2	9,2	5,6

* M = male; F = female.

BMF was collected are given in Table 55. A veterinarian was present for post-mortem examinations of carcasses eight and nine. As yet no results of tissue examination have been received that have been helpful in diagnosing cause of death.

Carcass five was a young adult male which died during April with no predator sign but with a heavy infestation of *R. appendiculatus*. Fat reserves were low as judged by a KFI of 10 and a femur marrow fat content of 2,6 per cent.

Carcass seven was a juvenile male killed by cheetah. It appeared to be in good condition and had milk in the omasum.

Carcasses eight and nine were both adult females which died during drug immobilisation using minimal tranquilisation in 1976 (see Chapter 7). Both animals had been panting heavily prior to death following much muscular activity under drugs. Animal nine had a rectal temperature of 43,6 °C at death, which was the highest recorded; that of animal eight was 42,6 °C. Post-mortem examination of animal nine revealed massive haemorrhaging of the respiratory muscles suggesting respiratory collapse as the cause of death. Haemorrhaging was not as acute in animal eight but the same cause of death was diagnosed. Both animals were immobilised under hot conditions (35 °C) and these results emphasise the need for adequate tranquilisation at such times to limit uncoordinated muscular activity.

Carcass 15 refers to a young adult male that died as a result of territorial fighting during winter. The animal was examined while still alive some 12 hours after fighting. It was lying at the bottom of a 6 m donga with a broken back; the animal was shot and a post-mortem examination made. All tissue analyses were indicative of very poor condition. Both perinephric and bone marrow fat reserves were much depleted, serum total protein, cholesterol, albumin and total lipids were low, but PCV and globulin were well within the recorded waterbuck range. Blood urea nitrogen was elevated indicating either a renal disorder, perhaps resulting from dehydration, or that muscle was being catabolised as an energy source. Blood slides showed a fairly low level piroplasm infection and evidence of slight anaemia in the form of young erythrocytes.

Carcass 26 exhibited an even poorer condition profile than the animal just discussed. It also died after territorial fighting but no serious wounds or injuries were sustained. The animal was seen to stagger for approximately one hour after a fight before collapse

Table 55. Details of waterbuck carcasses examined in the Umfolozi Game Reserve from which tissue samples other than bone marrow were taken.

Carcass number	5	7	8	9	15
Sex	Male	Male	Female	Female	Male
Age (years)	6,5	0,5	10,0	6,0	5,0
Date of death	23/4/76	1/6/76	6/6/76	6/6/76	24/7/76
Cause of death*	N.P.	cheetah	Im.	Im.	T.F.
Body condition	moderate	good	good	good	moderate
Body length (cm)	200	117	199	202	203
Shoulder height (cm)	127	84	114	109	137
Chest girth (cm)	-	-	130	130	144
Neck girth (cm)	73	42	52	54	75
Tick infestation	heavy	moderate	moderate	moderate	low
Incidence of *Theileria* sp. piroplasms in red blood cells	-	-	absent	absent	1/1 000
Kidney fat index	10,0	-	37,4	91,5	13,3
Bone marrow fat (per cent), femur or humerus	2,6	-	83,2	44,8	2,4
Bone marrow fat (per cent), tibia or radius	21,7	-	82,1	93,8	3,1
Bone marrow fat (per cent), metatarsus or metacarpus	-	-	85,5	90,2	2,9
Serum total protein (g/dl)	-	-	5,7	8,6	6,6
Serum cholesterol (mg/dl)	-	-	165	205	130
Serum urea nitrogen (mg/dl)	-	-	15,8	23,0	38
Serum albumin (g/dl)	-	-	2,2	3,4	1,5
Serum globulin (g/dl)	-	-	3,5	5,2	5,1
Albumin:globulin ratio	-	-	0,6:1	0,7:1	0,3:1
Serum total lipids (mg/dl)	-	-	380	425	350
Packed cell volume (per cent)	-	-	33	43	35

* N.P. = non-predator; Im. = during drug immobilisation; T.F. = territorial fighting.

continued

Table 55, continued.

Carcass number	26	30	28	40	41
Sex	Male	Male	Male	Female	?
Age (years)	6,5	10,0	0,5	1,0	0,5
Date of death	16/9/76	6/11/76	11/2/77	24/3/76	21/5/76
Cause of death	T.F.	N.P.	N.P.	N.P.	lion
Body condition	moderate	moderate	poor	moderate	-
Body length (cm)	207	208	102	150	-
Shoulder height (cm)	125	132	69	103	-
Chest girth (cm)	141	142	54	92	-
Neck girth (cm)	72	91	28	40	-
Tick infestation	low	-	low	severe	moderate
Incidence of *Theileria* sp. piroplasms in red blood cells	absent	-	1/47	1/3 000	absent
Kidney fat index	7,7	-	-	0	-
Bone marrow fat (per cent), femur or humerus	-	10,5	-	11,2	-
Bone marrow fat (per cent), tibia or radius	0,6	-	52,9	9,2	-
Bone marrow fat (per cent), metatarsus or metacarpus	1,2	-	46,8	5,6	-
Serum total protein (g/dl)	3,5	-	-	5,5	-
Serum cholesterol (mg/dl)	95	-	-	140	-
Serum urea nitrogen (mg/dl)	56	-	-	-	-
Serum albumin (g/dl)	-	-	-	1,9	-
Serum globulin (g/dl)	-	-	-	3,6	-
Albumin:globulin ratio	-	-	-	0,5:1	-
Serum total lipids (mg/dl)	375	-	-	-	-
Packed cell volume (per cent)	-	-	-	-	-

and death. Extremely low fat reserves and a very elevated BUN level suggest that death was owing to terminal depletion of energy resources following strenuous activity. Blood slides revealed a very high incidence of one cell in 10 being immature as evidenced by chromatin fragments and anisocytosis. This suggests that the animal had undergone blood loss in the recent past and was compensating for this by mobilising immature erythrocytes. The lack of piroplasms suggests that this was an absolute blood loss rather than a haemolytic one and may have been due to previous tick infestations; alternatively it could be directly related to nutritionally induced poor condition. The finding of very poor condition in this animal and carcass 15 may be indicative of the difficulties young adult males have in setting up and keeping territories.

Carcass 30 was an old male that died of non-predatory causes at the beginning of summer, again with low fat reserves.

Carcass 28 refers to a juvenile that died of non-predatory causes during February. Its mother was still nearby with a full udder a number of hours after death. *Theileria* sp. piroplasms were present at a high erythrocytic infection rate of 1/47 cells. *Babesia* sp. piroplasms were also present, the only occasion in all carcasses examined. Piroplasmosis is the suspected primary cause of death in this animal. The only other juvenile carcass from which a blood slide was taken was animal 41 which resulted from lion predation; here piroplasms were absent. Piroplasm infections resulting in haemolytic anaemia have been identified as a possibly important cause of mortality in roan and sable calves (Wilson *et al.* 1974).

Carcass 40 was a one year-old female which died with a severe infestation of *R. appendiculatus* during March (Fig. 91). Blood chemical analyses are all indicative of poor condition. Although it was not possible to carry out a PCV test the blood was recorded as thin. No evidence of compensation for an anaemic state was seen in the blood slides and the fairly low level piroplasm infection suggests that haemolytic anaemia was not occurring. The severe tick infestation is implicated in the death of this yearling possibly through blood loss anaemia. Similar post-mortem results were recorded by Herbert (1972) for an immature female waterbuck where again *R. appendiculatus* was the main tick involved.

Although the number of carcasses examined were few a number of trends can be tentatively recognised. Evidence from carcasses eight,

Figure 91. A yearling female waterbuck (carcass 40) that died in the Umfolozi Game Reserve during March 1978, with a severe infestation of the brown ear tick (*Rhipicephalus appendiculatus*).

nine and 15 support the findings of Brooks *et al.* (1977) that KFI declines before BMF. Again it is seen that all blood chemicals are lowered in a poor condition animal, except BUN which rises probably owing to protein catabolism. External appearance is confirmed to be a poor indicator of condition in waterbuck. Packed cell volume appears to be maintained in even as poor condition an animal as number 15. This finding could be significant when coupled with the assays for carcass nine. This female is in good condition as judged by fat reserves and all her blood assays are above the average for immobilised animals, well above for PCV and total lipids which both may be better indicators of condition than other assays that mainly reflect immediate diet. If a figure of 43 per cent haematocrit represents a healthy waterbuck then many of the adult animals sampled during immobilisation could be in poor or only moderate condition at the beginning of winter. This is emphasised by finding the PCV of poor condition male 15 to be approximately equal to the population mean. The truth of this speculation will only be seen when blood assay results become available from waterbuck elsewhere.

Waterbuck and ticks

Balashov (1968) has discussed how certain animals will suffer higher tick infestation rates than others when all are exposed to the same potential numbers for attachment. This is largely a little understood field but in young animals lack of previous exposure likely plays a role whereas in older animals poor condition and breakdown of acquired resistance mechanisms are implicated. Pederson (1977) found that in mule deer (*Odocoileus hemionus Rafinesque*) it is the younger and older individuals that have most ticks. Ferrar and Kerr (1971) have shown that reedbuck in poor condition can have heavy tick infestations which represent an important proximate cause of death. The occurrence of poor condition before higher infestations rather than the reverse is supported in the present study by the results from immobilised animals. At the time of sampling nymphs predominated which are not believed to be causally related to the three body condition classes. However, the four cases of high infestation were recorded on four of the five animals not classed as in good body condition.

At the present time waterbuck is the only species in UGR showing severe infestations of successfully engorging adult ticks. It is likely that this is so because the population is stressed. This conclusion is supported by results given in Chapters 8 and 9 where waterbuck are seen to be outcompeted by other species and forced into sub-optimal coarse long grass habitats. Not only is it likely that waterbuck have become more susceptible to successful engorgement by adult R. *appendiculatus* because of competition, but their shift in habitat usage probably means that their exposure to this tick has also been increased. This is supported by the observation that the only other ungulate in UGR showing heavy infestations of adult brown ear ticks is buffalo which also occupies this long grass habitat for much of the year. *R. appendiculatus* is known to increase in long grass bushed areas and to decrease where overgrazing occurs (Theiler 1964). Waterbuck are at a further disadvantage since the changes in habitat condition since 1970 in terms of increased grass height and increased bush encroachment (see Chapter 2) would both have favoured an overall increase in abundance of R. *appendiculatus* in UGR.

It is concluded that the present severe infestation of R. *appendiculatus* on particularly young animals reflects a stressed condition in the waterbuck population. It is possible that waterbuck may normally suffer more from ticks than other species since waterbuck will not tolerate the presence of ox peckers (*Buphagus erythrorhyncus*) (Attwell 1966, pers. obs., Stutterheim[1] pers. comm.), but it is likely that the observed losses of young animals from severe infestations would not have occurred without the ultimate predisposing factor of inter-specific competition.

Severe adult tick infestations can cause irritation with reduced feeding and lowered condition, or death through blood loss anaemia. Severe or lower infestations of adults or young tick stages can cause death from piroplasmosis, tick paralysis and from other ill defined toxic effects (Blood and Henderson 1963). Since mortality is mainly associated with severe infestations of adult ticks it is likely that direct blood loss anaemia, probably coupled with worrying and reduced feeding, is the main tick induced cause of death in waterbuck.

CONCLUSION

Lion predation is a main cause of death in adult waterbuck in UGR and waterbuck are among the preferred prey species of this predator. Non-predator deaths of adults are probably underestimated and the

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observed increase in adult mortality during winter suggests that poor condition may play a part in the deaths of many animals. One process identified as occurring during winter is the death of young adult males from territorial conflict where the proximate mortality factor is depleted energy reserves. Adult mortality data from the main study area indicate an annual population loss rate of between four and nine per cent given the present poor calf survival.

It is difficult to assess blood assays from immobilised animals without having comparative information for another waterbuck population of known demography. It is possible that juveniles are in poorer condition than adults and that even adults may be mainly in poor or only moderate condition at the beginning of winter, but more data are needed to confirm this.

The seasonality of juvenile deaths indicates that their main cause is different from that in adult waterbuck. The high incidence of juvenile non-predator deaths suggests that factors covered by this heading may be the main cause of death in young waterbuck. Much evidence has been presented that points to severe infestations of *R. appendiculatus* as the main proximate cause of death in these young animals. However, it has been argued that the ultimate cause of death is interspecific competition as described in Chapters 8 and 9. The importance of calf mortality in causing the present decline in density of waterbuck in UGR has already been demonstrated in Chapter 5.

CHAPTER 7

BEHAVIOUR

INTRODUCTION

A number of studies have recently related the ecology of ungulates to social organisation and behaviour and have shown the possible uses of behavioural data in the management of large herbivores (Cowan 1974, Jarman 1974, Estes 1974). As reviewed by Crook, Ellis and Goss-Custard (1976) the structure and function of a mammalian social system can be thought of as the product of species attributes and environmental variables, where species attributes include morphology and physiology and environmental variables refer to factors such as resource dispersion and predators. Using this viewpoint Jarman (1974) was able to correlate group size, social organisation and feeding strategy in African bovids and suggest that the social organisation observed for each species is that which most fully suits the species' feeding style, habitat and group size. Behavioural attributes are not inflexible though and for one species they can be expected to vary between populations and within populations through time, as conditions within the population and external to it change. Quantification of behavioural variation can help to explain the relationships of a species population with its environment.

For this project a study was made of waterbuck movement, social organisation and activity, to provide data that might assist in determining the overall condition of the species in UGR. No detailed behavioural observations were made. A number of previous studies have included in depth accounts of waterbuck behaviour particularly in relation to sexual interactions, territoriality and aggression (Kiley-Worthington 1965, de Vos and Dowsett 1966, Hanks *et al.* 1969, Spinage 1969c, Herbert 1972).

METHODS

Animal movement

Immobilisation and marking of waterbuck

During May and June 1976 28 waterbuck were captured in the main study area and marked to allow the movement of individuals to be followed. Four animals were captured in July 1977, two of which were recaptures for use in age determination studies (see Chapter 4). In all 11 males and 13 females aged two years and above and six juveniles were handled. Capture details are given for each animal in Appendix 2. Details of other procedures carried out on captured animals are given in Chapters 4 and 6.

Capture methods. Three capture methods were employed. The first was drug immobilisation using a projectile syringe fired with either a crossbow (Van Rooyen, Kruger National Park) or a converted 20 bore shotgun (Van Rooyen, Kruger National Park), both from a Landrover. Each weapon employed "Van Rooyen" darts that injected an immobilising drug using the acid-bicarbonate reaction. Only two individuals were captured using this method because during this period another four waterbuck were hit with a dart but not recovered. This was because once darted an animal usually ran into thick vegetation and could travel a considerable distance in the three to 16 minutes it took the drug to take effect (see Appendix 2). The remaining individuals were captured using two helicopter techniques; either direct darting from a helicopter or by herding waterbuck into a net and plastic sheeting boma as developed by Oelofse (1970). Once in the boma individuals were darted using the shorter range Cap-Chur gun and darts that use a small cartridge detonator for drug injection (Palmer Company, U.S.A.). This gun was also used for darting waterbuck from the helicopter. All the weapons and projectile syringes mentioned above have been described in detail by Pienaar (1973).

Of the thirty captures made using helicopter techniques 18 were by the boma method and 12 by individual darting. Individual darting was preferred as it involved less disturbance than the boma method. Once an animal was darted it could be followed using the helicopter until it collapsed; radio contact with the researcher on the ground allowed the animal to be reached quickly. All captures involving a helicopter were carried out by the NPB capture team and the helicopters used were those employed for game censusing in 1976 and 1977 (see Chapter 3).

Immobilising drugs. Doses and types of the immobilising drugs used are given in Appendix 2 for each individual immobilised. Apart from animals one and two, drug combinations were decided upon by the NPB capture team. A very satisfactory combination was a mixture of the narcotics M99 (etorphine hydrochloride, Reckitt, U.K.) and Fentanyl (Janssen Pharmaceutica, Belgium) with the tranquilizer Azaparone (Janssen Pharmaceutica), which was used in 1977. Use of just Fentanyl and Azaparone, as employed by Herbert (1972) for waterbuck, produced slightly less satisfactory sedation. Harthoorn (1973) suggested a combination of either Fentanyl or M99 with Azaparone as that best suited for waterbuck. Hanks (1967) found a 1:1 combination of M99 and Acepromazine (Boots Pure Drug Co., U.K.) well suited to immobilisation of waterbuck. In 1976 in UGR Phenergan (promethazine hydrochloride, Maybaker, U.K.), which like Acepromazine is a phenothiazine derivative, was used as a mild tranquilizer along with the narcotic drugs. Although time from darting to collapse was equivalent to that when Azaparone was used, the level of sedation was much lower. As described in the last chapter this low tranquilisation state led directly to the death of two animals. The parasympatholytic drug Hyoscine (hyoscine hydrobromide) formed part of the drug mixture of four animals in 1976, against the wishes of the author. Hanks (1967) showed that any benefits resulting from the inclusion of Hyoscine were outweighed by the photophobia it produced, particularly in an area where lion predation is common. Two of these four animals fell repeatedly after the antidote was given and were effectively blinded for an unknown period.

For all animals the effects of the narcotic drugs were antagonised by either Lethidrone (nalorphine hydrobromide, Burroughs Wellcome and Co., U.K.) or M285 (cyprenorphine hydrochloride, Reckitt).

As shown in Appendix 2 all but three waterbuck were successfully released after immobilisation. An additional three are believed to have died as a direct result of capture. Female 15 was found dead near the boma site and probably died of the same syndrome as Females 14 and 16 (see Chapter 6). Female 10 was observed reunited with her calf (Juvenile 11) three days after capture but she could hardly walk, all her legs giving way, suggesting that capture myopathy had set in (Basson and Hofmeyr 1973). She was killed by lion the next night but her calf was not taken. Male 24 did not fully recover from the drug immobilisation and was found eaten by crocodile soon after. Thus a total of six animals out of 32 captures died as a result of capture. Some other animals were not resighted (see Appendix 2) so it is possible that the final death rate was slightly higher.

Marking. Waterbuck were marked with both collars and ear tags as suggested by Hanks (1969). Ear tags were applied to all animals while collars were fitted only to those believed adult and which were later found to be three years old and above for females and four years and above for males. Coloured, numbered Dalton ear tags (Dalton Supplies Ltd., U.K.) were affixed to the dorsal edge of the ear using a special applicator. Penicillin cream was placed on the piercing part of the tag to reduce the chance of infection. Single tags were used for animals with collars to aid in their identification should the collars become worn or completely lost (Fig. 92), while different coloured tags were affixed to each ear of young uncollared animals so that they could be individually recognised.

Collars were made of two layers of "Sterkolite" plastic (Kahn and Kahn Plastics Ltd., Johannesburg) reinforced by strips of 2,0 mm thick perspex secured between the "Sterkolite". Various letters and symbols were cut out of the top layer of "Sterkolite" so that when glued together the collar could be uniquely recognised as a base colour (upper layer) with differently coloured symbols (lower layer) (Fig. 92). Rivets and glue were used to bond the two layers firmly together. Collars were made 20 cm wide and either 70 cm or 100 cm in length.

Collars were wrapped moderately tightly around the neck of an immobilised animal and any surplus length cut off. Three pairs of overlapping holes were made at the ends using a leather punch and the collar secured with nuts, bolts and large washers. The head side of the bolts were against the neck and the threads were burred with a file to prevent the nuts loosening.

Sampling marked animals

Marked animals were recorded whenever seen. Their location was noted to a 250 m x 250 m block subdivision of the grid system described in Chapter 2. The only other waterbuck resighting data routinely included with these observations were a few made by a NPB research officer carrying out collar resighting patrols for other marked species in UGR and HGR. Other details noted when a marked waterbuck was observed are as described below for all waterbuck group sightings.

Figure 92. Immobilised female waterbuck showing the single ear tag and the "Sterkolite" plastic collar (yellow circles on green background).

Group composition and activity

Records of all waterbuck group sightings were made on a standard sheet. The date, time and 500 m grid location were recorded. Group size and composition were noted using the field age classes given in Chapter 4. Activity of animals was recorded separately for males and females as either feeding, walking, lying, sexual or other; other mainly comprised aggressive behaviour. If an animal was disturbed no activity was recorded. Under field observation conditions ruminating animals could not usually be differentiated from those resting. A number of environmental variables were recorded with which to compare activity budgets. Topographic location was classified as either near to or at a hill-top or ridge, or elsewhere. Grass height was recorded as one of four classes; less than 10 cm, 11 cm to 30 cm, 31 cm to 50 cm or greater than 50 cm. Woody vegetation was described as open canopy, open to closed canopy, closed canopy, dense shrubs predominating, or as edge. Edge referred to a definite boundary between dense shrubs or closed woodland and open canopy woodland. These broad habitat features were only recorded to allow an examination of activity under varying conditions and cannot be used to assess proportionate use of the habitat as observations were not collected evenly through the study area. Habitat utilization by waterbuck and the other main grazers in UGR is examined in Chapter 8. Weather conditions were also recorded for analysis with activity budgets. Shade temperature was taken with a mercury bulb thermometer, wind was classified as absent, light, moderate or strong and rain was noted.

RESULTS AND DISCUSSION

Animal movement

Males

Of the eleven males marked one died soon afterwards as a result of capture and a further four were not resighted (see Appendix 2). One of the remaining six, Male 4, died of unknown cause near to where it was marked with only two sightings having been made. A record was kept of the location of a naturally marked one horned male (1H), making long-term movement data available for a total of six males.

Resightings of these six males are plotted on Figs. 93 to 96 for the period May 1976 to March 1978. The males can be split into

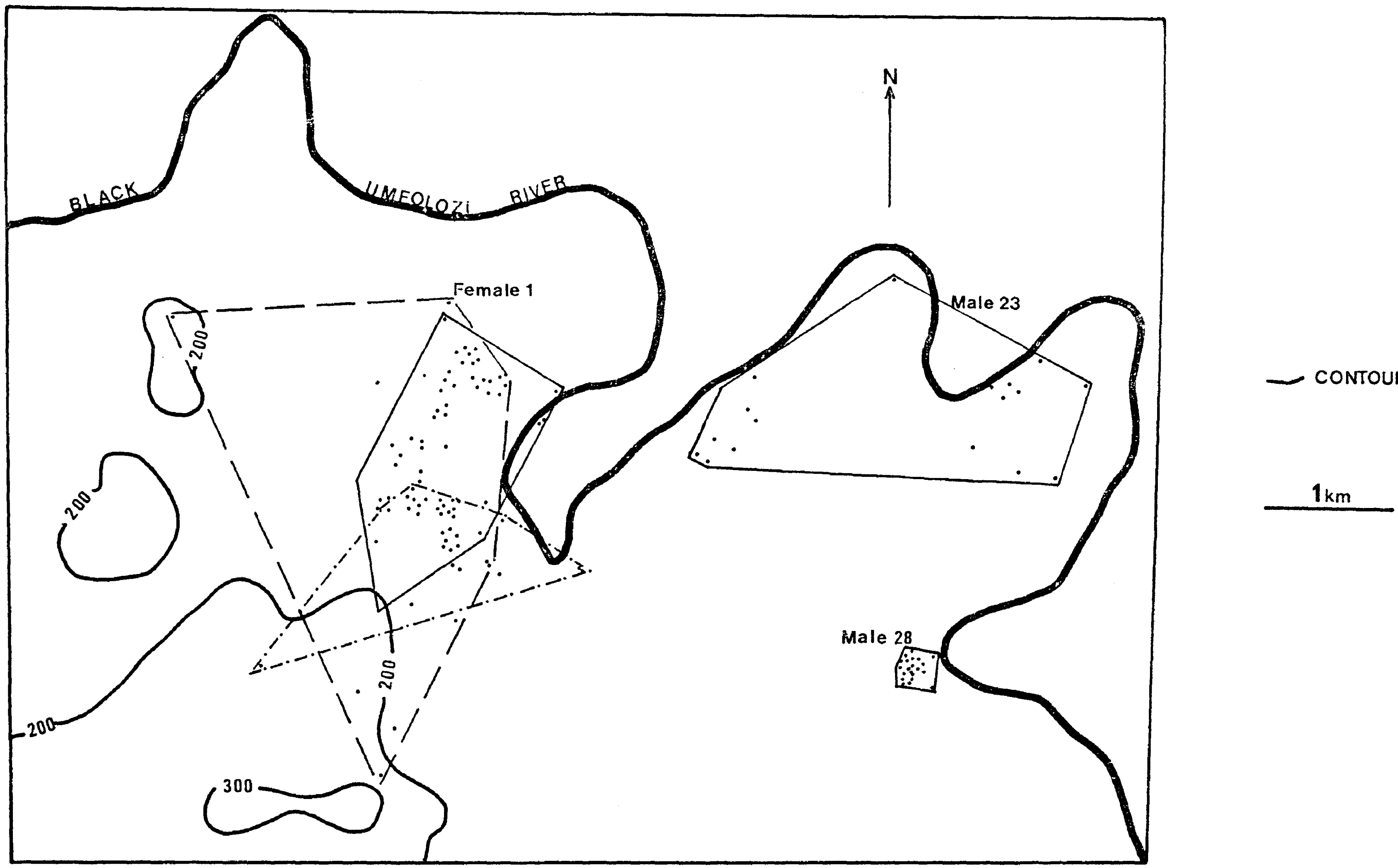

Figure 93. Resightings of marked waterbuck in the main study area: Female 1 winter 1976 (——), summer 1976-1977 (— — —), winter 1977 (-·—·); Male 23 whole period; Male 28 whole period.

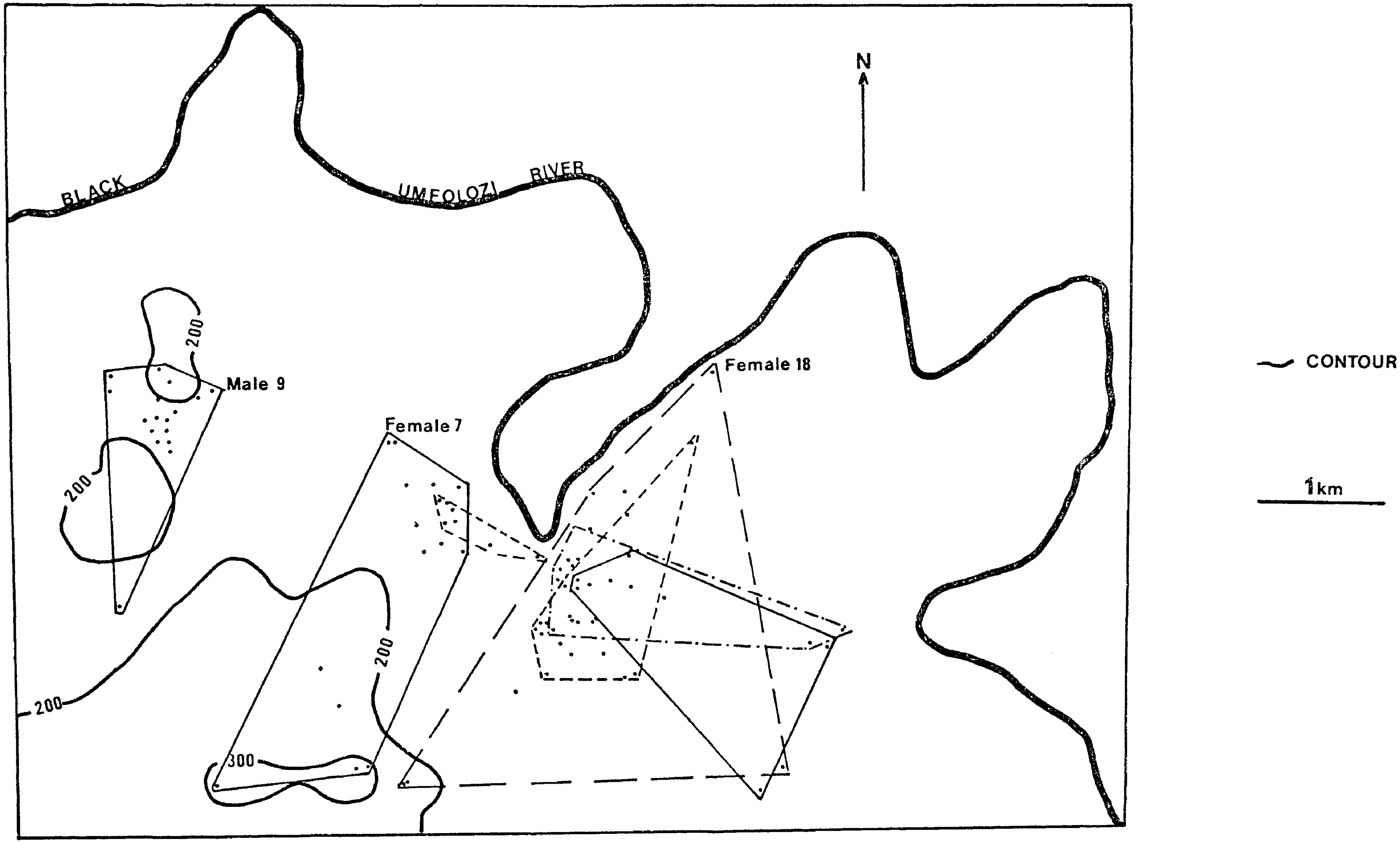

Figure 94. Resightings of marked waterbuck in the main study area: Male 9 whole period; Female 7 summer 1976-1977 (——), summer 1977-1978 (----); Female 18 winter 1976 (——), summer 1976-1977 (———), winter 1977 (—·—·), summer 1977-1978 (----).

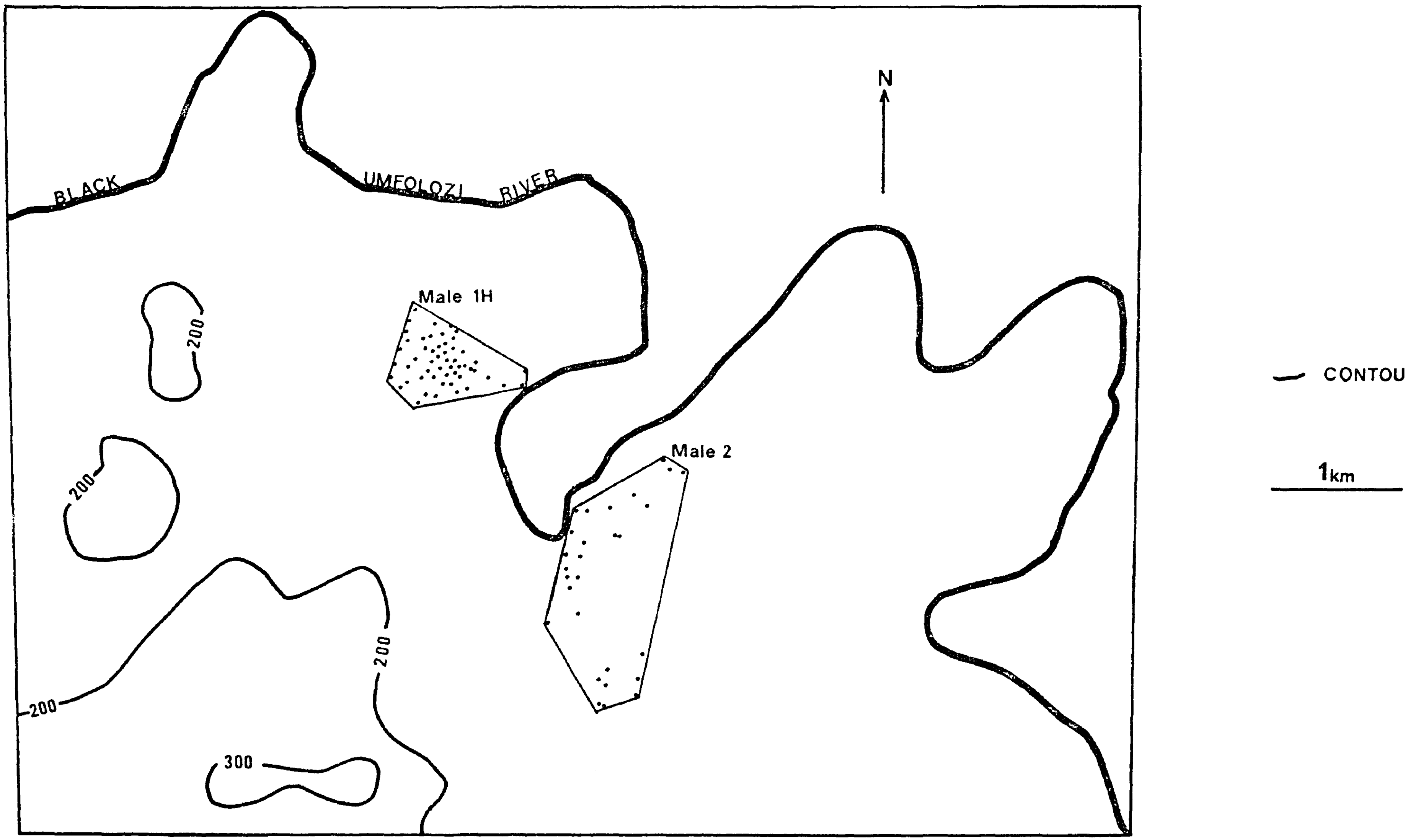

Figure 95. Resightinas of marked waterbuck in the main study area: Male 1H whole period; Male 2 whole period.

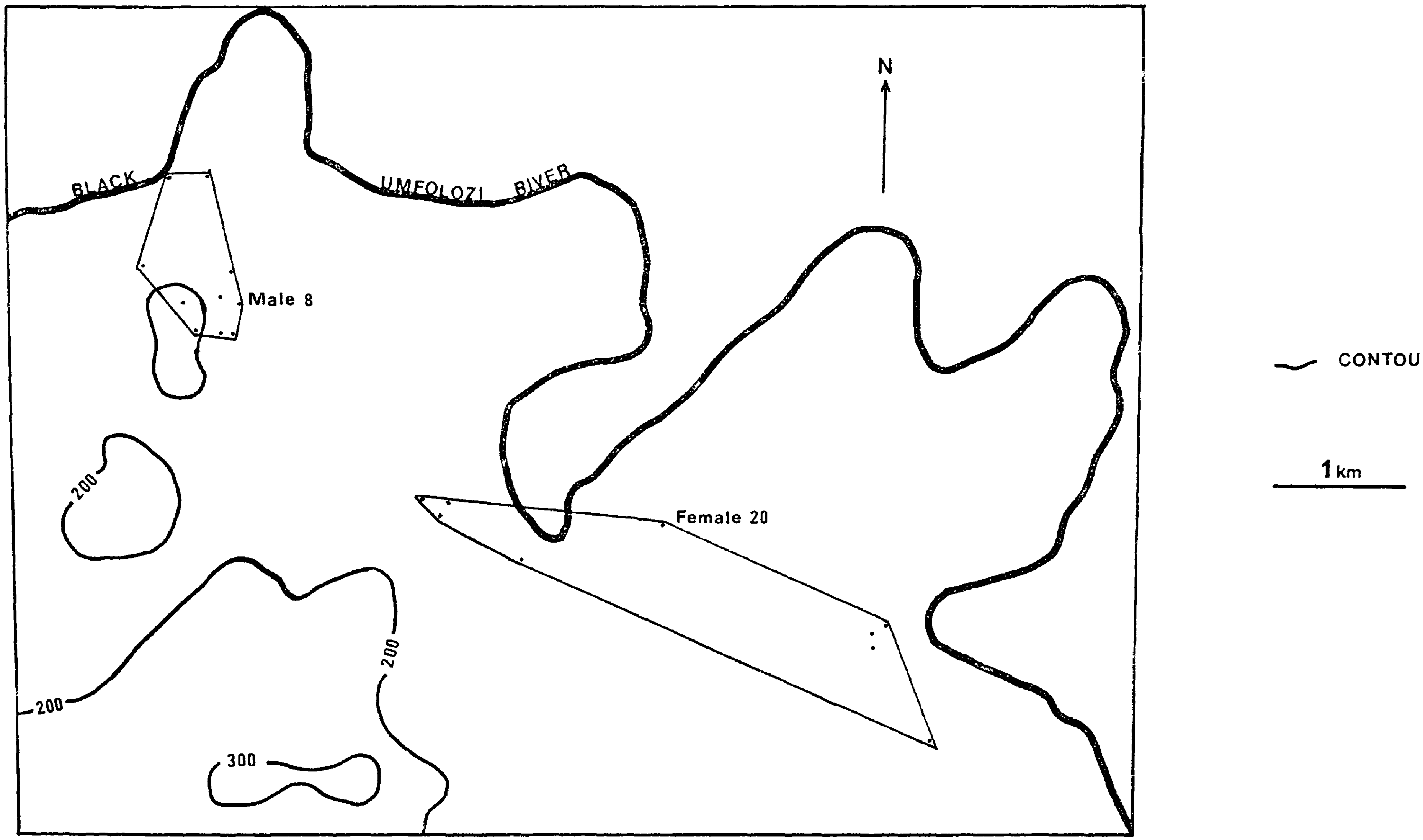

Figure 96. Resightings of marked waterbuck in the main study area: Male 8 winter 1976; Female 20 whole period.

two types because of their age and social groupings. Males 2, 8, 28 and 1H were fully adult; the three handled were either nine or 10 years old. Male 9 and Male 23 were sub-adult aged three years and two years respectively when captured in 1976. The four adult males were often observed alone or with females, while the sub-adults usually associated with other males forming groups of up to eight animals. These observations make it possible to term the adult males territorial males and the young males bachelor males. This classification is in agreement with all previous behavioural observations on waterbuck as reviewed by Herbert (1972) and with behavioural sequences seen during this study.

The size of territories, or home ranges of non-territorial animals, is calculated by joining all peripheral resighting points on a map and measuring the enclosed area with a planimeter (Jewell 1966). As discussed below, such quantification of range utilization is simplistic as it does not take into account the nature and frequency of utilization patterns within the enclosed area. However, this method is convenient for the present study as it allows for seasonal comparisons within UGR and for comparisons between UGR and other areas.

Territories were occupied year round with no observed change in area utilization with season. The data for Male 8 refers only to winter 1976 as this animal was poached in August 1976 (see Chapter 6). The territory size of Males 2, 8, 28 and 1H were 0,78 km^2, 1,22 km^2, 0,14 km^2 and 0,15 km^2 respectively with a mean of 0,66 km^2.

Although the data are few, bachelor males appear to move over larger areas than territorial males, their mean home range being 2,27 km^2. Much larger areas than this may be regularly utilized by some young individuals in UGR as it is believed that Male 9 left the study area for much of the summer of 1976-1977 and then left again in the winter of 1977 remaining away for the rest of the study period. These findings are based on a lack of sightings in the study area coupled with unconfirmed tourist observations of the animal some 15 km to the south. It would be necessary to have more data as regards the frequency and purpose of such large movements before they could be classified in terms of dispersion, migration or size of home range (Jewell 1966).

Spinage (1969c, 1974) gave territory sizes for waterbuck in Uganda or between 0,4 km^2 and 2,1 km^2, while the mean home range of bachelor males was 1,1 km^2. Territory size appeared to be related to age in Uganda as younger and older males had smaller territories than animals aged eight and nine years. Likewise Kiley-Worthington (1965) believed that the larger most dominant males had larger territories. Herbert (1972), however, found no correlation between the social status of a male and his territory size and Spinage (1974) reported that density of waterbuck had an overriding effect on territories, their size decreasing as density increased. Elliott (1977) also recorded very small territories of mean size 0,13 km^2, in a fertile area with a high density of waterbuck.

It seems likely that territory size in waterbuck is mainly related to availability of resources, particularly nutritious grass, rather than the social status of the animal. As found in UGR and elsewhere (Hanks *et al.* 1969, Spinage 1974) territories are maintained throughout the year whether breeding is seasonal or not. They therefore must contain all resources necessary for both wet and dry periods. Considering the energy that must be spent on maintaining a territory, it is reasonable to conclude that territory size is the minimum necessary to fulfil these requirements, as has been described for a number of bird species (Wynne-Edwards 1962, Newton 1976, Miller and Watson 1978). The smallest territory in UGR was in mainly closed woodland containing much *Panicum* sp. grassland, which is highly favoured by waterbuck especially during winter (see Chapter 9). All territories were near permanent water and all included a prominant hill or ridge. A hill may be important for display or more likely because of temperature effects as described in Chapter 2.

Spinage (1974) found that bachelor males were not segregated away from territories whereas Hanks *et al.* (1969) did record this during the breeding season. Tomlinson (1978) concluded that territorial male waterbuck affected the local distribution of bachelor males in the population which he studied in Rhodesia. No obvious segregation was noted in UGR, but such may be occurring during winter on a finer scale with respect to grassland utilization (see Chapter 8). Even so it is fair to conclude as done by Spinage (1974) that territoriality of males does not affect substantially the way the non-territorial bulk of the population obtains food. Also territory size has been shown to shrink with increasing density and is therefore unlikely to have any damping effect on population increase. Thus territoriality in waterbuck is probably not ever an ultimate population regulating factor and its importance is expected to lie in regulating reproductive competition and maintaining a prime breeding stock.

Females

As summarised in Appendix 2, four of the 13 females captured died during or soon after immobilisation and three more were not resighted. In addition two females were observed seldom and will not be discussed in detail. These were Female 6, which was only seen once before being killed by lions and Female 30 which was marked in 1977 and from the few observations made appeared to frequent the same area as Female 18.

The locations of the remaining four females are given by season in Figs. 93, 94 and 96; winter is taken as April to September and summer as October to March. The first feature to note is that Female 7 and Female 20 both left and main study area during the winters of 1976 and 1977. Female 7 was absent from July to October inclusive in 1976 and from May to October in 1977. Female 20 was absent from May to November in 1976 and from May to September in 1977. Female 7 spent at least part of the winter of 1976 to the north of Mpila, some 12 km to the south-east of the range she occupied in the study area. At the beginning of each summer Female 20 was initially resighted at the extreme south-east of her range, suggesting that she too had migrated towards Mpila. These observations may reflect a general movement of females away from the study area, which would explain the lower winter density of waterbuck in the study area and the increase in the male to female ratio at that time (see Chapters 3 and 5). The reason for such a migration is not known. In Chapter 9 it will be shown that no obvious macronutrient incentive could be found in vegetation, but this cannot be ruled out as a possibility. Spinage (1969c) also described a female utilizing two areas but not the intervening parts and returning to one area to calve, which agrees with the seasonality of movement in UGR. Herbert (1972) recorded increased movement of females at the peak of conceptions, which he believed to be directly related to sexual behaviour.

The mean home range of the animals that stayed in the study area throughout 1976 and 1977 was 4,42 km^2 in summer and 1,71 km^2 in winter. It appears that female waterbuck in UGR contract their home range in winter, in general staying nearer the river (Figs. 93 and 94), but this may be preceded by a migration to a new area.

There was no relationship between migration and age as the animals that remained, Females 1 and 18, were 3,5 yr and 5,0 yr respectively in 1976, while those that left, Females 7 and 20, were 10,0 yr and 6,0 yr. Spinage (1969c) found that young females sometimes dispersed to new areas, travelling up to 30 km.

The increase in home range size in summer coincides with an increased utilization of the upland grass *Themeda triandra* which was actively growing and of reasonable nutrient content at that time (see Chapter 9). It is suggested that winter shrinkage of home range reflects limited availability of areas of acceptable food. A similar diminuition of home range in winter was described by Sinclair (1974b) for buffalo. There may also be a general tendency for waterbuck to utilize upland areas as found by Spinage (1970) who suggested the presence of cooling breezes to be an attractant. In UGR this may only be possible during summer when most grasses are green and water is abundant.

Hanks *et al.* (1969) found an overall shrinkage of female home range in summer, which like in UGR coincided with the calving period. A similar pattern was observed in UGR but this has been masked in the longer term seasonal data just discussed. Female 1 was with a young calf when marked on 19 May 1976 and was always observed with this calf until the end of July 1976. During this period only 0,13 km^2 of her 2,14 km^2 winter range was utilized. Female 7 was pregnant when she returned to the study area in November 1977 and was always located in an area of 0,14 km^2 compared to 3,00 km^2 during the summer of 1976.

Waterbuck females therefore generally range farther than males, their movements covering a number of male territories. Home ranges are relatively constant from year to year although the possibility of winter migration means that annual and lifetime ranges would be much greater than the home ranges given here. The shrinkage of home range in winter is believed to reflect limited areas of acceptable food and is in accordance with the findings given in Chapters 8 and 9. Seasonal migration is also probably connected with obtaining adequate resources but the reasons remain unknown.

Juveniles

One of the six juveniles captured died during restraint and one more was not resighted (Appendix 2). The few sightings of the other four are given in Table 56. Juvenile 11 joined Juvenile 13 after the former's mother (Female 10) died because of capture myopathy on 10 June 1976. Juvenile 13 was probably the offspring of one of the other females that died as a result of the capture operation. It is possible that all four died before the end of winter 1976, which would agree with the high calf mortality described in Chapter 5, but one or more may have left the study area. Juvenile 17 was the young of Female 18 and stayed with her until about eight months of age, which is when males first permanently associate with bachelor groups (Spinage 1969c).

Group size

Waterbuck group size in UGR has been quantified by calculating maximum group size, mean group size and typical group size, considering all age and sex classes together.

Mean group size = N/G,

where N = number of animals sampled

and G = number of groups sampled.

$$\text{Typical group size} = \frac{(g_i^{\,2}.f_{g_i}^{\,2})}{N},$$

where g_i = group size of the ith group

and f_{gi} = frequency of occurrence of groups of the ith rank.

This latter expression was suggested by Jarman (1974) to represent best animal groupings as it is the size of group in which the average animal finds itself. Figure 97 shows the frequency histogram of 1 759 waterbuck groups classified by size. The maximum size is 32, mean size is 3,68 and typical group size is 6,66. The shape of the frequency distribution is equivalent to that found by Spinage (1969c) when waterbuck groups of mixed ages and sex were considered and suggests that there is no selection for certain group sizes.

Figure 98 shows monthly variation in group size compared with rainfall. All three measures of group size show an increase during wet summer months. The regression of group size on rainfall is not significant though ($P > 0,05$), for either maximum group size (r = 0,14), mean size (r = 0,20) or typical group size (r = 0,10). All

Table 56. Resighting details for four juvenile waterbuck marked on the 5th and 6th June 1976 in the main study area.

Animal number	Sex	Date	Time	Grid location	Other members of group	Activity
5	M	19 July 1976	16h15	8177ab	3F(a)+1F(1yr)+1J	feeding
		23 July 1976	17h05	8177ad	1F(a)	feeding
		24 July 1976	07h35	8177ad	9F(a)+1M(a)+2J	walking
11	M	9 June 1976	11h00	8276db	F-10+2J	bleating
		10 June 1976	09h05	8276dc	F-10	-
		12 June 1976	11h15	8276db	J-13	feeding
		31 July 1976	11h20	8575ac	4F(a)+F-18	-
13	F	12 June 1976	11h15	8276db	J-11	feeding
		31 July 1976	11h20	8575ac	4F(a)+F-18+J-11	-
17	M	10 June 1976	16h00	8276db	alone	feeding
		21 July 1976	11h20	8276dd	F(a)+F-18+1J	standing
		14 September 1976	10h05	8474cb	F-18	standing

F = female; M = male; J = juvenile; (a) = adult.

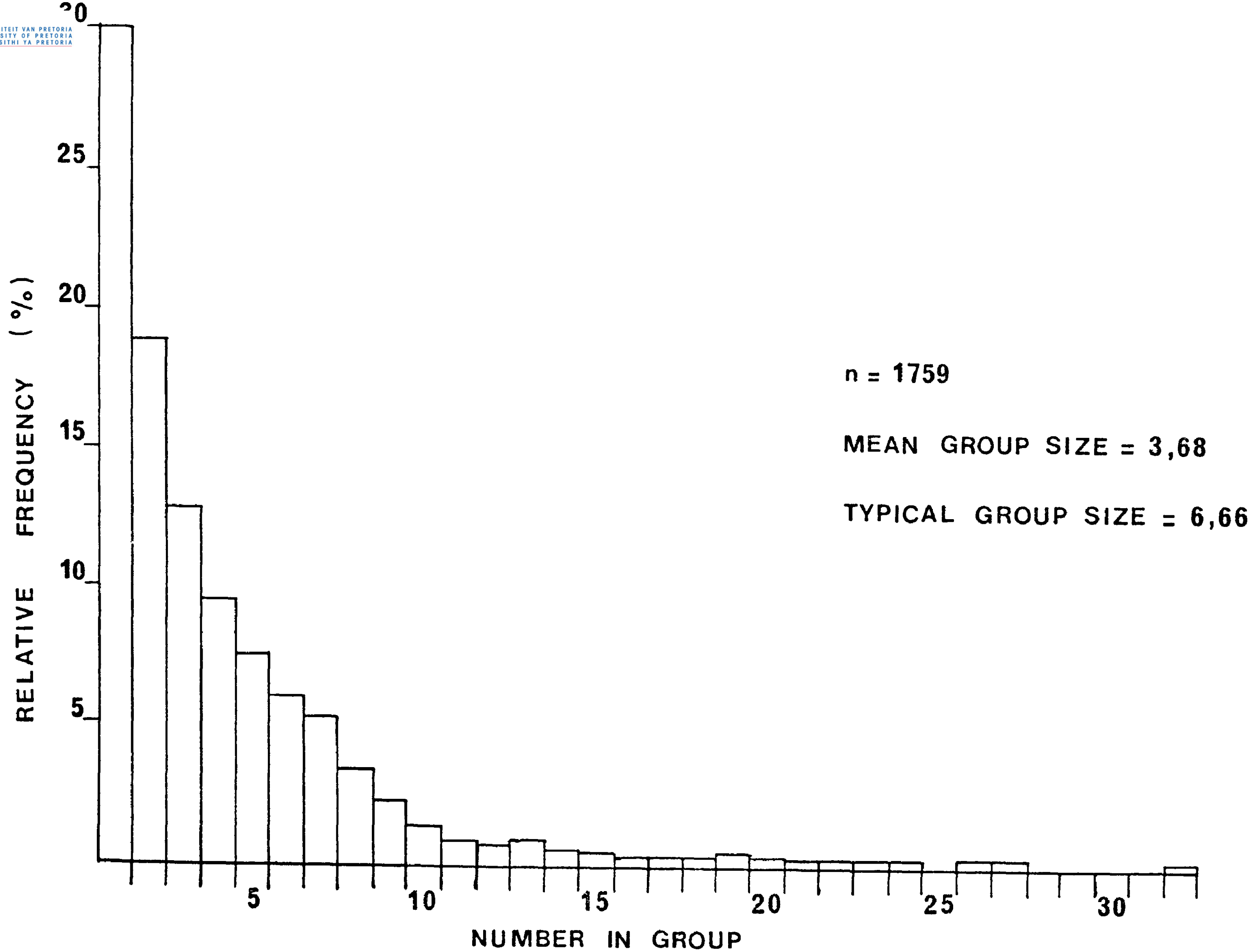

Figure 97. Frequency histogram of 1 759 waterbuck groups observed in the Umfolozi Game Reserve classified by size.

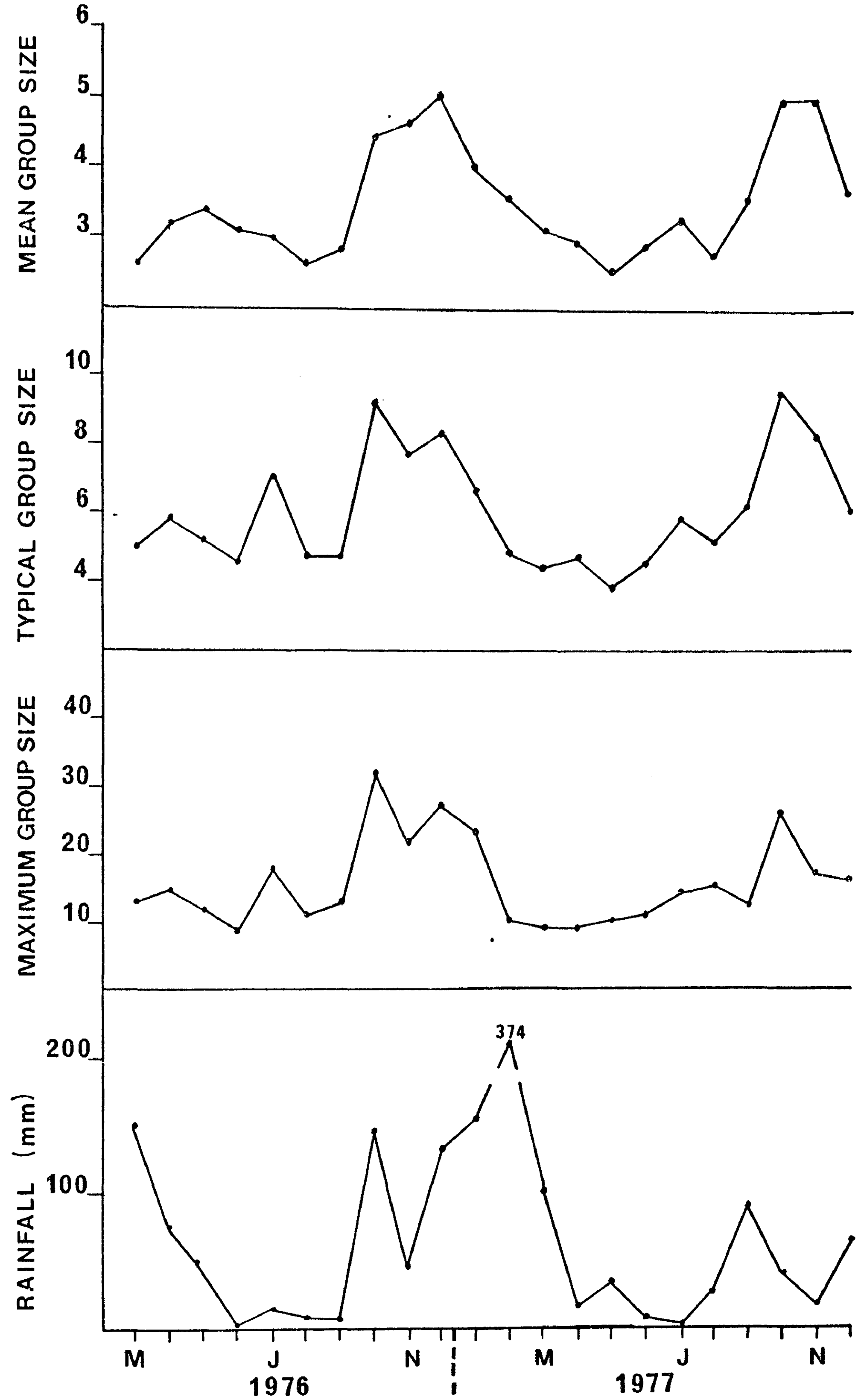

Figure 98. Monthly variation in waterbuck group size in the Umfolozi Game Reserve compared with rainfall.

regressions of group size on the maximum number density estimate are positive and significant ($P < 0,05$), the correlation coefficients being 0,57, 0,48 and 0,52 for maximum size, mean size and typical size respectively. These results confirm that particular group sizes are not selected for and that waterbuck group size is a function of local density of animals. It is likely that local density only increases after the onset of the rains when good quality food becomes abundant (see Chapter 9). conversely, lowering of group size occurs during winter, which is the pattern expected if suitable areas of food were small and scattered (Crook *et al.* 1976). The initial lowering of group size actually occurs before the end of summer which may be owing to females being less gregarious during the calving period in late summer. The small increases in group size in June and July (Fig. 98) are possibly associated with the herding activity of territorial males, since this is the period when most conceptions are expected (see Chapter 5).

Child and von Richter (1969) recorded a range in waterbuck group size of one to 37, with a mean of 8,1 if lone animals were excluded. With the same omission Spinage (1969c) found group sizes to lie mainly between three and six animals and Herbert (1972) gave a mean figure of 6,9. If singletons are omitted from UGR data the mean group size becomes 4,8 and the typical group size is 7,15. It is difficult to use data from other populations in a comparative manner as it appears that waterbuck may also congregate during stressed periods presumably because acceptable grazing occurs in large isolated areas rather than in small clumps. Thus Hanks *et al.* (1969) found an increase in female herd size during winter when animals came together on favoured winter grassland and a decrease in summer attributable to calving.

Waterbuck group size largely results from random contact which increases as local density increases. It will be shown below that certain behavioural constraints are imposed on group structure and that these findings refer particularly to females. In UGR local density and group size increase during summer months when suitable food is abundant. Group size is then lowered in late summer because of calving and never increases substantially during winter. This continued fragmentation during winter suggests that there are strong advantages for animals following divergent feeding paths as would occur if acceptable food were of low density and a scattered distribution (Jarman 1974, Crook *et al.* 1976). Since most conceptions occur during winter it is possible that ecological requirements are outweighing the herding behaviour of territorial males at this time.

Group structure

The absolute and relative frequencies of 22 group types from 1 759 group observations are given in Table 57. As found in other studies (de Vos and Dowsett 1966, Child and von Richter 1969, Herbert 1972) lone males were most commonly observed, which reflects the territorial nature of the species. Groups of females without calves were the next most common, followed by groups of females plus one adult male. Sub-adult males were mixed with adult males in at least 6,5 per cent of groups; although all adult males are not territorial, this probably indicates a certain level of tolerance by territorial males. A single adult male with females constituted 9,1 per cent of groups while females plus more than one adult male only formed 1,0 per cent, which suggests that territorial animals do not usually tolerate other adult males.

The percentage occurrences of four broad group types are given by season in Table 58. Breeding groups with a single adult male are most common at the end of summer and the beginning of winter, which coincides with the post-calving period. The results just presented indicate that these breeding groups are generally not large, particularly during early winter. Lone adult males are most frequent at the end of winter which may be attributable to general fragmentation of groups at that time. Groups of females become most common at the beginning of summer which corresponds with the observed increase in group size and supports the suggestion that it is mainly females that determine group size. Bachelor group occurrence shows no relation to season.

A main point emerging from these data is the great flexibility in group structure, a feature which has been emphasised in previous studies on waterbuck (de Vos and Dowsett 1966, Hanks *et al.* 1969, Spinage 1969c, Herbert 1972). This flexibility is more clearly demonstrated by a few group composition records for two marked animals (Table 59). Certain individuals may associate regularly, such as Female 1 and Female 7, but in general groups vary considerably, even on the same day.

Table 57. Waterbuck herd structure in the Umfolozi Game Reserve based on 1 759 observations made throughout the study period.

Type of grouping	Absolute frequency	Relative frequency (per cent)
1 M(a)	343	19,5
1 M(a) + 1 F	53	3,0
1 M(a) + >1 F	160	9,1
1 M(a) + 1 F + 1 C	13	0,7
1 M(a) + >1 F + ≥1 C	83	4,7
>1 M(a) + >1 F	17	1,0
>1 M(a) + >1 F + >1 C	12	0,7
1 M(a) + ≥1 M(sa)	47	2,7
>1 M(a) + ≥1 M(sa)	32	1,8
≥1 M(sa)	67	3,8
>1 M(a)	56	3,2
1 F	132	7,5
>1 F	316	18,0
1 F + 1 C	64	3,6
>1 F + >1 C	142	8,1
≥1 M(a) + ≥1 M(sa) + ≥1 F	9	0,5
≥1 F + ≥1 M(sa)	21	1,2
1 F(a) + 1 F(1yr) + 1 C	6	0,3
≥1 J	14	0,8
≥1 I	1	0,1
≥1 M(a) + ≥1 M(sa) + ≥1 F + ≥1 C	27	1,5
Other combinations of sex and age classes	144	8,2

M = male; F = female; C = calf; J = juvenile; I = infant; (a) = adult; (sa) = sub-adult.

Read "≥1" as "one or more".

Table 58. Percentage occurrence of four waterbuck group types in the Umfolozi Game Reserve by season.

		Per cent composition							
		Summer 1976	Winter 1976		Summer 1976-1977		Winter 1977		Summer 1977
Herd type	Composition	Mar	Apr-Jun	Jul-Sep	Oct-Dec	Jan-Mar	Apr-Jun	Jul-Sep	Oct-Dec
Solitary males	1 M(a)	20,7	16,1	29,4	15,8	14,2	23,2	27,8	18,9
Breeding herd	1 M(a) + ≥1 F ± ≥1 C	41,3	21,5	8,0	13,9	25,5	18,9	9,6	18,5
Bachelor males	>1 M	3,4	18,8	15,1	14,2	7,9	6,1	4,8	10,1
Female herd	>1 F	24,1	7,2	13,9	22,9	19,4	9,8	18,3	25,9
Sample size		29	223	238	367	325	164	126	286

Symbols as for Table 57.

Table 59. A few consecutive group composition records for two marked waterbuck to demonstrate flexibility in group structure.

	Date	Time	Other members of group	Activity
Female 1	2 November 1976	17h50	17F(a)+2F(1yr)+1J+4M(1yr)	feeding
	9 November 1976	16h45	3F(a)+1F(1yr)+1J	lying
	10 November 1976	18h20	F-7	feeding
	11 November 1976	17h45	10F(a)+F-7+3J+1M(a)	feeding
	19 November 1976	08h45	1F(a)+F-7+2M(a)+1M(2yr)+2M(1yr)	standing
	19 November 1976	15h20	Alone	walking
Male 28	7 October 1976	15h40	5F(a)+2J	walking
	28 October 1976	08h30	1F(a)+1J	standing
	30 October 1976	10h10	1M(a)	fighting
	4 November 1976	14h25	8F(a)+3J	sexual
	17 November 1976	15h55	3F(a)	feeding

Symbols as for Table 57.

Activity

Activity and time of day

Activity budgets for male and female waterbuck aged one year and above are presented in Fig. 99, based on 2 039 records of male behaviour and 4 179 records of female behaviour obtained whenever waterbuck were sighted throughout the study period. Overall, males spent 34,6 per cent of their time feeding, 10,3 per cent walking, 27,1 per cent standing, 22,9 per cent lying, 2,3 per cent in sexual activity and 2,9 per cent in other, mainly aggressive, activity. Females spent 40,8 per cent of the time feeding, 18,3 per cent walking, 22,7 per cent standing, 17,6 per cent lying, 0,5 per cent in sexual activity and 0,2 per cent in other activities.

Feeding occurred throughout the day but with a main feeding period during the late afternoon and a smaller increase in the early morning. This agrees with previous records of feeding activity for waterbuck (Spinage 1968, Hanks *et al.* 1969, Herbert 1972, Elliott 1977, Tomlinson 1978). Females spend more time feeding than males, but Spinage (1968) found that this could be compensated for by increased feeding by males during the night. Females also spent more time walking than males, particularly in the early morning and evening, which probably reflects the generally larger home ranges of females. The male is more active in social and aggressive behaviour, although females were observed to butt other females and one animal apparently died of injuries so sustained (see Chapter 6).

Activity and season

Male and female activity budgets are shown by season in Table 60. Little variation occurred in the proportion of time spent in these broad activity classes with the time of year. Males spent more time standing during winter which may indicate increased territorial display, although no increase in sexual or territorial behaviour was seen. There is no change in the amount of feeding done by either males or females through the year. Tomlinson (1978), working in Rhodesia, also found little seasonal variation in the proportion of time that waterbuck spent feeding. Elliott (1977) recorded decreased feeding and increased ruminating in waterbuck in dry months, which she attributed to a more fibrous diet at those times.

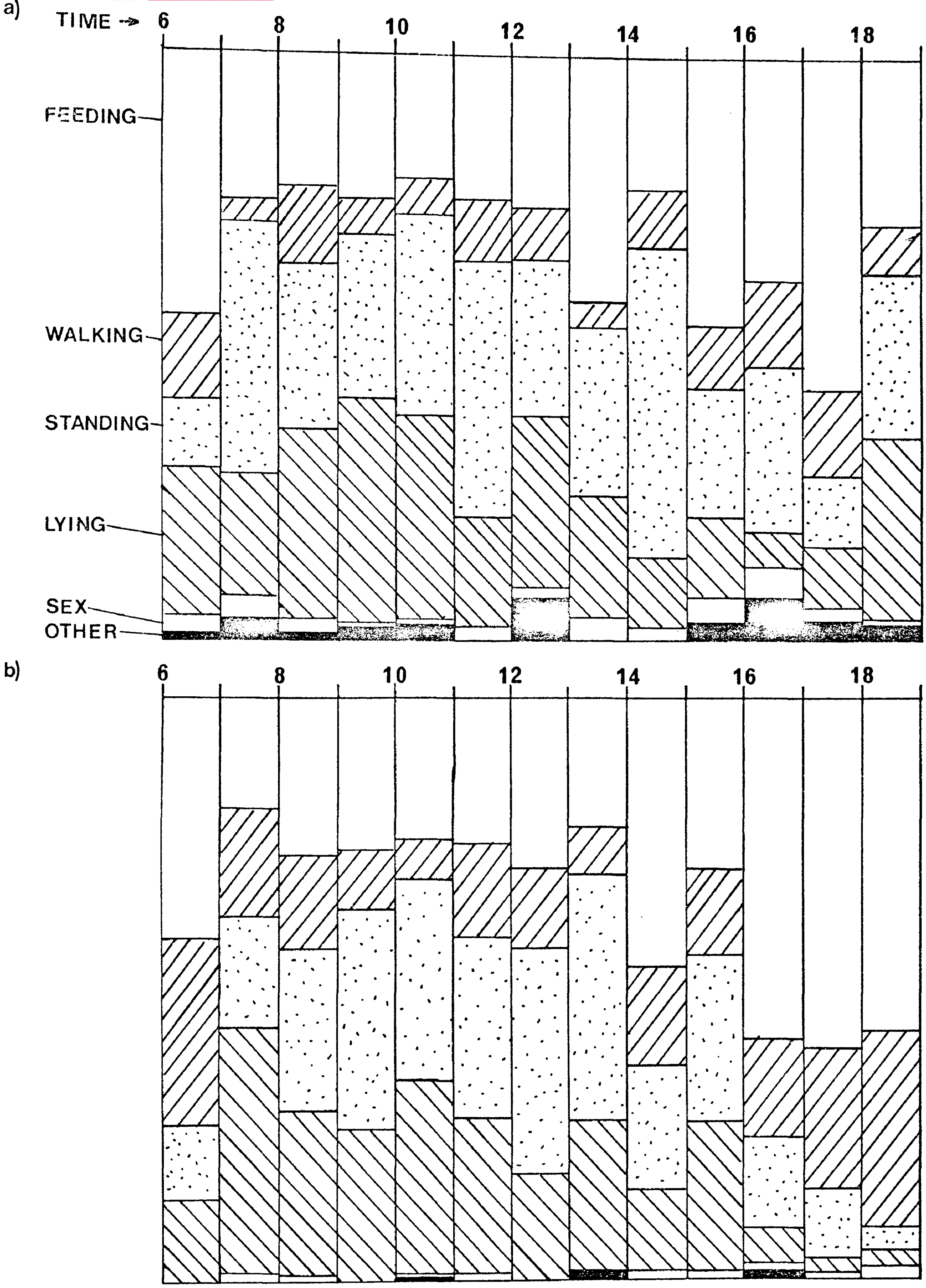

Figure 99. Daily activity budgets for a) male waterbuck (2 039 observations) and b) female waterbuck (4 179 observations), based on sightings made between March 1976 and December 1977 in the Umfolozi Game Reserve.

Table 60. Activity of male and female waterbuck in the Umfolozi Game Reserve by season.

	Per cent of observations				
	Winter 1976 Apr-Sep	Summer 1976-1977 Oct-Mar	Winter 1977 Apr-Sep	Summer 1977 Oct-Dec	Total period
Male					
Feeding	31,3	37,3	32,9	30,6	34,6
Walking	13,5	8,5	12,2	9,7	10,3
Standing	31,9	25,1	33,2	19,4	27,1
Lying	18,1	24,1	16,6	34,5	22,9
Sexual	2,4	1,7	2,4	4,5	2,3
Other	2,8	3,2	3,4	1,0	2,9
Sample size	498	1 066	205	206	1 975
Female					
Feeding	41,8	39,9	37,4	43,2	40,8
Walking	15,2	20,6	19,9	15,5	18,3
Standing	30,1	23,2	30,0	13,4	22,7
Lying	12,4	15,4	14,1	27,6	17,6
Sexual	0,1	0,7	0,4	0,3	0,5
Other	0,3	0,2	0,2	0	0,2
Sample size	741	1 909	468	972	4 090

Activity and group size

Both male and female waterbuck show a reduction in feeding when in groups comprised of only one or two animals (Table 61). This is particularly marked for lone animals, where more time is spent standing. For males this is partly accounted for by territorial display, but for females it likely reflects increased vigilance when alone and points to a main function of grouping. Groups may form a type of cover for individuals and reduce the chance of predation through higher collective vigilance.

Activity and woodland type

The only obvious trend in activity with woodland type is for an increase in the aggressive behaviour of males in ecotones (Table 62). This may reflect the use of distinct woodland edge as a marker of territory or it may be that territories are selected to include much edge indicating the need for both open and closed woodland so that nutrient and energy requirements are fulfilled year round. The lack of other trends suggest that it is the proportionate usage of these habitat types that regulates the use of the environment rather than changes in activity in different areas.

Activity and grass height

More time is spent lying and less time feeding in grass less than 10 cm tall (Table 63). This agrees with findings presented in Chapter 8 where waterbuck are shown to favour intermediate height grassland. The decline in feeding by males when in tall grass may be an artifact of small sample size, although both males and females do lie down more in long grass than in grass of the two intermediate height classes.

Activity and topography

Males spend less time feeding on hill-tops and ridges and more time standing or lying, which may indicate that vantage points are important for display purposes (Table 64). Females show no change in activity pattern with topographic location.

Activity and rain

Both males and females spent more time standing and lying and less time feeding and walking when it rained (Table 65). Sexual activity, however, was not damped by rain.

Table 61. Activity of male and female waterbuck in the Umfolozi Game Reserve separated by group size.

	Per cent of observations					
	1 waterbuck	2 waterbuck	3-5 waterbuck	6-10 waterbuck	11-15 waterbuck	15 waterbuck
Male						
Feeding	14,8	36,9	40,1	50,2	33,3	34,8
Walking	8,4	12,9	11,3	8,6	18,7	17,4
Standing	46,4	22,4	24,5	14,8	12,0	13,0
Lying	29,3	19,7	19,1	20,6	20,0	17,4
Sexual	0,2	2,0	2,4	3,3	10,7	8,7
Other	0,9	6,1	2,7	2,5	5,3	8,7
Sample size	547	295	551	514	75	46
Female						
Feeding	22,7	32,8	38,1	43,4	41,7	49,8
Walking	22,0	21,3	10,9	19,9	18,5	22,4
Standing	44,1	25,5	30,1	17,3	20,0	16,4
Lying	10,3	18,5	19,9	18,9	19,6	11,4
Sexual	0	0,6	0,6	0,6	0,2	0
Other	0,7	0,6	0,4	0	0	0
Sample size	145	329	911	1 561	496	580

Table 62. Activity of male and female waterbuck in five woodland types in the Umfolozi Game Reserve.

	Per cent of observations				
	Open woodland	Open to closed woodland	Closed woodland	Dense shrubs	Edge
Male					
Feeding	36,2	32,8	32,6	27,6	44,0
Walking	9,8	8,9	4,8	11,5	14,9
Standing	25,7	29,4	31,6	32,2	12,4
Lying	30,0	26,4	25,1	25,3	16,1
Sexual	2,6	2,1	2,7	1,1	1,9
Other	2,7	0,3	3,2	2,3	10,6
Sample size	1 179	326	187	87	161
Female					
Feeding	47,4	37,7	34,0	38,0	36,4
Walking	20,1	13,3	14,7	14,5	23,5
Standing	13,0	28,7	32,5	25,9	27,2
Lying	18,7	20,1	17,8	21,7	11,5
Sexual	0,7	0	0,5	0	0,9
Other	0,1	0,1	0,5	0	0,5
Sample size	2 358	855	415	166	217

Table 63. Activity of male and female waterbuck in the Umfolozi Game Reserve in relation to grass height.

	Per cent of observations			
	Grass <10 cm	Grass 11-30 cm	Grass 31-50 cm	Grass >50 cm
Male				
Feeding	28,9	38,9	38,4	20,7
Walking	7,6	8,0	10,4	17,0
Standing	29,4	24,4	36,0	24,5
Lying	30,9	24,4	12,8	30,2
Sexual	2,9	2,1	0	3,8
Other	0,3	2,3	2,4	3,8
Sample size	343	866	125	53
Female				
Feeding	35,3	48,1	43,3	40,2
Walking	12,7	20,4	14,0	13,0
Standing	21,7	19,7	31,1	17,4
Lying	30,3	10,6	11,4	29,3
Sexual	0,3	1,2	0	0
Other	0,1	0,1	0	0
Sample size	1 278	1 429	263	92

Table 64. Activity of male and female waterbuck in the Umfolozi Game Reserve in relation to topography.

	Per cent of observations	
	Hill-top	Flat or gently sloping ground
Male		
Feeding	30,0	43,9
Walking	8,7	11,2
Standing	30,1	22,6
Lying	26,2	17,3
Sexual	2,3	2,5
Other	2,8	2,6
Sample size	1 303	608
Female		
Feeding	39,4	43,0
Walking	19,8	14,4
Standing	21,2	24,0
Lying	18,9	17,9
Sexual	0,3	0,7
Other	0,3	0
Sample size	2 566	1 659

Table 65. Activity of male and female waterbuck in the Umfolozi Game Reserve in relation to rain.

	Per cent of observations	
	Not raining	Raining
Male		
Feeding	37,6	22,3
Walking	11,2	5,8
Standing	25,7	34,1
Lying	20,0	36,7
Sexual	2,5	5,0
Other	3,0	1,9
Sample size	1 676	363
Female		
Feeding	41,6	35,8
Walking	18,6	12,5
Standing	21,4	36,4
Lying	18,4	14,3
Sexual	0,5	0,6
Other	0,2	0,6
Sample size	3 869	343

Activity and temperature

Males stand more at high temperatures rather than lying or feeding (Table 66). Females also stand more but feeding is not reduced. These findings suggest that waterbuck are adversely affected by temperatures over 35 °C and they probably stand to obtain the cooling effects of breezes. Taylor *et al.* (1969) found that cutaneous evaporation of waterbuck tripled when ambient temperature increased from 25 °C to 45 °C.

Activity and wind

The only trend is for reduced feeding when there is no wind (Table 67). This may be a temperature induced effect or it may be artificial since wind in UGR seemed more prevalent during the afternoon, which coincides with the main feeding period. Strong winds certainly do not reduce feeding.

CONCLUSION

Social organisation, movement and activity of waterbuck in UGR are similar to populations studied elsewhere. It is likely that territory size, home range size and group size are all functions of resource abundance and dispersion. Fragmentation of groups and reduction of home range during winter indicate that acceptable food is limited and scattered during this season. The generally small variations in activity with change in habitat suggest that it is the amount of time spent in these different areas that is important in determining resource utilization rather than variation in behaviour in the different areas.

Table 66. Activity of male and female waterbuck in the Umfolozi Game Reserve in relation to temperature.

	Per cent of observations				
	< 20 °C	20-25 °C	26-30 °C	31-35 °C	> 35 °C
Male					
Feeding	33,7	35,2	30,5	45,6	22,4
Walking	6,7	10,1	5,3	8,0	14,3
Standing	34,8	24,7	27,9	23,9	38,8
Lying	19,1	22,7	31,4	17,4	16,3
Sexual	1,1	3,2	2,3	0,7	0
Other	4,5	4,1	2,6	4,3	8,1
Sample size	89	344	656	138	49
Female					
Feeding	28,7	38,1	36,6	38,5	37,1
Walking	15,6	19,0	12,9	10,7	11,2
Standing	32,9	21,6	29,7	29,3	35,0
Lying	22,8	20,7	19,3	21,5	16,8
Sexual	0	0,3	1,3	0	0
Other	0	0,2	0,3	0	0
Sample size	237	1 004	1 017	410	143

Table 67. Activity of male and female waterbuck in the Umfolozi Game Reserve in relation to wind.

	Per cent of observations			
	No wind	Light wind	Moderate wind	Strong wind
Male				
Feeding	20,1	37,1	38,5	50,0
Walking	4,6	12,1	11,4	11,0
Standing	37,6	25,3	23,2	8,0
Lying	33,7	20,4	18,4	26,0
Sexual	1,5	2,6	4,4	1,0
Other	2,4	2,4	3,9	4,0
Sample size	412	495	228	100
Female				
Feeding	28,1	42,8	37,8	42,0
Walking	18,9	18,1	13,0	20,4
Standing	29,9	20,5	23,4	19,9
Lying	22,4	18,1	23,9	17,1
Sexual	0,6	0,3	1,5	0,6
Other	0	0,1	0,2	0
Sample size	491	1 469	528	181

CHAPTER 8

HABITAT UTILIZATION AND COMPETITION

INTRODUCTION

This part of the study is based on Hutchison's (1958) redefinition of the niche, a term coined almost simultaneously by Elton (1927) and Grinnell (1928) to mean somewhat different things. Elton's definition emphasised what may be termed the trophic niche whereas Grinnell was thinking of a more holistic community niche. Hutchison brought these rather vague ideas together and defined the niche as a n-dimensional hypervolume, where the dimensions are equivalent to environmental pressures. It is obviously impossible to quantify all those biological factors that can affect habitat utilization. The approach adopted here is to limit niche dimensionality to those parameters which particularly help to separate species (Levins 1968).

From these considerations it can be seen that in order to define the niche of waterbuck in terms of environmental stress and competition, it is also necessary to define the niches of all the other main grazing species. The analytical method used first extracts from a set of environmental measurements only those that are important in separating species and then defines the niches of all the main grazers with respect to these variables, at the same time producing indices of niche overlap. All these computations are made using a single multivariate statistical method, discriminant function analysis (DFA). This method has been used recently to investigate habitat relationships for invertebrates (Green 1971), birds (Conner and Adkisson 1976) and ungulates (Ferrar and Walker 1974, Hudson 1976, Page 1977).

METHODS

The basic method whereby habitat parameters are allotted to animal species is to note the location of animals in the study area with reference to the 500 m x 500 m grid system. Each grid square (block) is defined for a set of habitat parameters, some updated monthly. The presence of a species in a block automatically allocates one set of parameter values to that species.

This approach differs somewhat from two recent studies which have used multivariate methods to examine ungulate-habitat relationships.

Ferrar and Walker (1974) also employed discriminant function analysis, but their habitat values were based mainly on measurements made within a 5 m radius of the location of an animal. The grid system used here is considered preferable as it allows the overall environment around an animal to be defined more completely. For example a waterbuck under a tree may be under that particular tree because the whole area is characterised by clumped trees, few shrubs and a high grass height diversity. A disadvantage of this method is the possibility of producing meaningless means for certain variables if their within-block variance is high. In practice it was found that the scale of habitat feature variability allowed for good description using this system. The method used here is more similar to that of Hirst (1975) who made a detailed habitat map in advance of sampling animals, each habitat type being quantitatively defined for a set of environmental characters. He then used principal components analysis and multiple linear regression equations to define niche occupancy.

Habitat variables

Table 68 lists all 42 variables used in discriminant function analyses. The variables were chosen as those thought likely to influence the distribution of grazing animals. Grazers have previously been shown to be able to select for grass species, plant parts and for certain areas with a particular structure to the herbaceous layer (Gwynne and Bell 1968, Field 1972, Jarman 1974 and McNaughton 1976). Many variables have therefore been included that describe both structure and species composition of herbaceous vegetation. Per cent contribution to biomass was used to describe grass species composition as it is likely that an index of the amount of a grass is more important than just presence-absence or frequency data.

The influence of woody vegetation on grazers is expected to be largely confined to physiognomic attributes rather than species composition. Therefore parameters describing woody vegetation are confined to gross structural aspects.

Each of the 132 500 m x 500 m blocks was defined for these variables. The vegetation descriptions were obtained during February and March 1977 using the general methods of Walker (1976). For the purpose of this study a tree is defined as woody vegetation over 2 m in height; a shrub as woody vegetation between 1 m and 2 m high and scrub as woody vegetation less than 1 m high. Tree density, shrub density and

Table 68. The 42 variables used in multivariate analyses; see text for explanation of terms.

Computer label	Variable	Units
TDEN	Tree density	no/0,05 ha
SDEN	Shrub density	no/0,05 ha
TDIV	Tree clumping	var/$\overline{x}$ ratio
SDIV	Shrub clumping	var/$\overline{x}$ ratio
CHIT	Ceiling height	m
SCRB	Scrub density	no/m^2
GSDV	Grass species diversity	number
HITD	Grass height diversity	var/$\overline{x}$ ratio
CWEG	Closed woodland edge	per cent
SLOP	Slope	number of 50 ft contours
COVE	Herb cover-abundance	per cent
PWAT	Distance to permanent water	km
DVPT	Distance to open vantage point	km
DTRD	Distance to a tourist road	km
ALTI	Altitude	m
PRED	Predator use index	number of lion kills in block during 1976 and 1977
BURN*	Time since burnt	month
DWAT*	Distance to any water	km
GHIT*	Grass height	cm
ACON	*Aristida congesta barbicollis*	per cent contribution to biomass
BINS	*Bothriochloa insculpta*	"
CIVR	*Chloris virgata*	"
CPLE	*Cymbopogon pleurinodis*	"
CGAY	*Chloris gayana*	"
DMAC	*Digitaria cf. macroglossa*	"
DAGY	*Digitaria argyrograpta*	"
DAUS	*Dactyloctenium australe*	"
DELU	*Diplachne eleusine*	"
ESUP	*Eragrostis superba*	"
ECUR	*Eragrostis curvula*	"
EPAS	*Eustachys paspaloides*	"
EMON	*Enteropogon monostachyos*	"
FAFR	*Fingerhutia africana*	"
HCON	*Heteropogon contortus*	"
PDEU	*Panicum deustum*	"
PCOL	*Panicum coloratum*	"
PMAX	*Panicum maximum*	"
SSPA	*Setaria sphacelata*	"
SSMU	*Sporobolus smutsii*	"
TTRI	*Themeda triandra*	"
UMOS	*Urochloa mossambicensis*	"
FORB	Forbs	"

*updated monthly.

mean celing height were determined in 20 500 m^2 quadrats per block. Scrub density, grass species diversity, grass height diversity, herbaceous cover-abundance and all grass species' per cent contributions to biomass, were measured in 20 1 m^2 quadrats per block. Non-woody dicots in the herb layer were lumped as forbs and measured in the same way as grasses in terms of per cent contribution to biomass, using the formulae of Mannetje and Haydock (1963) given in Walker (1976). The larger quadrats were in two sets of 10 placed on random 500 m transects placed across each block. The smaller quadrats were each located randomly within a larger quadrat.

Tree clumping, shrub clumping and variability in grass height were calculated using the variance/mean ratio, where values of zero denote a random distribution and values greater than one a clumped (high variation) distribution (Southwood 1966).

Distance variables, slope and altitude were all taken from a 1:25 000 contour map compiled by A. Whateley.[1] Distances were measured from the centre of a block. The amount of closed woodland edge was measured by placing a 100 point grid, scaled to the size of one block, over a 1:25 000 photograph of the main study area (Trigonometric Surveys, Johannesburg). The number of points observed to intersect with closed woodland edge when viewed under a stereoscope gave a percentage value for the amount of edge in a block.

The values for three variables were updated monthly. The first was the time since burning; the second was the distance to any water, including temporary pans, temporary streams and the permanently flowing Black Umfolozi River. The third variable was grass height which was measured as suggested by Walker (1976) as the mean maximum height of the herbaceous layer, where individual measurements are of the highest live material in a 1 m^2 quadrat.

An additional 12 species of grass not given in Table 68 were recorded during the survey but left out of subsequent analyses because of their infrequent occurrence and low per cent contribution to biomass. Each occurred in less than eight blocks with per cent contribution to biomass values of less than five. The species were: *Brachiaria arrecta*, *Brachiaria serrata*, *Eragrostis racemosa*, *Eragrostis ciliaris*, *Eleusine indica*, *Rhyncheletrum repens*, *Sporobolus africanus*, *Tragus berteronianus*, *Alloteropsis semi-allata*, *Schmidtia* sp., *Cenchrus*

1. Mr A. Whateley, Natal Parks Board, HGR.

ciliaris and *Cynodon dactylon*.

Herbivore distributions

The method used to sample animal distributions has already been described under "Ground census" in Chapter 3, where each block was searched once a month and the numbers of all species seen recorded. It was important that the whole study area received an even coverage so that the animal records are representative of both abundance and habitat associations. Searches were confined to mornings, as early as possible, to ensure that aspects of the feeding niche were well represented. Data were collected for the same 16 months between July 1976 and December 1977 for which ground census results have been given.

For the purpose of this chapter,only the eight main grazing species are considered in detail. These are waterbuck, white rhino, impala, nyala, wildebeest, buffalo, zebra and warthog. Results of additional analyses including the other three grazing species, common reedbuck, mountain reedbuck (*Redunca fulvorufula*) and steenbok (*Raphicerus campestris*), plus browsers, will be published separately.

Data analysis

Multivariate analyses were carried out using the SPSS (statistical packages for the social sciences) program Discriminant on the University of Pretoria IBM 370 computer. Theory and details of computations are given by Hope (1968). Two files were created for raw data. One was a list of all 132 blocks defined for the 39 variables that did not change value by month. The other file was also a list of the 132 blocks, but each block contained records for each of the 16 months over which data were collected. For each month a block was defined for the three variables which were updated monthly and for the numbers of each species seen. In addition waterbuck were separated by age and sex into the following groups: all animals, males, females, sub-adult males and calves.

The raw data on habitat variables were measured in many units, some with ranges of zero to one and some from one to 100, and so on. If analyses were carried out using these units then results would be biased towards those parameters with the highest absolute values. For this reason all data were zero-one transformed (Ferrar and Walker 1974). Distance measurements were not $\log_e$ transformed as done by

Ferrar and Walker (1974) as it is considered equally likely that linear relations exist particularly for distance to water measurements.

The two files were combined to produce a third that was the basis for data input to the Discriminant program. It consisted of the total array of variable values encountered by each species for each month. Thus if warthog occurred in 30 blocks in one month there would be 30 lines of data each quantifying the 42 habitat variables. The use of presence or absence criteria rather than weighting the variables to the number of individuals was decided upon after trials using both methods. Using individual weighting caused a great reduction in within-species variance for most parameters and produced significance in the discriminating power of virtually all variables. The result was that many significant discriminant functions were produced whose biological meaning was difficult to interpret.

The following are the main output statistics obtained from the Discriminant program.

1. Number of observations of each species.
2. Mean values for each variable by species.
3. Standard deviations for each variable.
4. Wilks Lambda and univariate F ratios.
5. Within groups covariance matrix.
6. Within groups correlation matrix.
7. Total covariance matrix.
8. The relative percentage of total variance accounted for by each discriminant function (DF).
9. The significance of each DF.
10. Standardised and unstandardised DF coefficients.
11. Centroids in reduced space by species for each DF.
12. Species plots of discriminant scores on DF1 against DF2, plus species centroids.

Initially all 42 variables were used for any one analysis. Invariably the results were difficult to interpret because of this large number of variables. The output from this run was used to reduce the variable list for a second final run. First, the correlation matrix was examined and those variables showing a high correlation with one or more other variables ($r>0,8$) were discarded. Second, the univariate F ratios were considered; these show the significance of the strength of each variable to separate species of animal. Only those variables showing a significant F ratio ($P<0,05$) were usually utilized, giving 10 to 15 variables. If the number of significant variables was less than 10 then additional nearly significant variables were included. The Discriminant program was then re-run.

The discriminant functions finally obtained express the difference between species in terms of a few common orthogonal habitat gradients, instead of the original 42 habitat variables. The standardised DF coefficients indicate the degree to which each variable is associated with any DF. The mean of these discriminant scores is the species centroid which can be interpreted as the niche centre. The significance of species separation is shown by plotting species centroids and indicating plus and minus two standard errors of the centroid mean along each DF gradient. Where these overlap so do the species. The significance of separation on each DF is formally shown by calculating a t statistic in the following way (du Toit pers. comm.):

$$t = \frac{C_a - C_b}{\sqrt{\dfrac{N_a(\mathrm{Var}\ C_a) + N_b(\mathrm{Var}\ C_b)}{N_a + N_b - 2}}} \div \sqrt{\frac{1}{N_a} + \frac{1}{N_b}}$$

where: $\mathrm{Var}\ C_a \doteq \frac{1}{N_a}(U_1{}^2 S_1{}^2 + U_2{}^2 S_2{}^2 + \ldots + U_n{}^2 S_n{}^2)$

and where: the hypothesis tested is that the centroid of species a and species b are equal.

$\mathrm{Var}\ C$ = variance of a centroid,

N_n = sample size of species n,

U_n = unstandardised DF coefficient for variable n,

$S_n{}^2$ = variance of variable n, and

C_n = centroid of species n.

The "approximate" sign is used in the centroid variance equation for two reasons; first, because population variances have been replaced by their respective sample variances and second, because covariance terms have not been considered, as variables that were statistically correlated were omitted from DF calculations.

In addition to running the program Discriminant, the SPSS program Factor was used to carry out principal components analyses as a possible preliminary method to choose variables for DFA. The analysis produces principal components (PCs) which like DFs represent common ecological gradients. The program also produced communalities for variables, these being the percentage variance in each variable accounted for by all PCs. These statistics are another criterion for ranking variables for inclusion in DFA. Although many of the results were interesting they usually added little over the method adopted here and when results were different from those of DFA their ecological interpretation was not straightforward. For these reasons the results of PCA will not be discussed further.

RESULTS

Variables useful in the niche definition of grazing species

Table 69 lists those variables which significantly ($P < 0{,}01$) helped to separate the eight main grazers as judged by their univariate F ratios. The most important parameter was altitude, followed by distance to permanent water. Third came the number of months since burning and ceiling height; fourth were grass height, distance to any water, the amount of *Panicum maximum* and the amount of *Heteropogon contortus*. These two grasses again emphasise altitudinal differences; *Panicum maximum* is mainly found at lower elevations in the shade of dense woody vegetation, whereas *Heteropogon contortus* occurs on higher ridges and rocky slopes.

An additional 11 variables were used to interpret DF gradients because of high standardised DF coefficients; these are given in Table 70. This means that 31 of the initial 42 habitat variables proved useful in describing habitat associations. The 11 not used were bulk contributions to biomass of grass species which generally occurred little within the study area.

Habitat utilization as shown by discriminant function analyses

The results of monthly DFAs are graphed in Figs. 100 to 115. For each month species centroids are plotted with respect to the main DFs that serve to separate species. In each case two or three DFs are used which together account for between 57 per cent and 83 per cent of the total variance in any one month (Table 71). The majority of first DFs show significance and although none of the second or third DFs are significant they can still be used to indicate trends.

Table 69. Parameters which significantly ($P<0,01$) helped to separate the eight main grazing species in the Umfolozi Game Reserve along discriminant function gradients as judged from their univariate F ratios.

Number of times variable significant	Variables*
10	ALTI
7	PWAT
5	BURN, CHIT
3	GHIT, DWAT, PMAX, HCON
2	TDEN, DMAC
1	SDEN, CWEG, SLOP, DTRD, BINS, ESUP, FAFR, SSMU, TTRI, FORB

* For the meaning of computer labels see Table 68.

Table 70. Additional parameters which proved useful in interpreting discriminant function gradients because of high standardised discriminant function coefficients.

Number of times parameter useful	Variables*
4	HITD
3	SCRB, ECUR
2	TDIV, SDIV, UMOS
1	GSDV, COVE, DVPT, PRED, PDEU

* For the meaning of computer labels see Table 68.

Table 71. Relative percentage of total variance extracted by discriminant functions and the significance of discriminant functions.

Month	DF1 (per cent)	DF2 (per cent)	DF3 (per cent)	Total (per cent)
1976				
Jul	33,2	30,7	-[1]	63,9
Aug	31,1*	27,9	-[1]	59,0
Sep	38,5	18,2	-[1]	56,7
Oct	42,5***	22,2	-[1]	64,7
Nov	54,8	13,1	-[1]	67,9
Dec	40,1	24,2	-[1]	64,3
1977				
Jan	29,6*	25,0	15,6	70,2
Mar	52,3***	21,4	8,3	82,0
Apr	35,8*	20,6	17,3	73,7
May	53,8**	15,4	-[1]	69,2
Jun	34,6*	26,6	13,7	74,9
Jul	42,0*	29,1	-[1]	71,1
Sep	48,1*	20,9	13,9	82,9
Oct	40,6**	20,1	16,0	76,7
Nov	37,5**	26,2	17,0	80,7
Dec	38,6	22,9	14,0	75,5

1. Not used.

* $P < 0{,}05$

** $P < 0{,}01$

*** $P < 0{,}001$

July 1976

Two DFs are graphed in Fig. 100. The main ecological gradient is from areas with much *Panicum maximum* and a low ceiling height to areas with a high ceiling and much *Eragrostis curvula*. Buffalo prefer high ceiling areas and is the main species isolated by this DF. Wildebeest prefer habitats similar to buffalo, whereas nyala are found at the opposite *Panicum maximum* end of the scale. Waterbuck occupy a neutral position with the four other species.

The second DF is dominated by the time since burning. July 1976 was one month after approximately one quarter of the study area, that part away from the Black Umfolozi River, was burnt (see Fig. 11). Zebra are the only species showing a strong attraction to the burn and buffalo and nyala are negatively associated with it. Again waterbuck occupy a neutral position indicative of both varied and intermediate habitat usage.

August 1976

Two DFs are graphed in Fig. 101. DF1 grades from areas near to the Black Umfolozi River with much *Sporobolus smutsii*, to areas away from the river. Buffalo are located right by the river. All other species occupy a neutral position, none preferring areas far from the river. The Umfolozi River represented virtually the only water source in the study area during this month.

DF2 concerns locations with few shrubs and much *Sporobolus smutsii* utilized by buffalo and white rhino and densely shrubbed areas used by nyala. Waterbuck overlap with zebra on DF2 as well as DF1 because of a slight preference for shrubbed areas.

September 1976

Two DFs are graphed in Fig. 102. DF1 grades from recently burnt areas with much scrub in the herb layer to areas with little scrub, while DF2 mainly separates *Panicum maximum* grassland from areas with much *Heteropogon contortus*.

The main species separated out are wildebeest utilizing recently burnt areas with a lot of scrub and buffalo living in *Panicum maximum* dominated habitats. Large standard errors as shown by buffalo are seen in a few months' results because of small sample size; when this occurs overlap with other species is not recorded in any summaries, unless their centroids are close together.

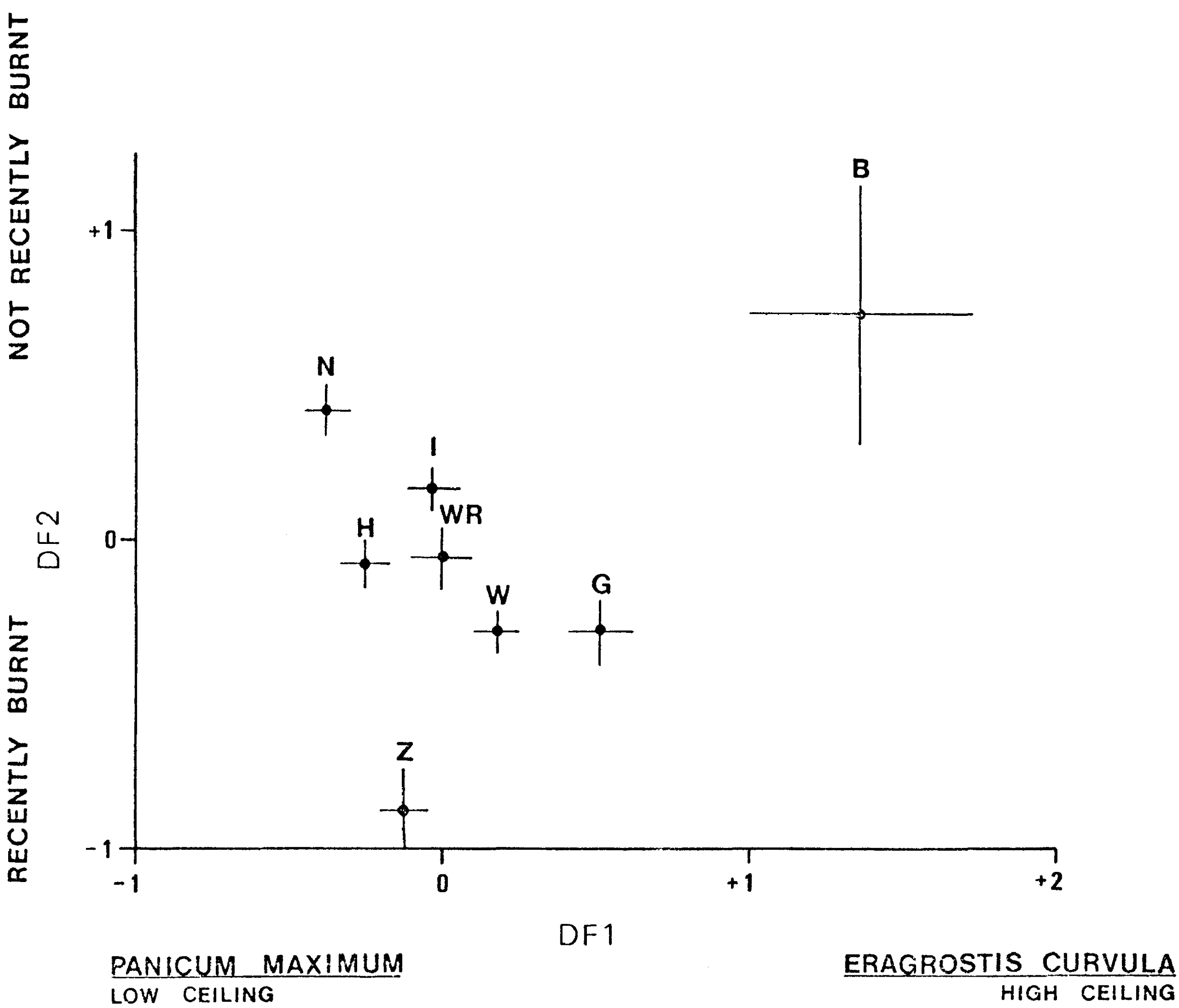

Figure 100. Habitat utilization in the main study area as shown by discriminant function analysis. The location of species' centroids with two standard errors on either side of the mean, July 1976. B = buffalo, G = wildebeest, H = warthog, I = impala, N = nyala, W = waterbuck, WR = white rhino and Z = zebra.

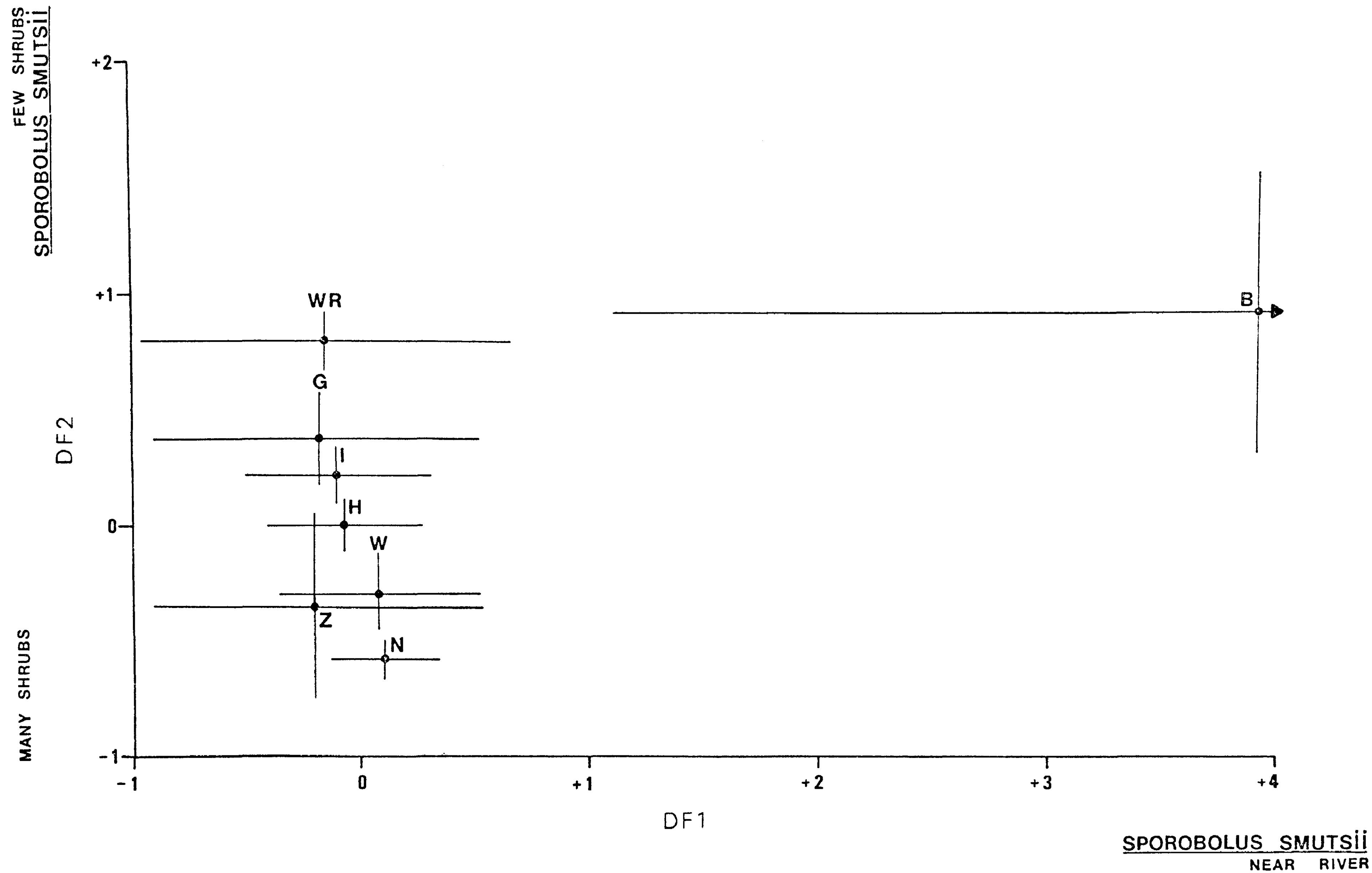

Figure 101. Habitat utilization in the main study area as shown by discriminant function analysis. The location of species' centroids with two standard errors on either side of the mean, August 1976; notation as in Fig. 100.

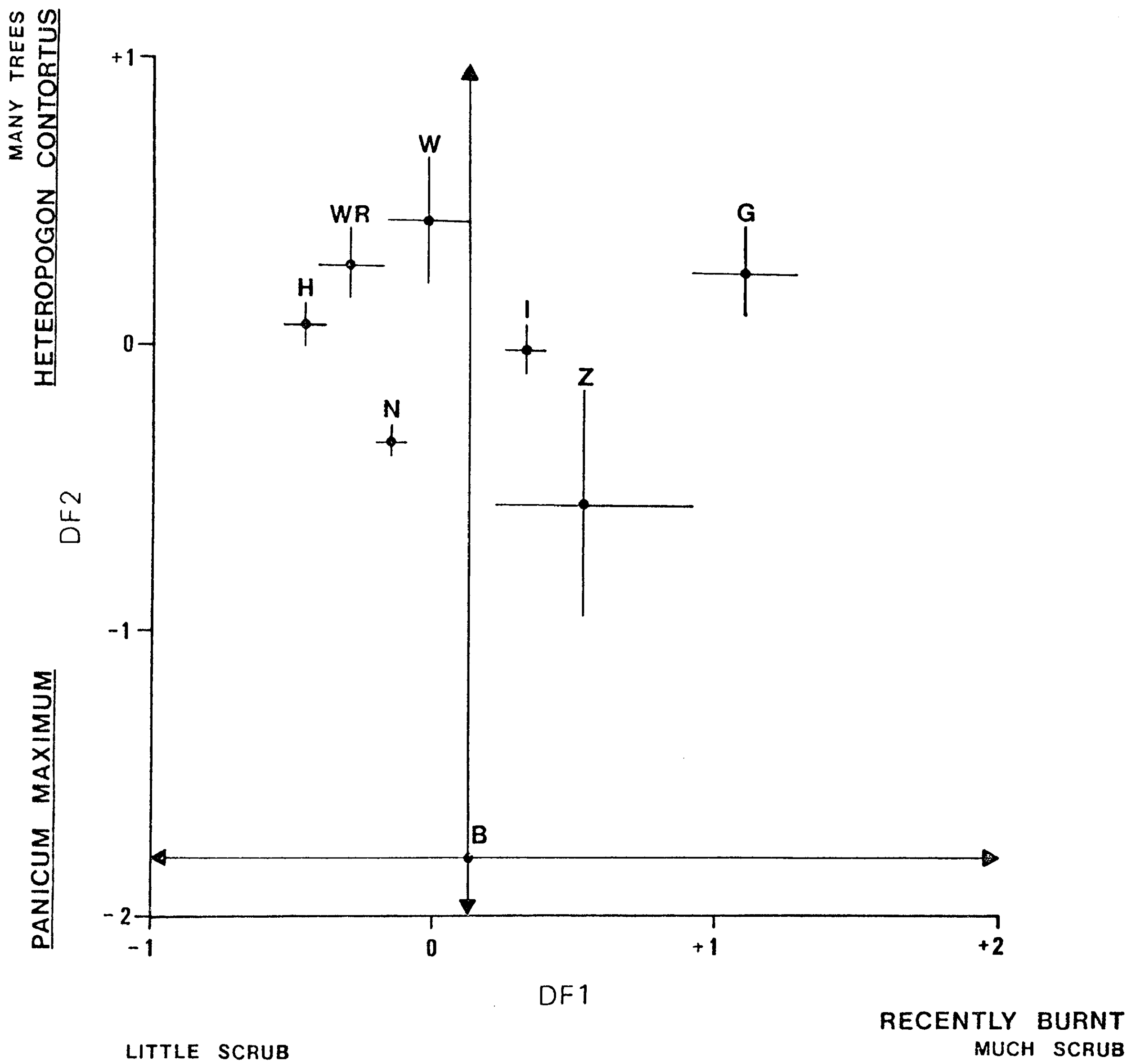

Figure 102. Habitat utilization in the main study area as shown by discriminant function analysis. The location of species' centroids with two standard errors on either side of the mean, September 1976; notation as in Fig. 100.

Waterbuck overlap with nyala on DF1 and with white rhino and wildebeest on DF2.

October 1976

Two DFs are graphed in Fig. 103. DF1 concerns the months since burning and the predator use index, while DF2 involves grass height and the distance from a tourist road. Buffalo and nyala are avoiding the four month old burn, separating them from the other species; the others, however, are also utilizing burnt areas little. October represents the end of four very dry months and the burn had not yet flushed with spring rains (Fig. 123). Buffalo, waterbuck and possibly zebra are separated from other species on DF2 by the utilization of longer grass areas and an avoidance of tourist roads. This means that during a critical period at the end of winter waterbuck are allied to long grass grazing buffalo. The only species utilizing short grass and having a negative association with the burn is nyala.

November 1976

Two DFs are graphed in Fig. 104. DF1 concerns height of the woodland ceiling and the amounts of *Panicum maximum* and *Heteropogon contortus* in the herb layer. DF2 grades from *Eragrostis superba-Themeda triandra* grassland to areas dominated by scrub. Buffalo and zebra utilize high ceilinged open habitats with much *Heteropogon contortus*, whereas nyala occupy the opposite extreme of low ceilinged *Panicum maximum* areas. Waterbuck are close to zebra and buffalo on DF2, all three preferring the *Eragrostis-Themeda* grassland; wildebeest are opposite to this, staying in scrubby areas likely indicative of overgrazing.

December 1976

Two DFs are graphed in Fig. 105. The nature of these two ecological gradients are quite similar: DF1 involves distance to water and the clumping of trees,DF2 involves distance to water and the density of trees. Zebra and wildebeest are the species showing distinctive habitat preferences this month, zebra particularly so because of a use of habitats away from water but with denser, clumped trees. Waterbuck are somewhat separated from other species by a strong association with water.

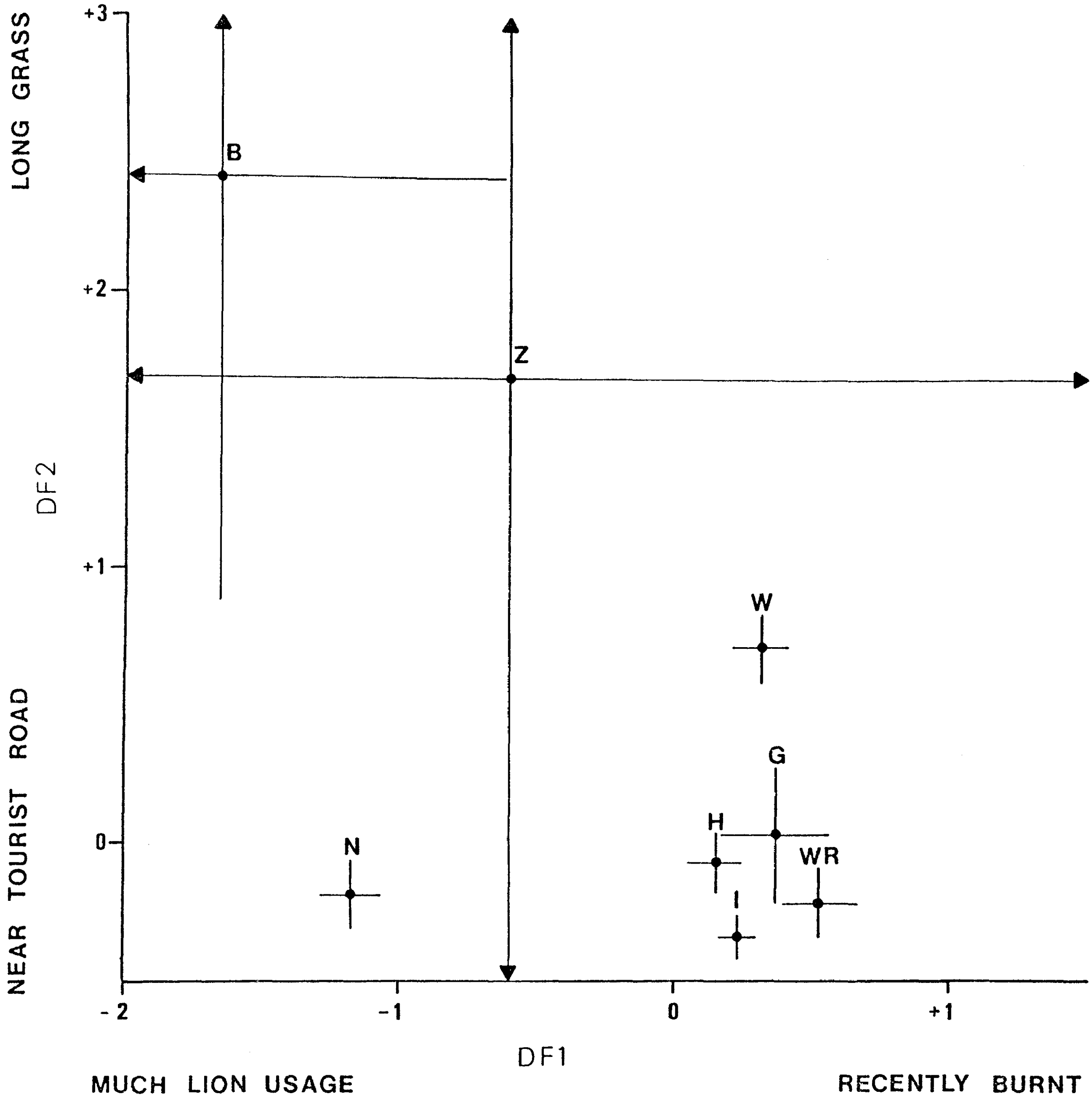

Figure 103. Habitat utilization in the main study area as shown by discriminant function analysis. The location of species' centroids with two standard errors on either side of the mean, October 1976; notation as in Fig. 100.

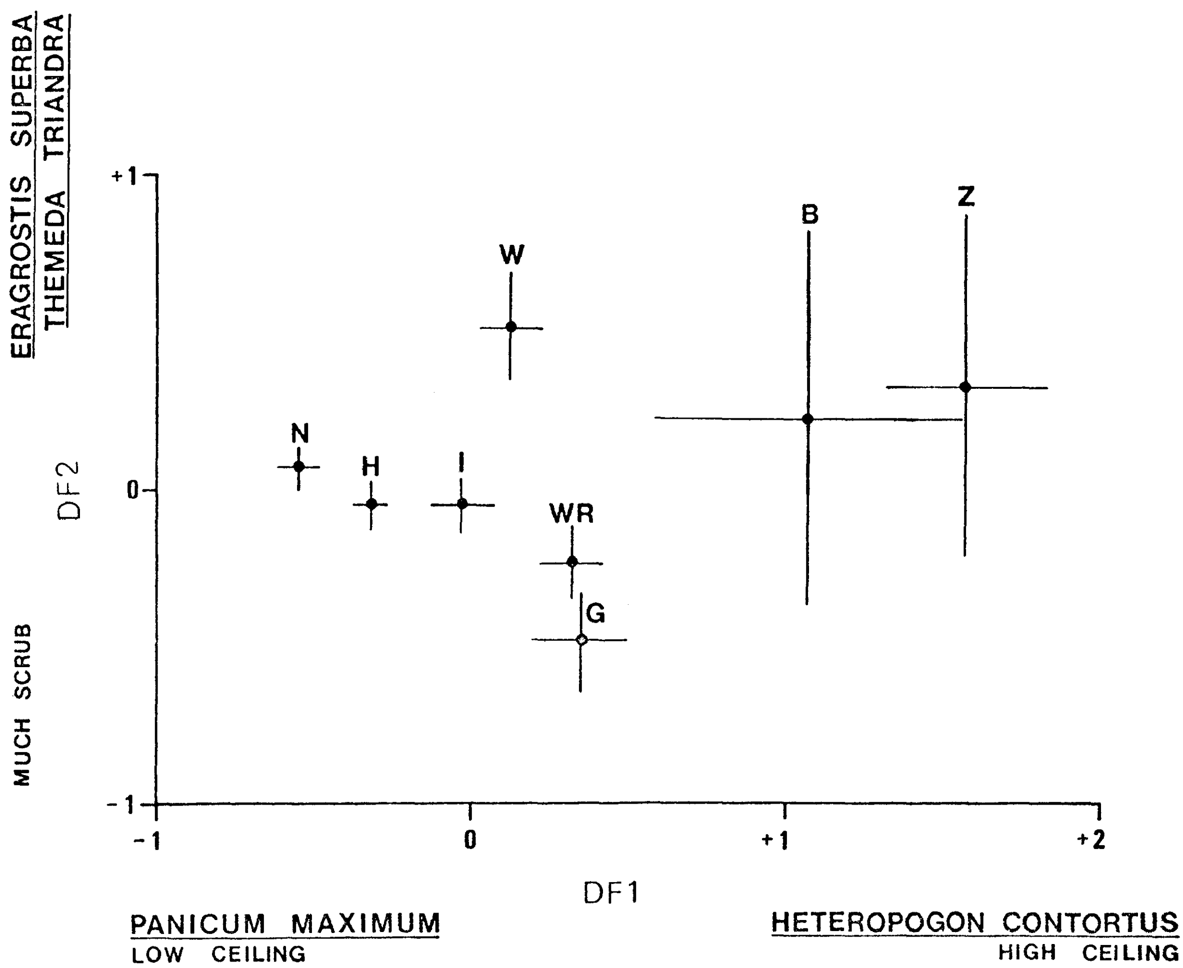

Figure 104. Habitat utilization in the main study area as shown by discriminant function analysis. The location of species' centroids with two standard errors on either side of the mean, November 1976; notation as in Fig. 100.

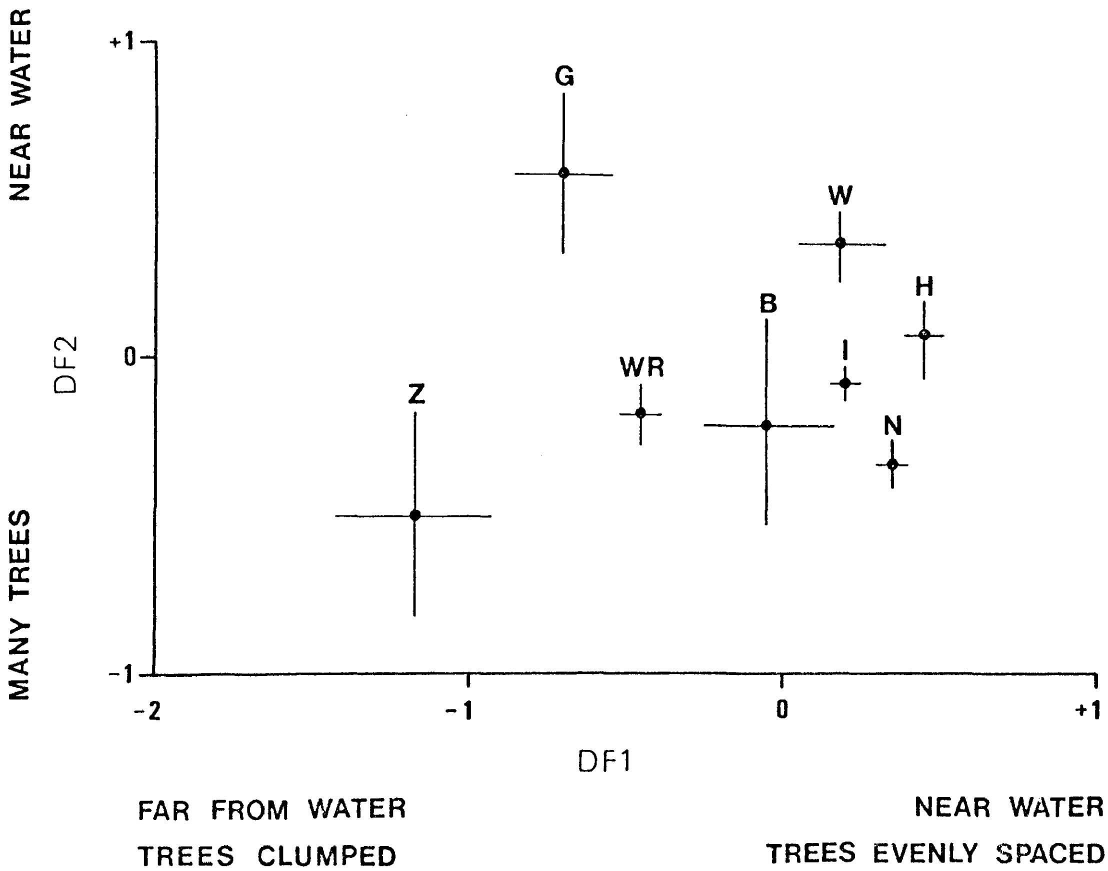

Figure 105. Habitat utilization in the main study area as shown by discriminant function analysis. The location of species' centroids with two standard errors on either side of the mean, December 1976; notation as in Fig. 100.

January 1977

Three DFs are used to define species separation by habitat type this month (Fig. 106). DF1 concerns time since burning, the amount of *Eragrostis curvula* and the clumping of shrubs. DF2 concerns the clumping of shrubs and the amount of *Panicum deustum* present. DF3 grades from low altitude areas with few shrubs to higher areas with many shrubs. Nyala, white rhino and warthog are isolated with respect to DF1 and DF2; buffalo are additionally separated on DF3. Waterbuck occupy a rather intermediate position with respect to all three habitat gradients indicative of a use of varied habitats. Waterbuck are closest to impala and wildebeest when all three dimensions are considered together.

March 1977

Three DFs are graphed in Fig. 107. DF1 serves only to separate buffalo with respect to the presence of an uncommon grass species *Fingerhutia africana*, an association that may be due to chance considering the small sample size for buffalo. DF2 represents an ecological gradient from areas with good grass cover to areas with poor grass cover and much *Panicum maximum*. The latter end of this gradient is characterised by nyala and buffalo. Moderate separation is achieved on DF3, which contrasts high ceilinged areas with few grass species, with low ceilinged areas with many grass species. Waterbuck again occupy the most intermediate position of all species with respect to all gradients.

April 1977

Three DFs are graphed in Fig. 108. One extreme of DF1 is linked to likely overgrazed areas with much *Sporobolus smutsii*, where wildebeest and nyala occur. The other extreme represents recently burnt areas with a high ceiling height, which buffalo, zebra and to a lesser extent waterbuck prefer. During April the mean height of grass on the 10 month old burn was 40 cm, higher than the unburnt areas (Fig. 123). Waterbuck are well separated from buffalo on DF2 and from both buffalo and zebra on DF3, by a preference for little shrubbed higher elevations.

May 1977

Two DFs are graphed for this month in Fig. 109. DF1 concerns

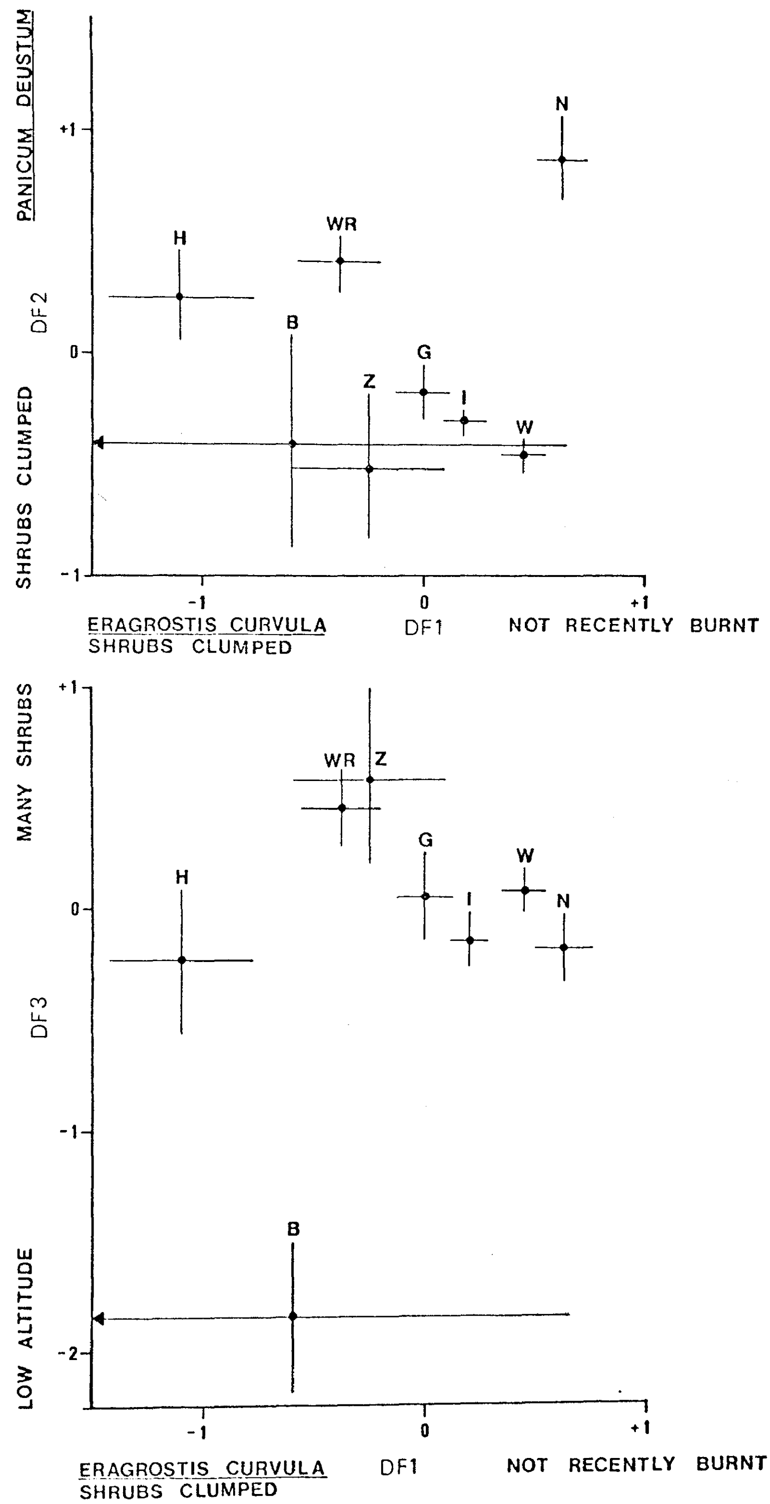

Figure 106. Habitat utilization in the main study area as shown by discriminant function analysis. The location of species' centroids with two standard errors on either side of the mean, January 1977; notation as in Fig. 100.

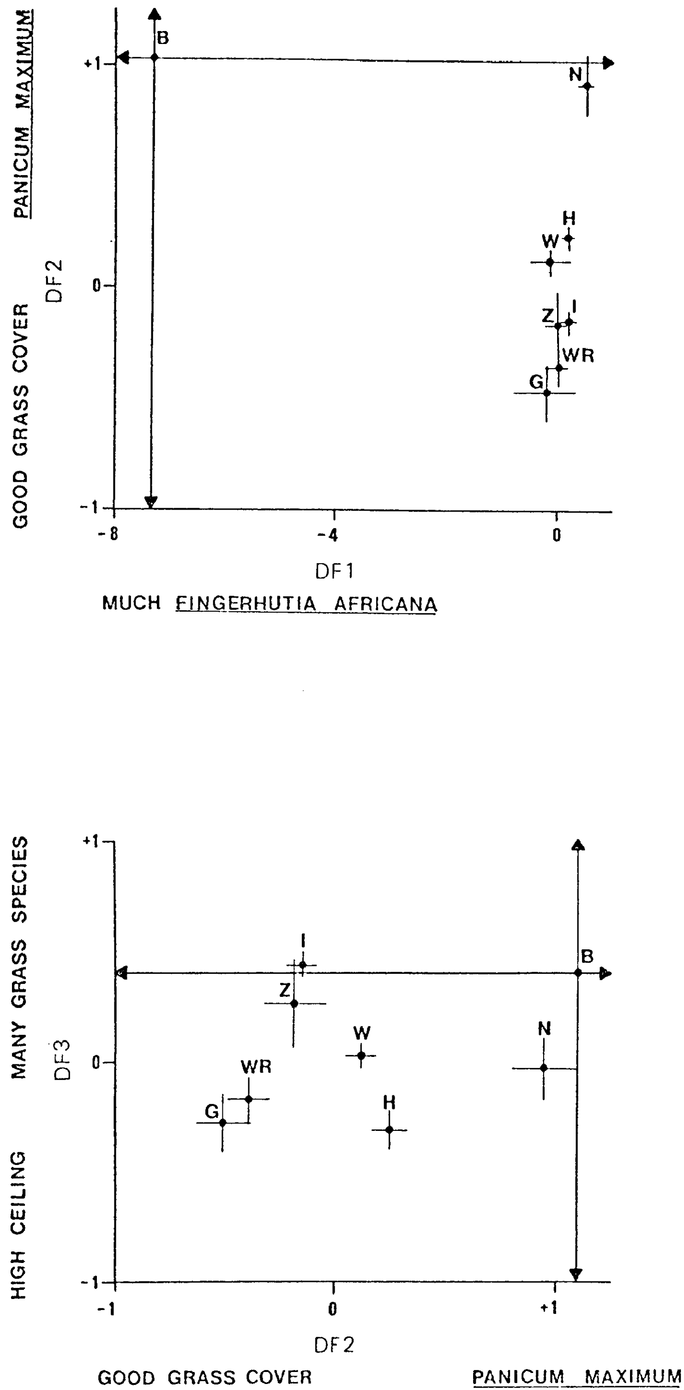

Figure 107. Habitat utilization in the main study area as shown by discriminant function analysis. The location of species' centroids with two standard errors on either side of the mean, March 1977; notation as in Fig. 100.

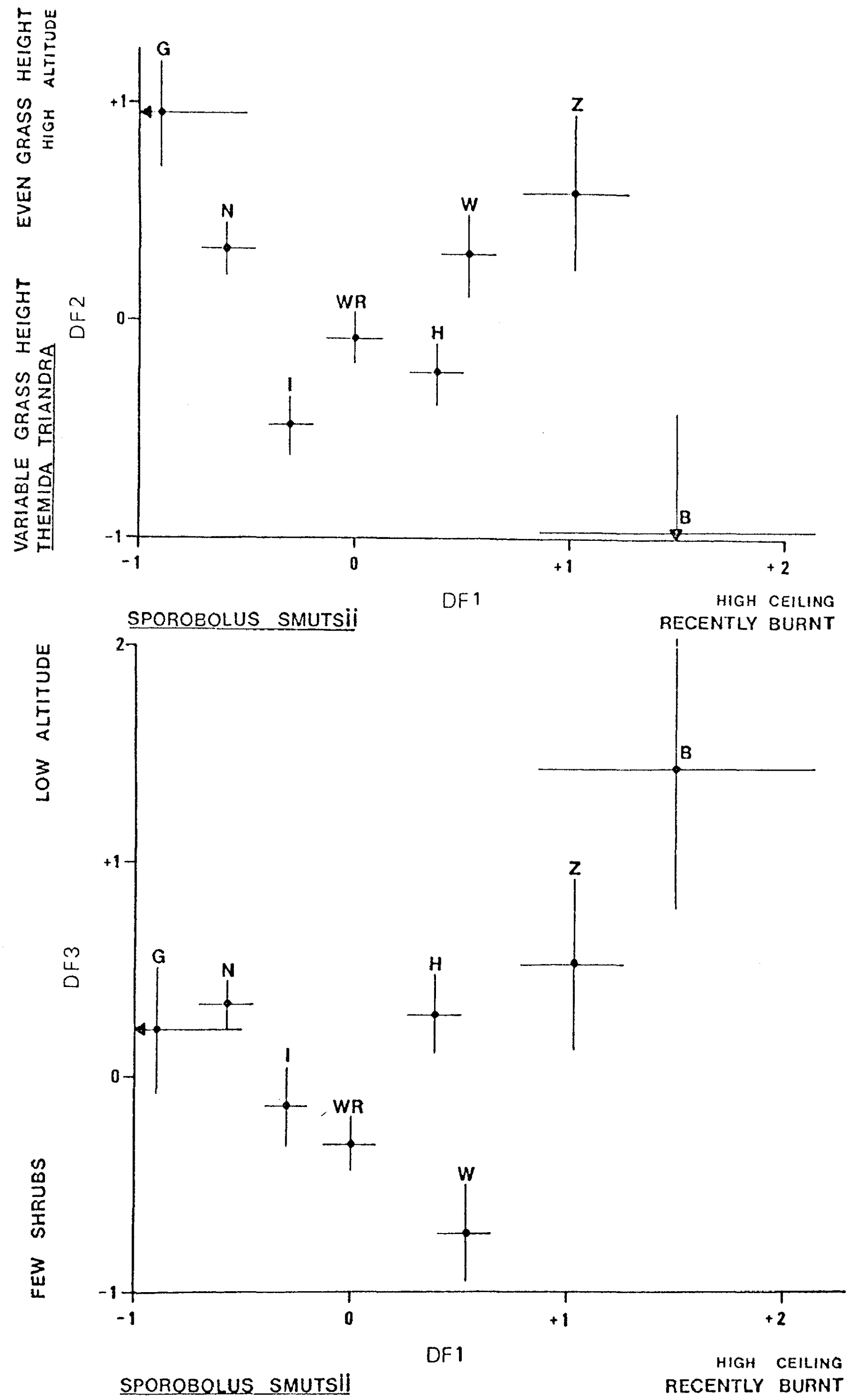

Figure 108. Habitat utilization in the main study area as shown by discriminant function analysis. The location of species' centroids with two standard errors on either side of the mean, April 1977; notation as in Fig. 100.

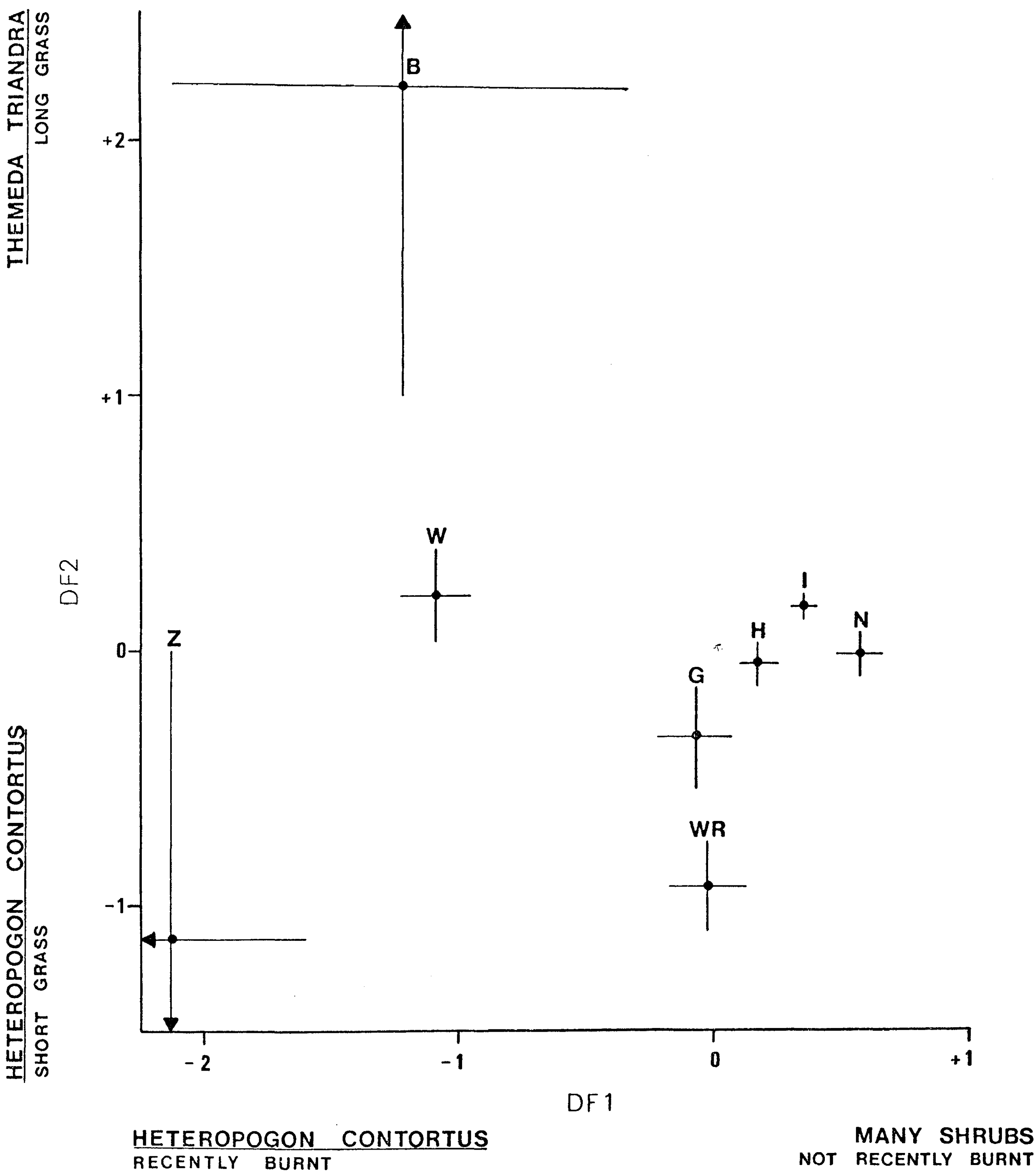

Figure 109. Habitat utilization in the main study area as shown by discriminant function analysis. The location of species' centroids with two standard errors on either side of the mean, May 1977; notation as in Fig. 100.

mainly the time since burning, while DF2 grades from long *Themeda* grassland to short *Heteropogon* grassland. Waterbuck, buffalo and zebra are separated from other species because of a preference for the area burnt 11 months before. Buffalo and zebra are themselves separated by the latter's preference for shorter grasses and the former's for longer *Themeda* grassland. Waterbuck have an intermediate position with respect to grass height.

June 1977

Three DFs are graphed in Fig. 110. DF1 represents the gradient from short grassland at low altitude to long grassland at higher altitude; DF2 grades from even height grassland dominated by *Themeda triandra* to grassland of variable height; DF3 concerns the distance to a vantage point. Buffalo stand out this month because of a preference for long grassland at higher altitudes. Waterbuck is the only other species showing a slight preference for such a habitat. Waterbuck are also separated by utilization of variable height grassland along with white rhino, the latter species staying at lower elevations.

July 1977

Two DFs are graphed in Fig. 111. DF1 grades from high altitude areas with little *Urochloa mossambicensis*, to low altitude areas where this grass is abundant. DF2 represents an ecological gradient from short grassland with much *Panicum maximum*, to tall grassland dominated by *Themeda*, but also with a high density of trees. Buffalo is again the main species separated out, because of utilization of tall *Themeda* grassland. Impala and nyala were found at lower altitudes, while wildebeest and white rhino showed the strongest preference for high altitudes. Waterbuck show a slight preference for higher altitude areas with longer grass.

September 1977

Three DFs are graphed in Fig. 112. DF1 represents an ecological gradient from high altitude areas with few shrubs, to lower altitude areas with many shrubs. DF2 concerns the amounts of *Panicum maximum* and scrub in the herbaceous layer, while DF3 grades from shrubbed areas with much *Panicum maximum* to areas with few shrubs and little *Panicum maximum*.

September broke the run of five dry months and was also the month

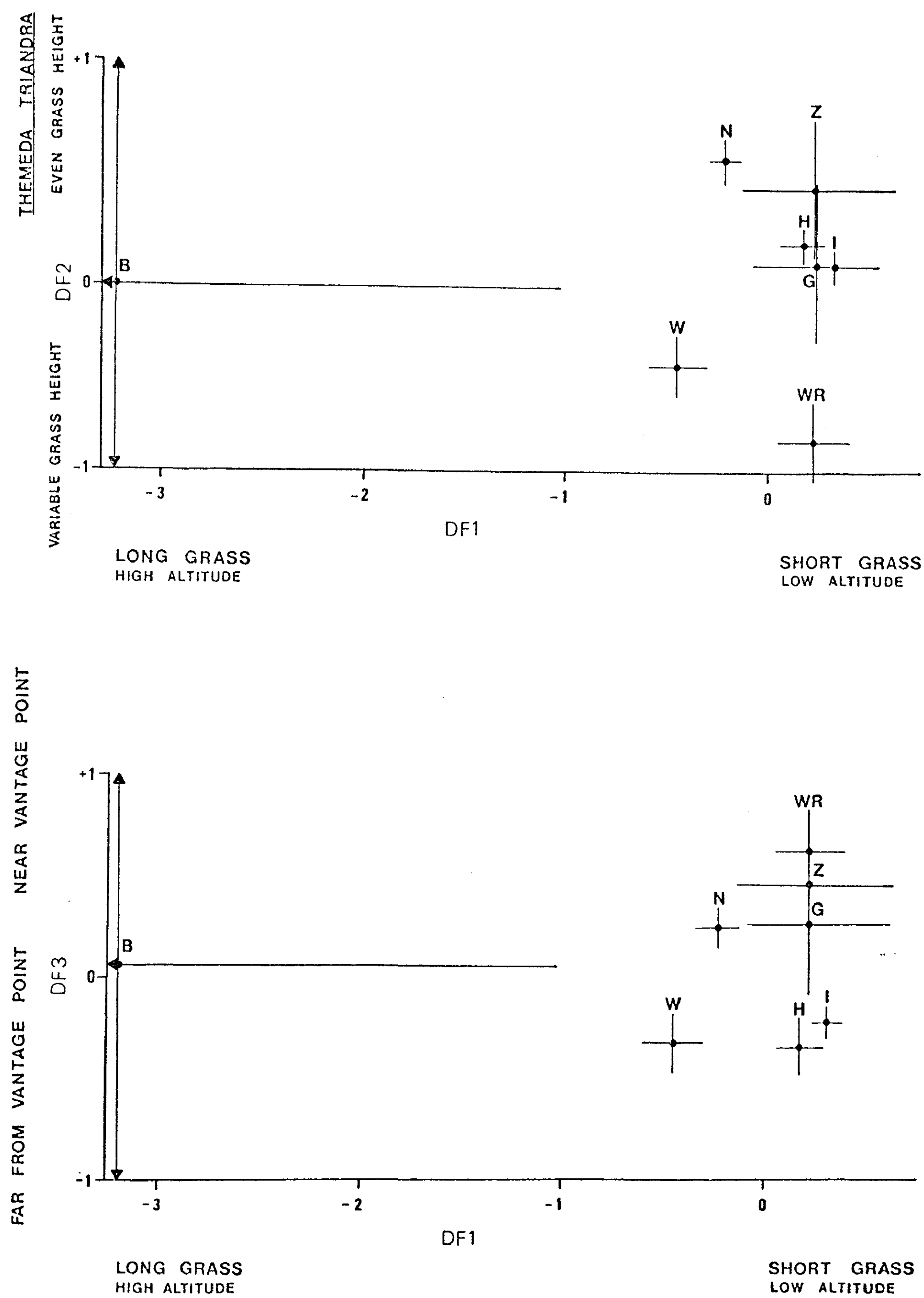

Figure 110. Habitat utilization in the main study area as shown by discriminant function analysis. The location of species' centroids with two standard errors on either side of the mean, June 1977; notation as in Fig. 100.

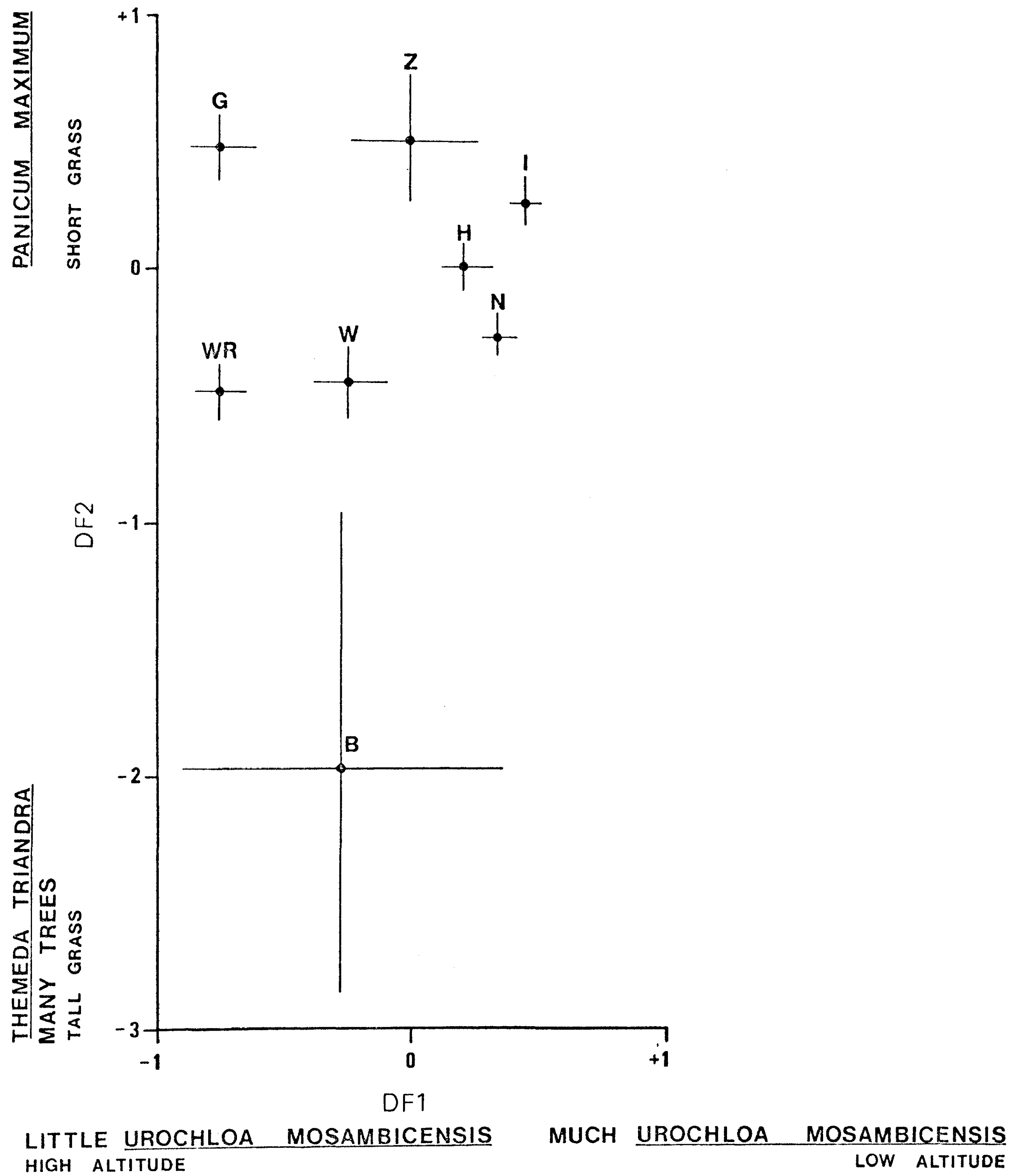

Figure 111. Habitat utilization in the main study area as shown by discriminant function analysis. The location of species' centroids with two standard errors on either side of the mean, July 1977; notation as in Fig. 100.

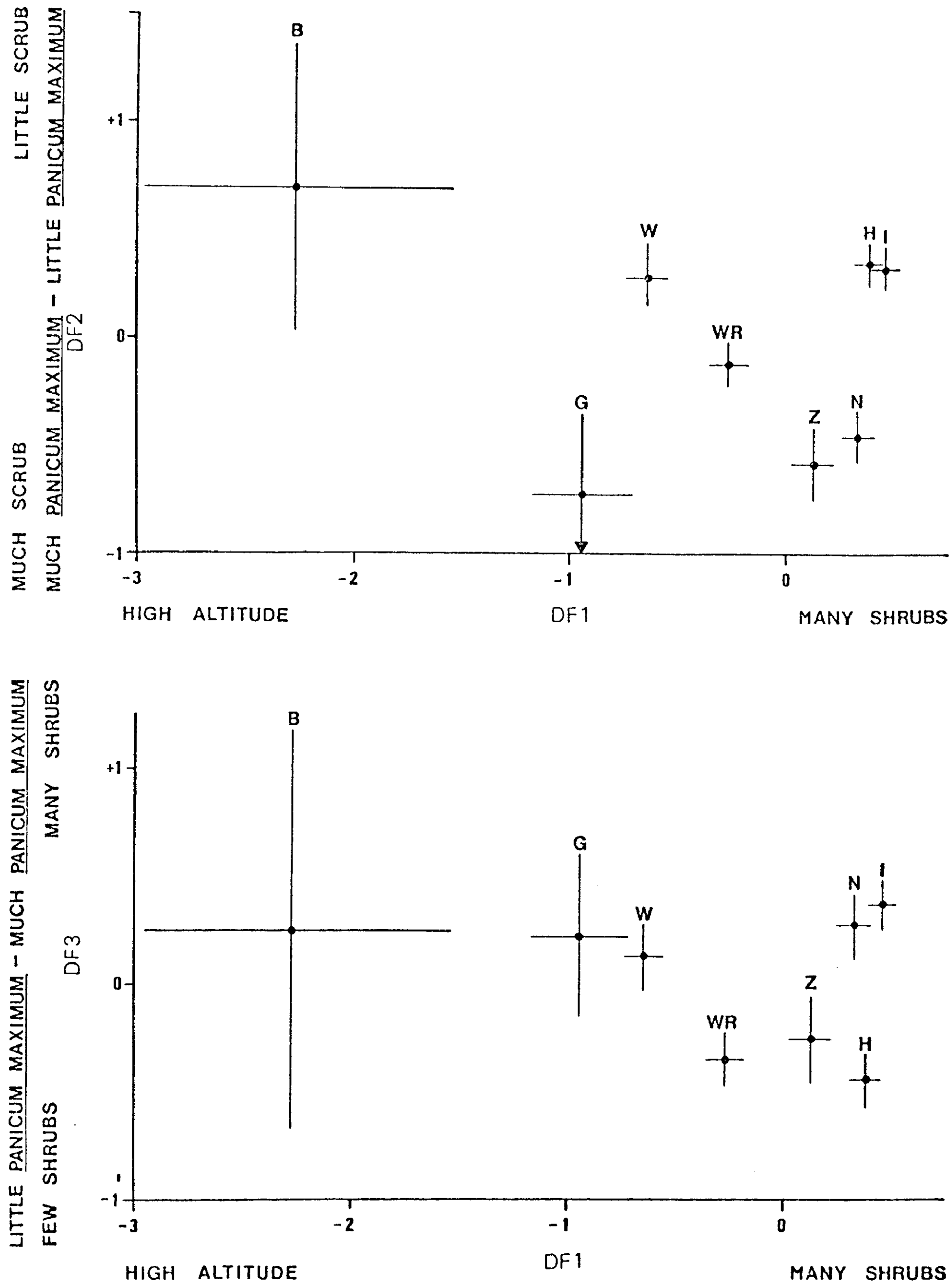

Figure 112. Habitat utilization in the main study area as shown by discriminant function analysis. The location of species' centroids with two standard errors on either side of the mean, September 1977; notation as in Fig. 100.

when all the study area not burnt in June 1976 was burnt (Fig. 11). There was virtually no green flush at the time of sampling (Fig. 123), but all species except buffalo and to a lesser extent wildebeest and waterbuck utilized the burn to some extent as judged from their neutral position with respect to altitude. Waterbuck exhibited no preferences on DF2 or DF3; nyala showed the most consistant pattern on these two gradients, by preferring shrubbed areas with much *Panicum maximum* and much scrub.

October 1977

Three DFs are graphed in Fig. 113. DF1 concerns distance to water, DF2 concerns mainly grass height and DF3 grades from high altitude areas with much closed woodland edge to lower altitude areas with little closed woodland edge.

October was again dry and little water occurred away from the Black Umfolozi River (Fig. 3). Zebra is the only species ranging far from water and nyala is the species staying closest to water. Waterbuck occupy an intermediate position on this gradient, but are separated out by preferring relatively longer grassland like white rhino and higher altitudes like buffalo.

November 1977

Three DFs are graphed in Fig. 114. DF1 represents an ecological gradient from closed woodland to open woodland with much *Bothriochloa insculpta*. DF2 concerns clumping of trees and the amount of *Eragrostis superba*. DF3 grades from recently burnt areas with short grass to long grass areas away from the burn.

This month waterbuck occupied open woodland areas with longer grasses such as *Eragrostis superba* and showed no preference for the recent burn. Little rain fell in November and grass on the burn was not increasing in height as it had by November 1976. Waterbuck overlap with buffalo on each DF, although their centroids are well separated on DF3.

December 1977

Three DFs are graphed in Fig. 115. DF1 grades from areas with an even grass height to areas with variable grass height and much *Bothriochloa insculpta*. DF2 grades from habitats close to the Black Umfolozi River to those far from the river and with variable grass

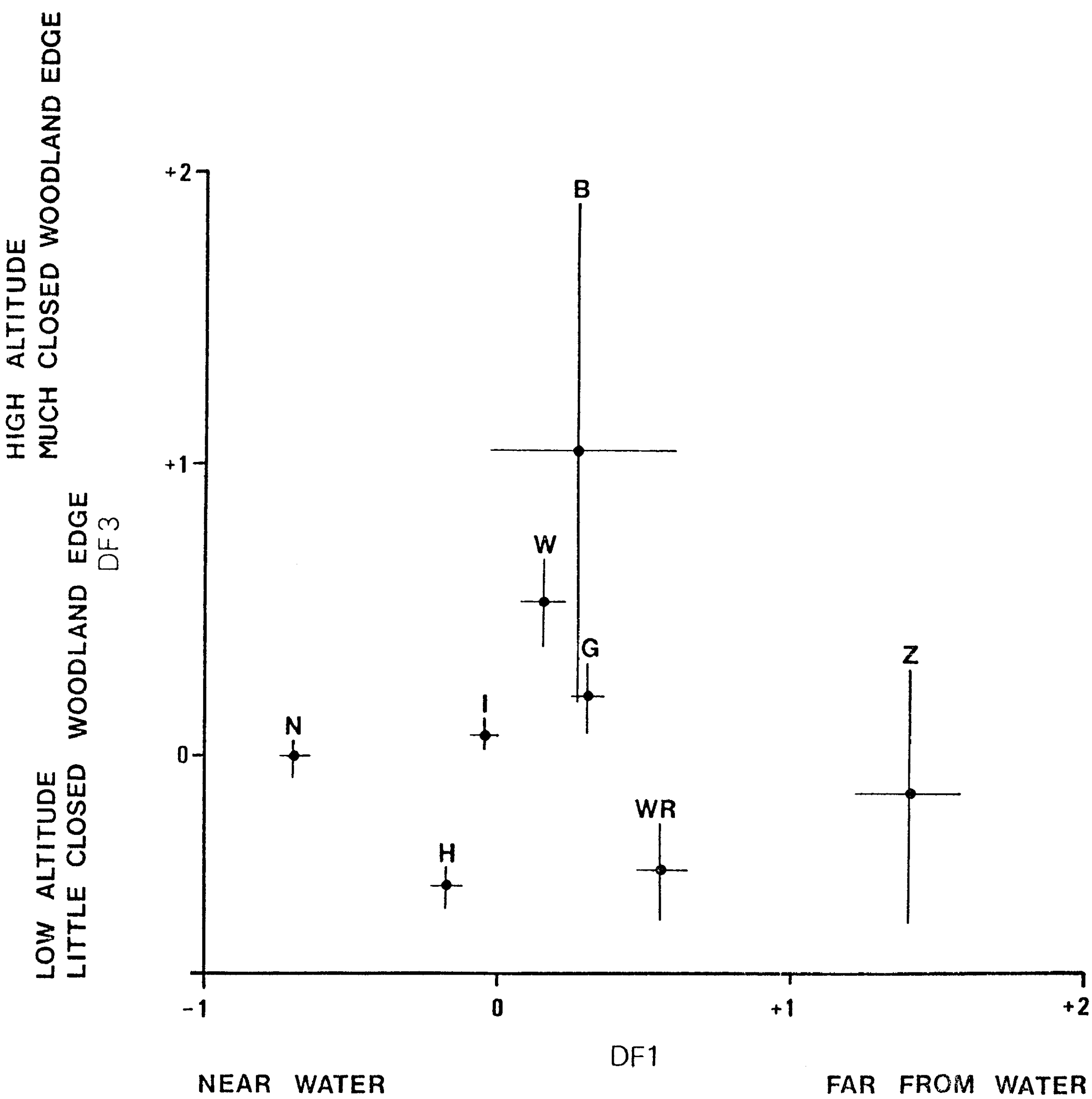

Figure 113. Habitat utilization in the main study area as shown by discriminant function analysis. The location of species' centroids with two standard errors on either side of the mean, October 1977; notation as in Fig. 100.

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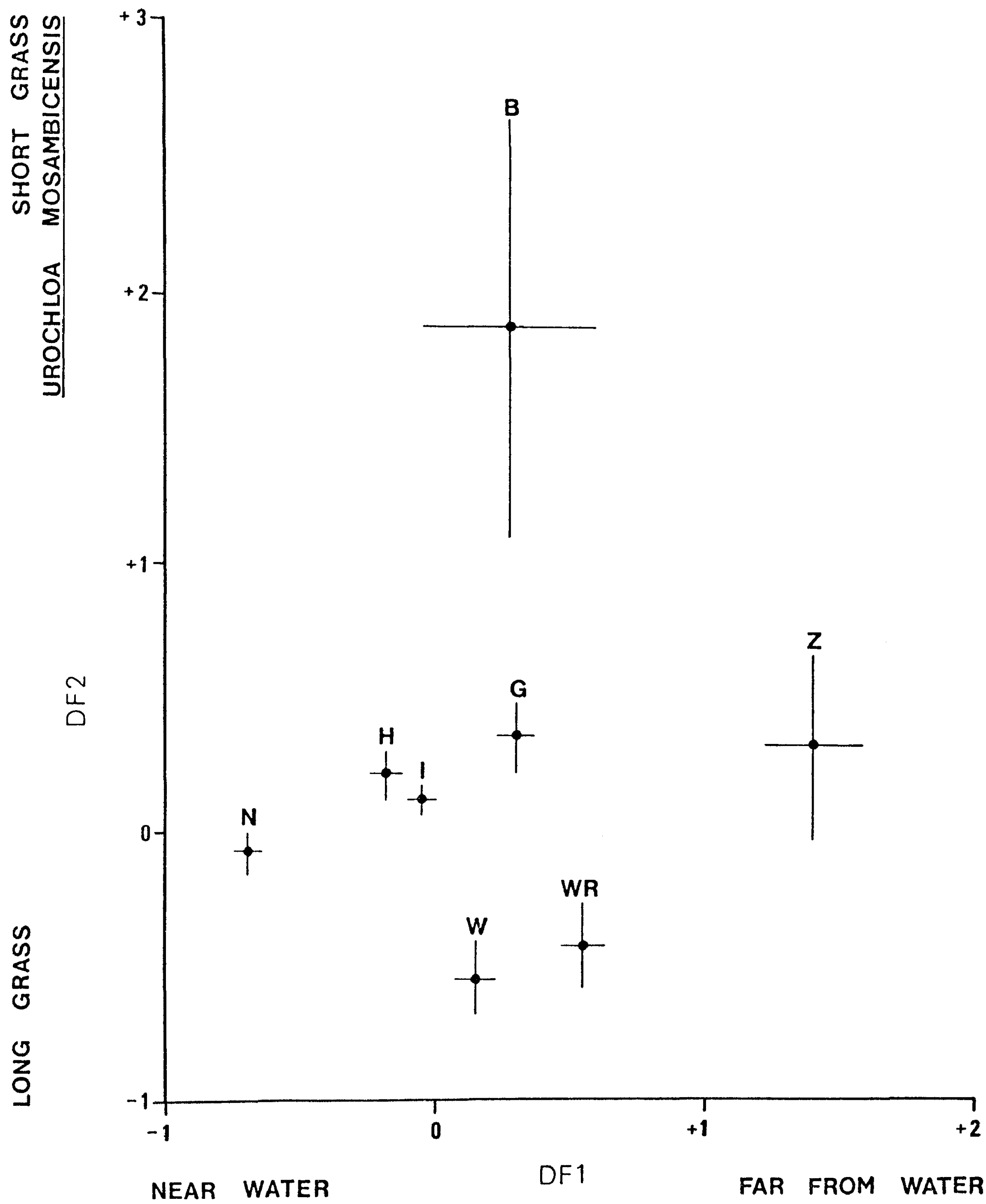


Figure 113, continued.

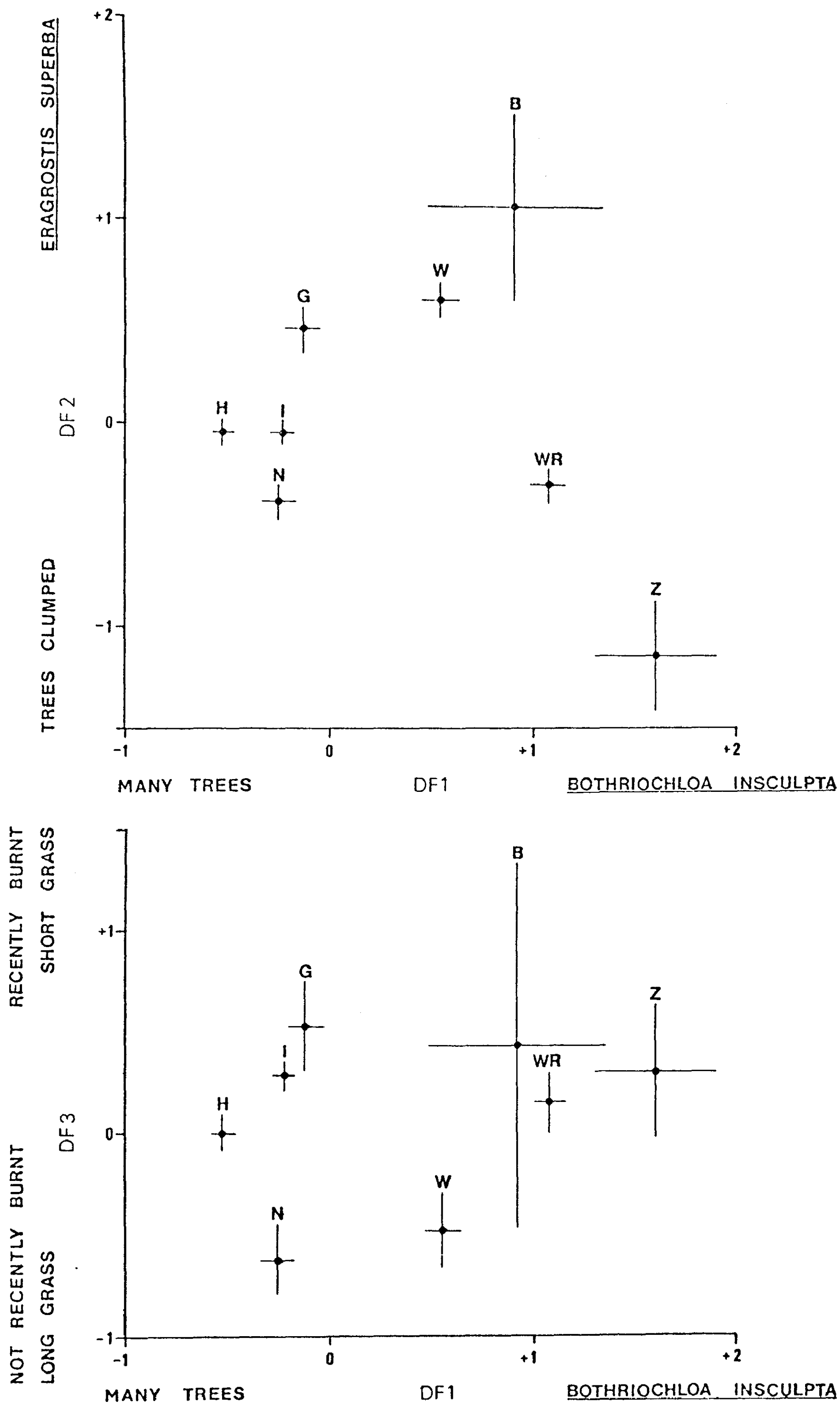


Figure 114. Habitat utilization in the main study area as shown by discriminant function analysis. The location of species' centroids with two standard errors on either side of the mean, November 1977; notation as in Fig. 100.

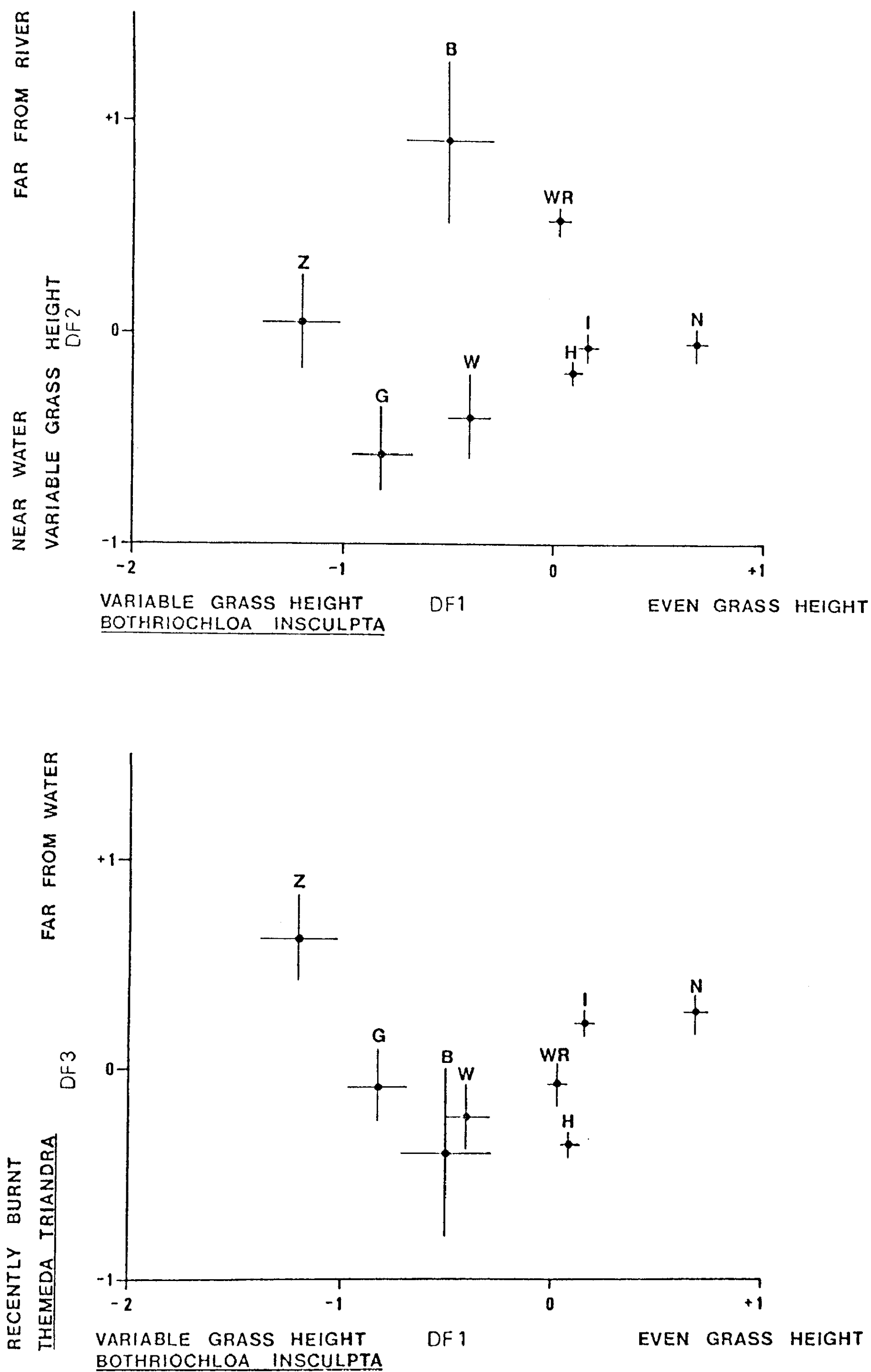


Figure 115. Habitat utilization in the main study area as shown by discriminant function analysis. The location of species' centroids with two standard errors on either side of the mean, December 1977; notation as in Fig. 100.

height. DF3 grades from areas close to any water source which were recently burnt, to areas not close to water.

Waterbuck show a very intermediate position this month, except for a slight preference to stay near the Black Umfolozi River in areas of variable grass height. The grass height on the burn did not increase this month due to a lack of rain; the rain recorded for December (Fig. 3) fell mainly towards the end of the month, after sampling was complete. It is likely that the choice of areas with variable grass height indicates the importance of leaving unburnt patches of long grass near the river, so that some bulk of grass exists should the rains come late.

Summary of DFA results

When the significance of overlap ($P < 0,05$) on the first DF is used as an index of competition, buffalo emerge as the main competitor with waterbuck in terms of habitat overlap on a year round basis (Table 72). The use of only the first DF is justified as it is only here that significant DFs occur (Table 71). By considering the reciprocity of overlap on DF1 the eight grazers can be split into four groups. First, buffalo, zebra and waterbuck, with impala sometimes associated with zebra. Second, white rhino and wildebeest; third, impala with warthog and fourth, nyala with waterbuck. The fourth association is weaker than the rest since it is not reciprocated by waterbuck to the same degree. All associations are on a year-round basis apart from nyala with waterbuck, which is confined to the dry season and early wet season, particularly in 1976. The lack of overlap in 1977 is largely attributable to the area near the river being burnt in 1977. Nyala are confined mainly to densely bushed areas which occur particularly near the river, and so remain on the burn, whereas waterbuck do not favour burnt areas at such an early stage.

Waterbuck stand out as the species showing preference for the widest range of habitat types as a regular strategy, from high open ridges to closed woodland by the Black Umfolozi River; hence the diverse competitors, buffalo and nyala.

These results do not mean that waterbuck are in a favourable position because of a flexibility in habitat usage. Indeed supplementary habitat association data and results on feeding ecology are going to be used to argue that the opposite is the case; that the primary habitat of waterbuck is that occupied year-round by nyala

Table 72. A summary of competition between the eight main grazing species in the Umfolozi Game Reserve based on significance of overlap on the first discriminant function.

Species	Main competitor(s)	Seasonality
White rhino	Wildebeest (7)*	Mainly dry months
Impala	Warthog (7)*	All year
Nyala	Waterbuck (5)*	Dry plus beginning of wet season
Warthog	Impala (7)*	All year
Zebra	Buffalo (6)*	All year
	Impala (6)*	All year
Wildebeest	White rhino (7)*	All year
Buffalo	Zebra (7)*	All year
	Waterbuck (7)*	All year
Waterbuck	Buffalo (7)*	All year

* Number of months in which overlap was significant ($P < 0,05$).

and what are recorded here are the results of competition with nyala for a limiting resource, pushing waterbuck into an unfavourable environment.

That such a process could be occurring can be seen more clearly by considering a DFA over the whole 1977 dry season (Fig. 116). Here waterbuck are split into males, females, sub-adult males and calves. All waterbuck classes prefer longer grass areas which separates them from nyala on DF1. There is some separation of waterbuck classes on DF2, with calves and females nearest to nyala because of a tolerance of slightly lower ceiling heights and poorer grass cover. There is a large separation of waterbuck classes on DF3. Calves and females are the most restricted to water of any waterbuck class or indeed any species, which brings them into overlap with nyala and impala. Waterbuck sub-adult males stay the furthest from water, bringing them into contact with zebra and white rhino. These results indicate a stress situation during the dry season, with the waterbuck age-sex classes on a habitat gradient from better quality grass of sub-optimal height to long grass of poor quality (see Chapter 9). That sub-adult males are in the most disadvantageous grassland suggests that this separation is not only physiologically oriented with relation to body size, but that social interactions are probably also important.

Supplementary data analyses

Grazing associations

The frequencies with which other species were observed grazing within a 10 m radius of a grazing waterbuck are given in Table 73. These data are not corrected for variations in density and so the low association with buffalo is to be expected considering their low mean density within the study area. Data for other species are considered indicative of co-utilization of grassland types, particularly within species on a seasonal basis.

The main overlap is with nyala, impala and zebra. Waterbuck graze with nyala particularly in dry months, with impala somewhat more during dry months and with zebra somewhat more during the wetter months. These results agree with those from DFA and confirm that the overlap with nyala during winter is important in terms of the trophic niche.

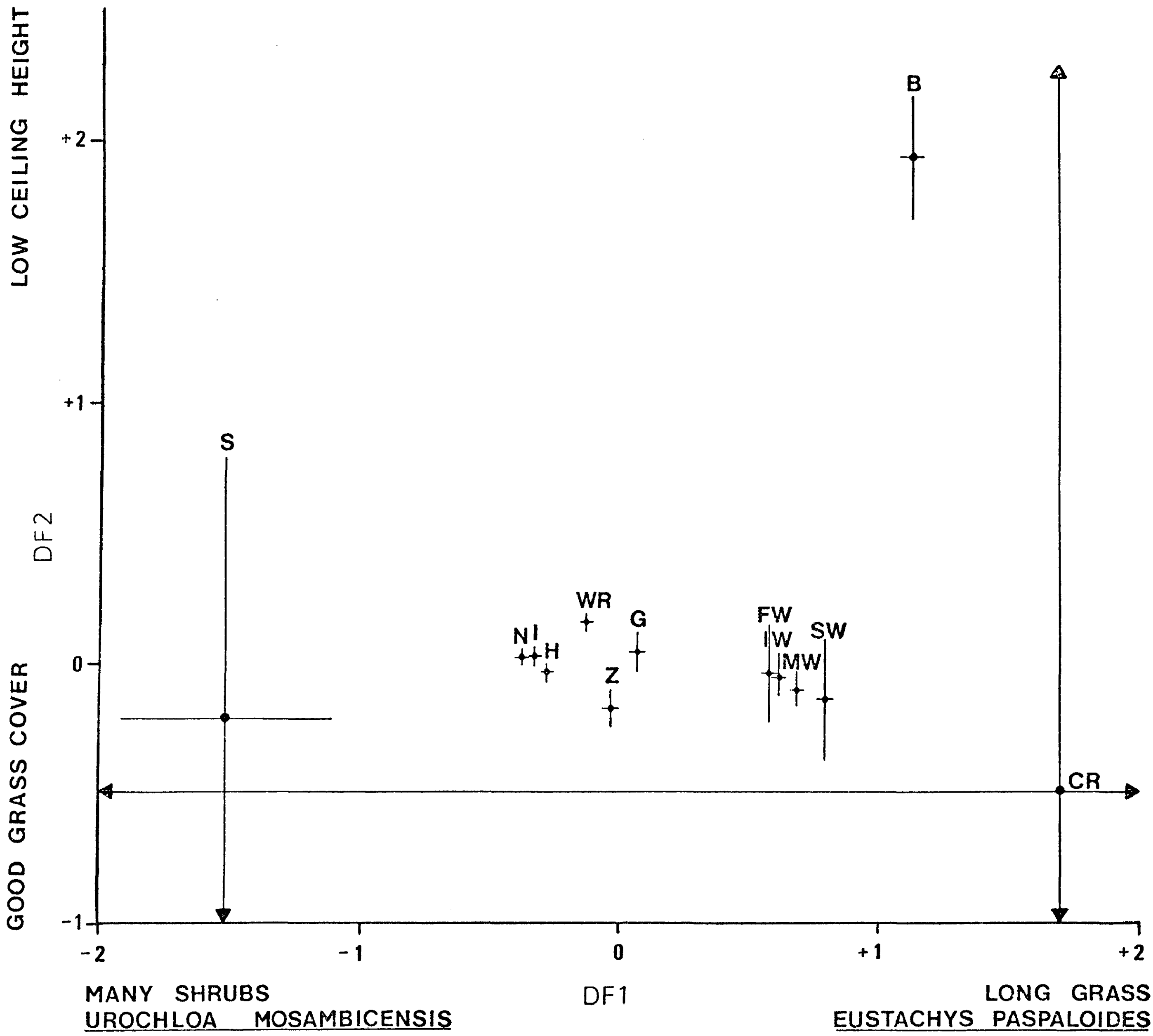


Figure 116. Habitat utilization in the main study area as shown by discriminant function analysis. The location of species' centroids with two standard errors on either side of the mean, for the dry months April to September 1977. Notation as in Fig. 100, plus: S = steenbok, CR = common reedbuck, FW = female waterbuck, MW = male waterbuck, IW = waterbuck calves and SW = sub-adult male waterbuck.

continued

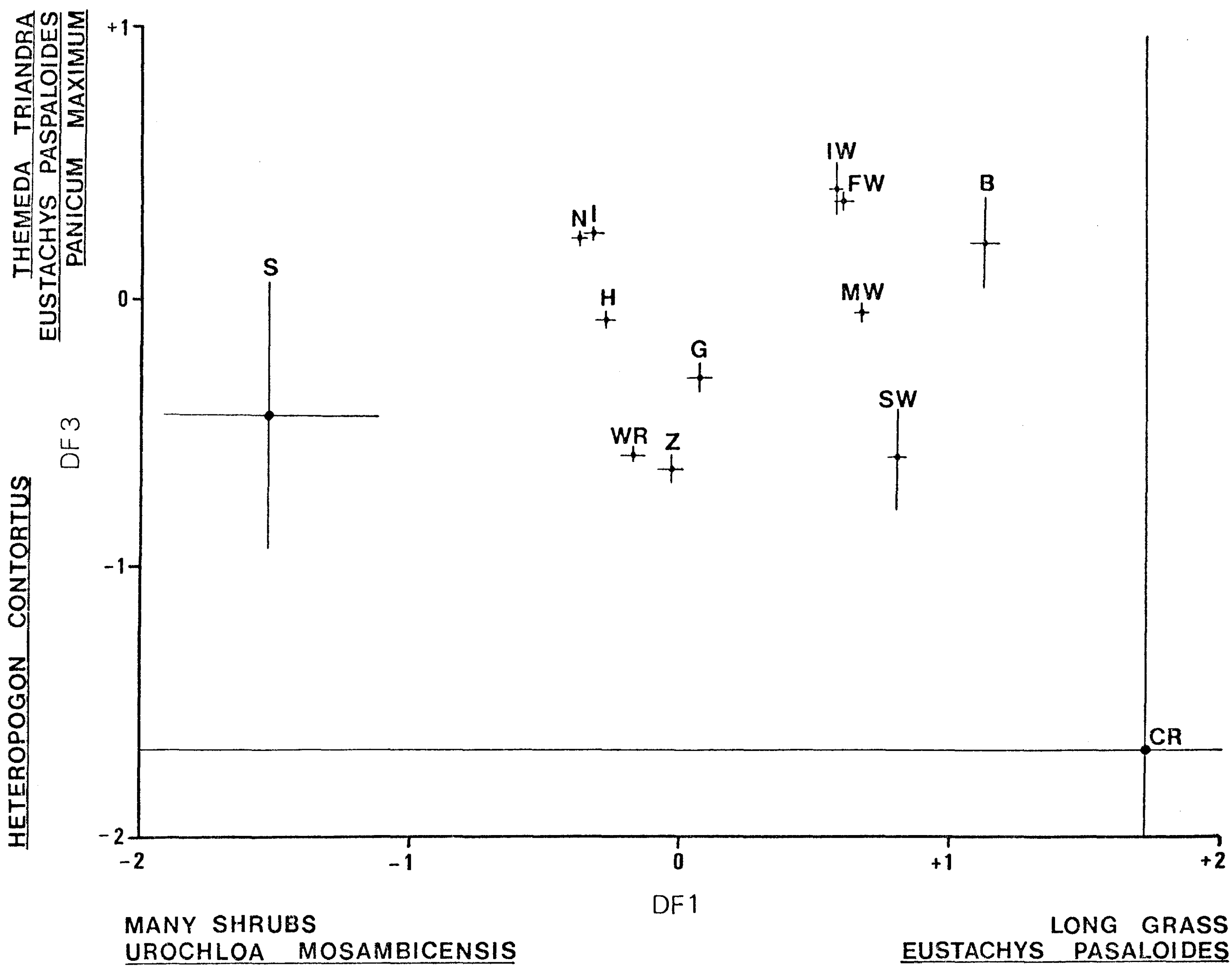


Figure 116, continued.

Table 73. The frequencies of other species observed grazing with grazing waterbuck in the Umfolozi Game Reserve expressed as percentages of total mixed feeding sightings.

	White rhino	Impala	Nyala	Warthog	Zebra	Wildebeest	Buffalo	Total number of observations
Jan-Mar 1976	0	33,3	0	0	33,3	33,3	0	6
Apr-Jun 1976	0	20,0	15,0	10,0	20,0	5,0	5,0	20
Jul-Sep 1976	0	41,4	37,9	3,4	3,4	13,8	0	29
Oct-Dec 1976	8,6	18,6	37,1	0	21,4	12,9	1,4	70
Jan-Mar 1977	5,9	14,7	17,6	0	41,2	20,6	0	34
Apr-Jun 1977	0	35,7	50,0	7,1	14,3	0	7,1	14
Jul-Sep 1977	10,5	15,8	31,6	5,3	26,3	5,3	0	19
Oct-Dec 1977	10,2	22,0	16,9	1,7	44,1	20,3	0	59
Total period	6,4	24,3	27,5	2,4	23,5	14,7	1,2	251

The grazing succession onto burnt areas

Since burning history was one of the top four variables important for species niche definition and also one of the few variables open to direct manipulation through management, it was examined further.

The association of a species with a burnt area was calculated on a monthly basis using data from the equal coverage ground censuses. The Association Index (AI) for species A =

$$\frac{\text{Per cent of total observations of species A on burn}}{\text{Per cent of study area burnt}}$$

An index of one indicates random association, greater than one positive association, and less than one negative association. In order to allow direct comparision between graphs and to make the ranges of possible positive and negative associations equal, the index is converted to a percentage of maximum values possible. For positive associations, per cent value =

$$\frac{(AI - 1)}{(MaxAI - 1)} \cdot 100$$

For negative associations, per cent value reduces to

$$(AI - 1) \cdot 100$$

since the negative range is always one to zero.

The monthly association indices for the eight main grazing species with the 1976 and 1977 burns are shown in Figs. 117 to 122. The monthly mean grass heights, taken from block records, for the area burnt in 1976 and the remainder of the study area burnt in 1977, are graphed in Fig. 123.

The June 1976 burn was on higher altitude *Themeda* grassland, accounting for 24,6 per cent of the study area. The only species to show a positive association during the first month was zebra. Wildebeest were the second main species to show a strong preference for the burn, this being maximal during the second month when the grass had reached 10 cm. Little rain fell during the first four months after the burn and apart from this utilization of the initial flush, use was reduced until a second flush occurred with November rains. Impala

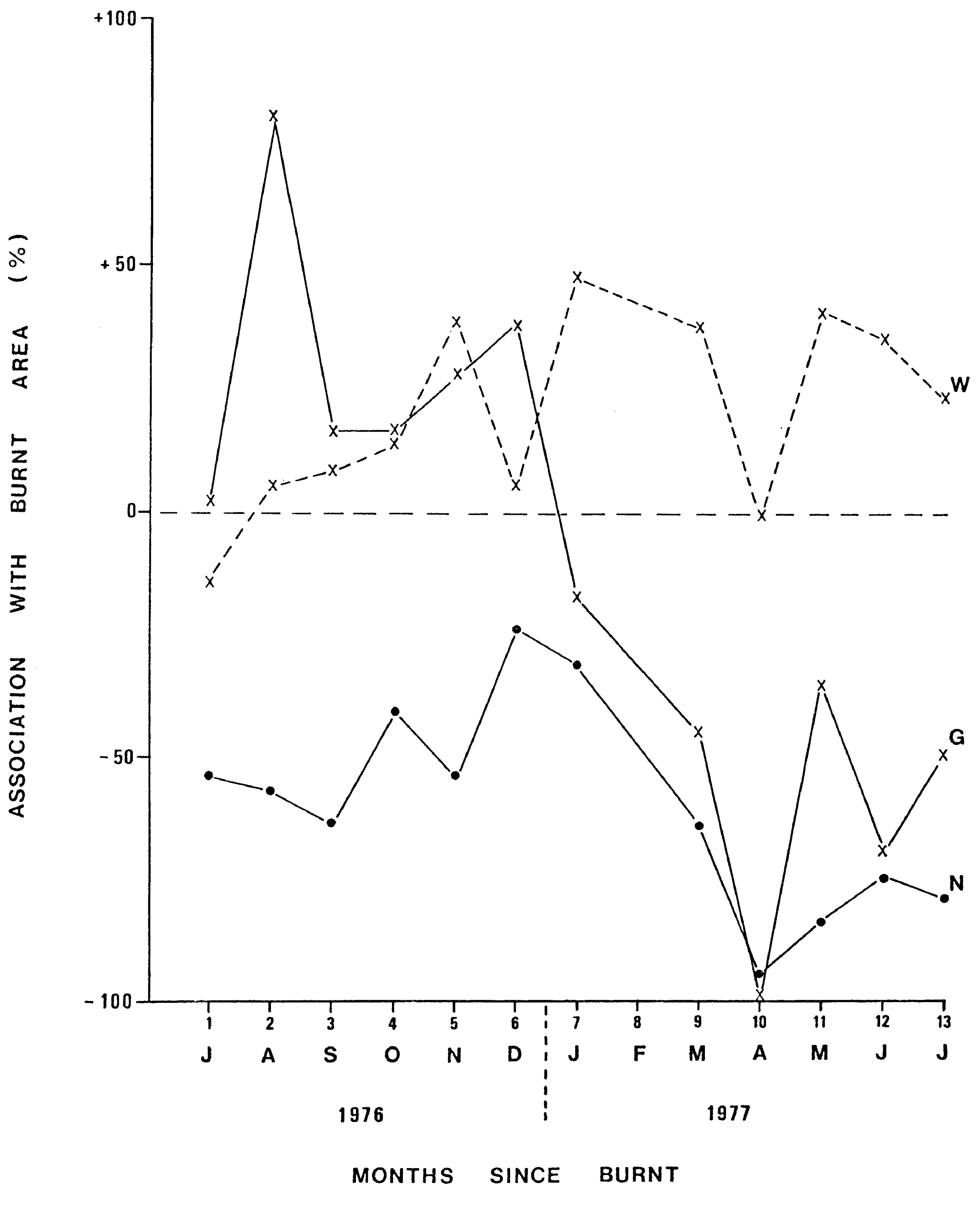


Figure 117. The association of waterbuck (–x –), wildebeest (-x-), and nyala (—•—) with the June 1976 burn in the main study area.

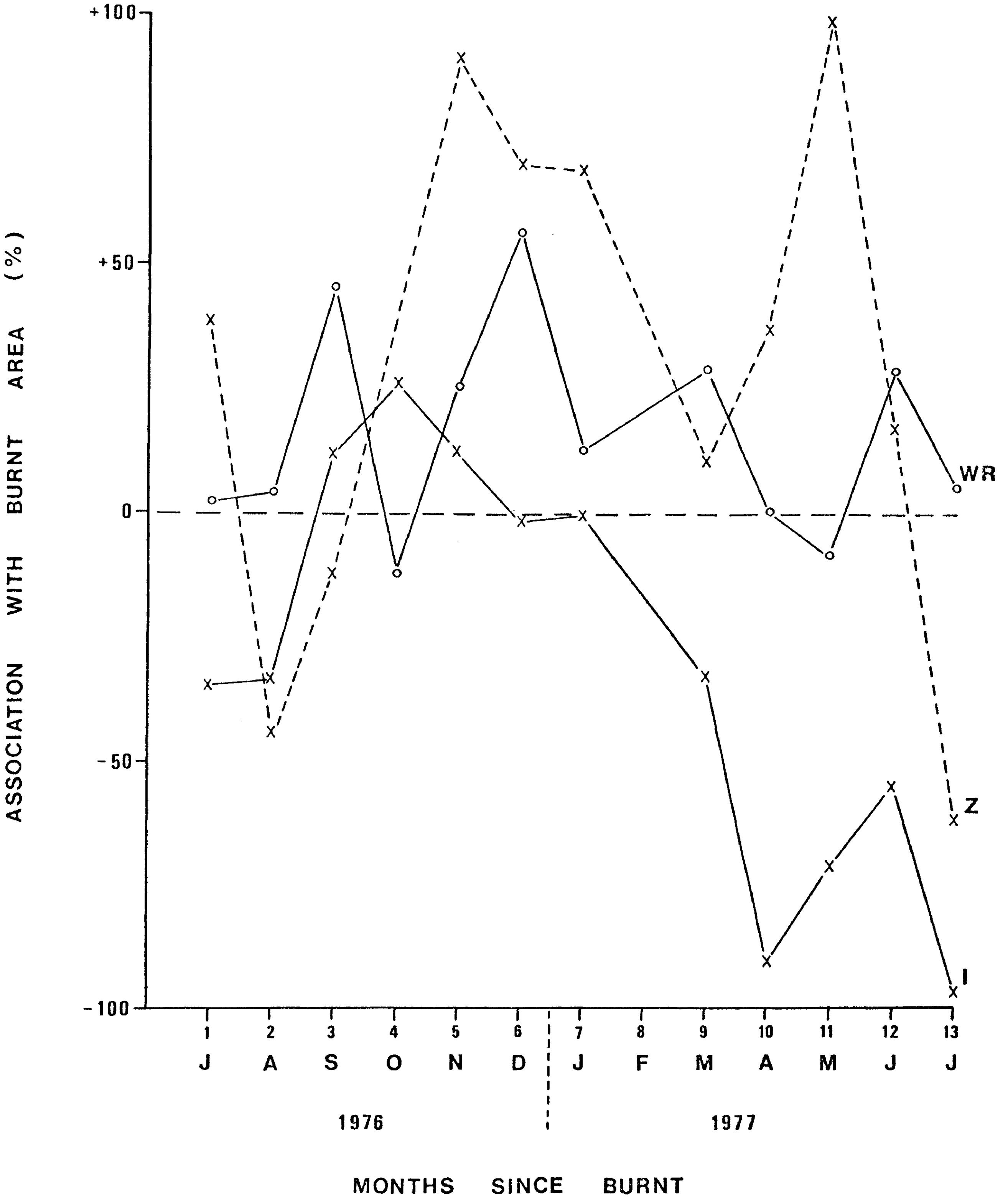


Figure 118. The association of zebra (–x–), impala (—x—) and white rhino (—o—) with the June 1976 burn in the main study area.

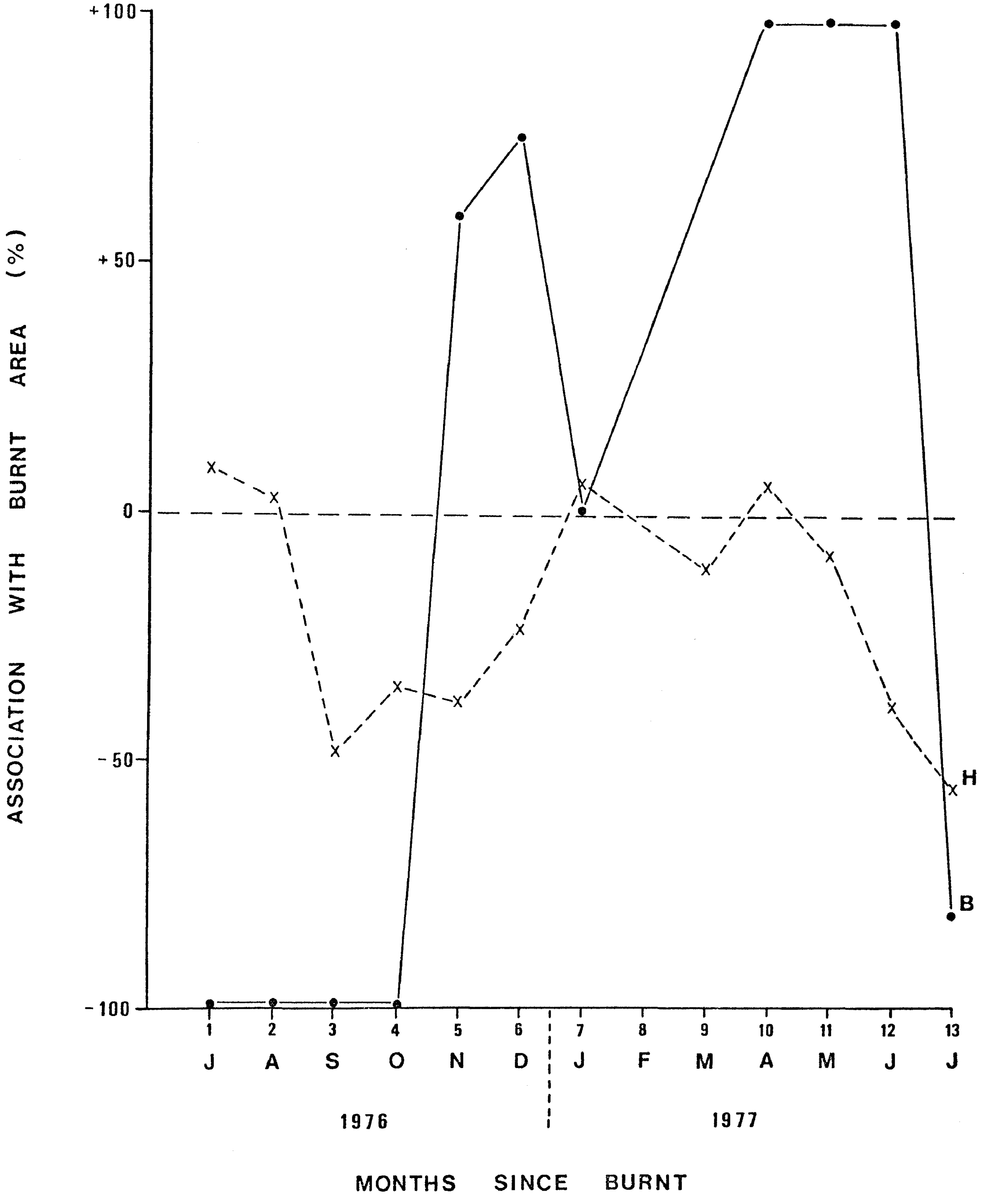


Figure 119. The association of buffalo (—•—) and warthog (-x-) with the June 1976 burn in the main study area.

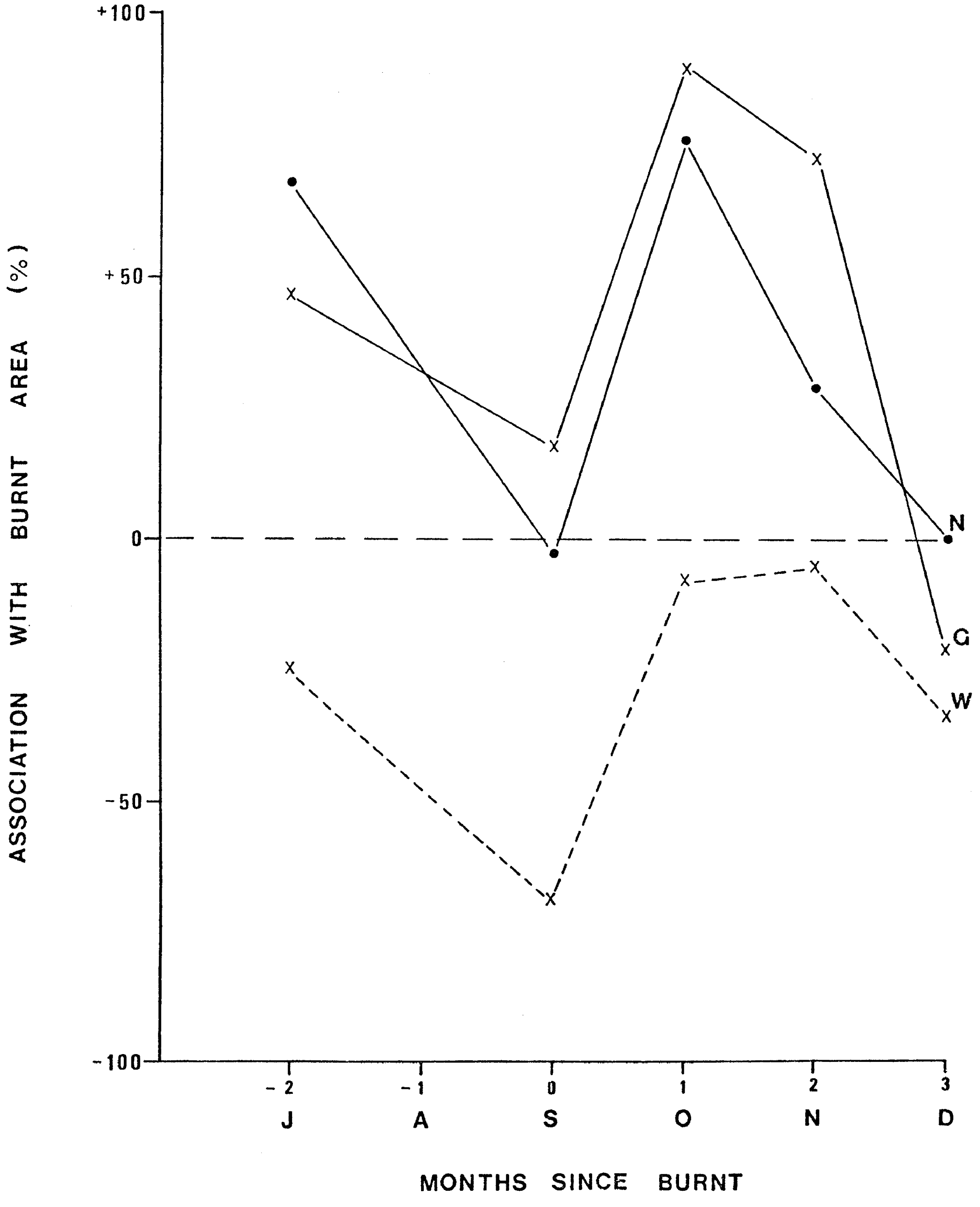


Figure 120. The association of waterbuck (-x-), wildebeest (—x—) and nyala (—•—) with the August 1977 burn in the main study area.

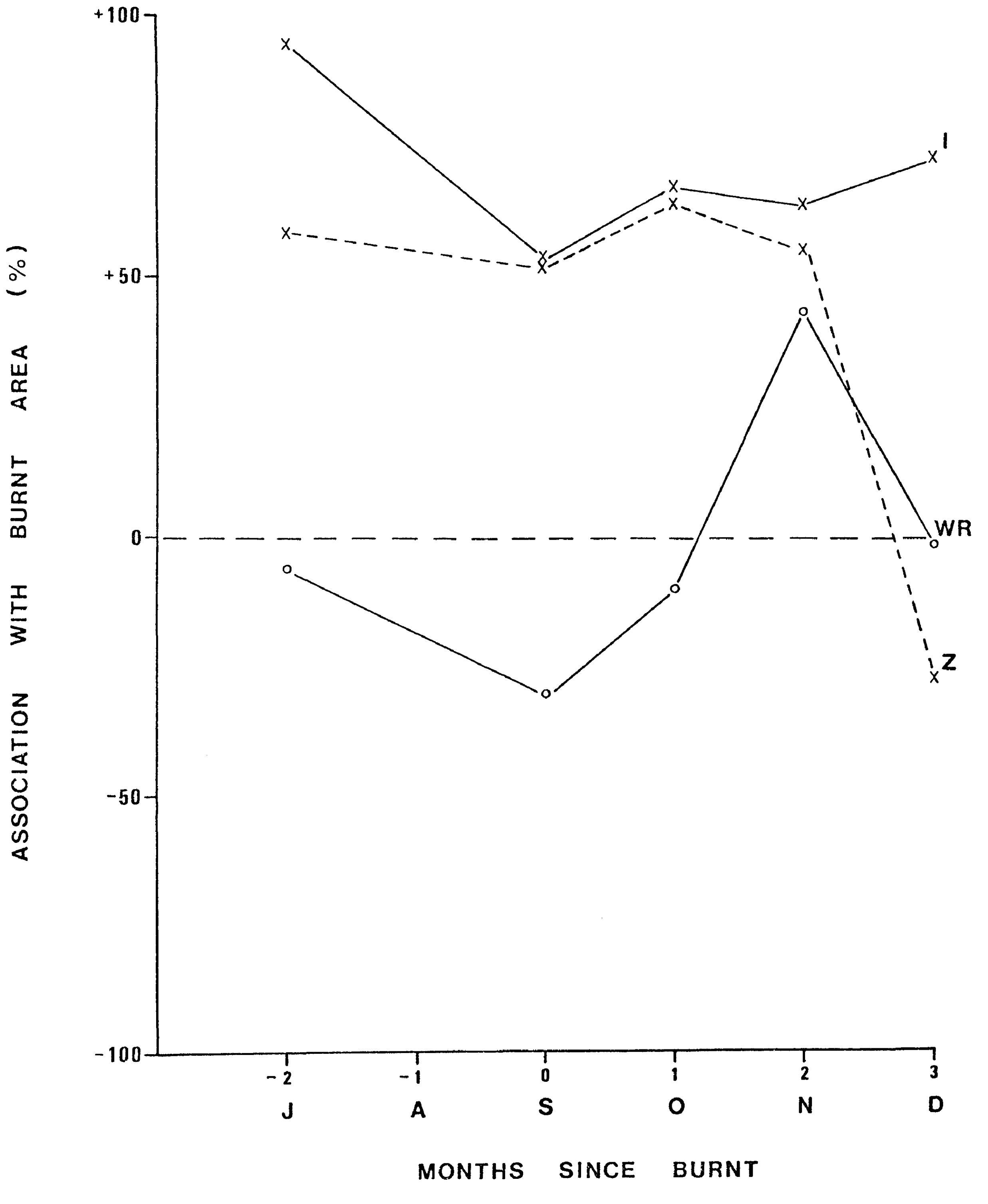


Figure 121. The association of zebra (–x –), impala (—x—) and white rhino (—o—) with the August 1977 burn in the main study area.

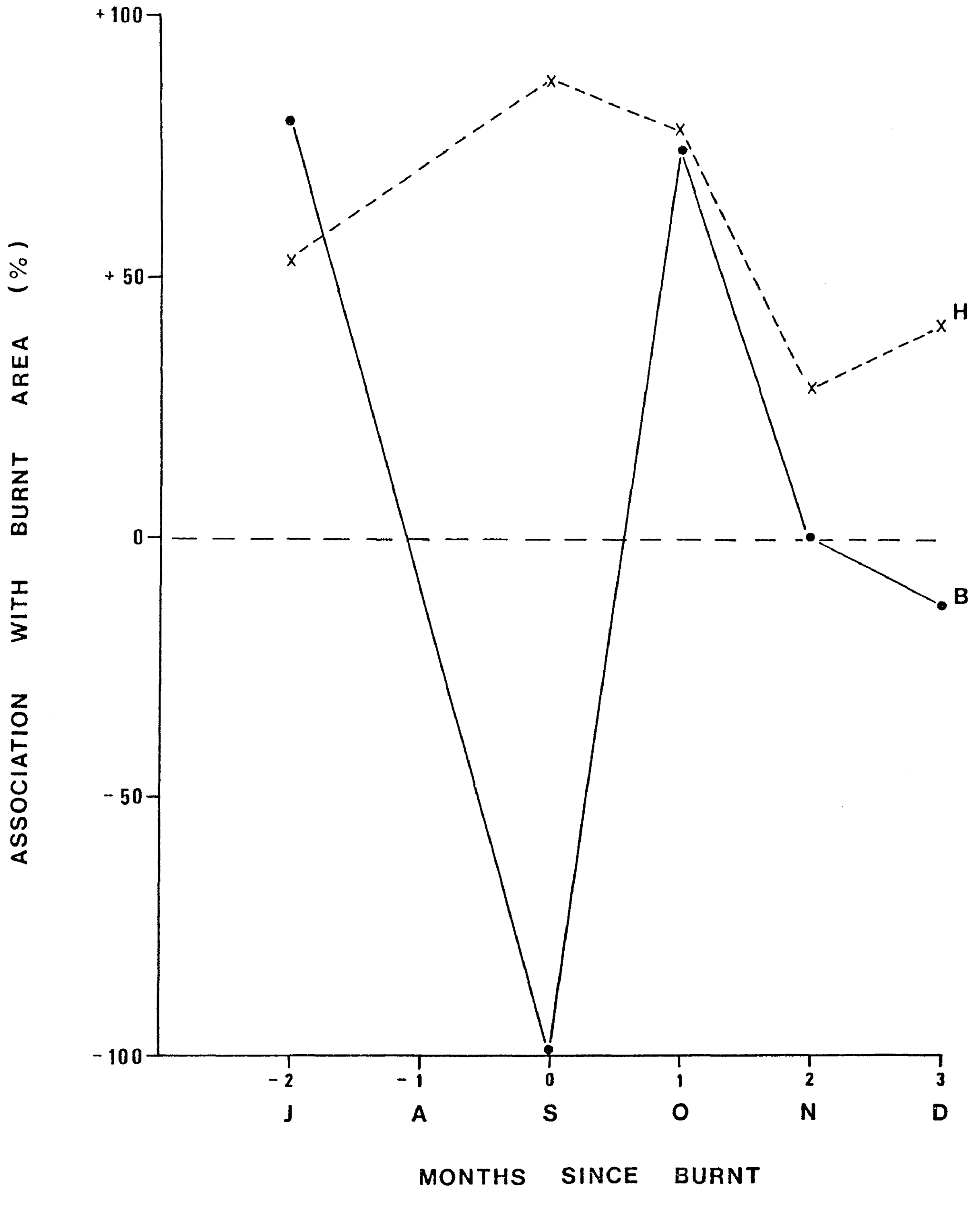


Figure 122. The association of buffalo (—•—) and warthog (–x–) with the August 1977 burn in the main study area.

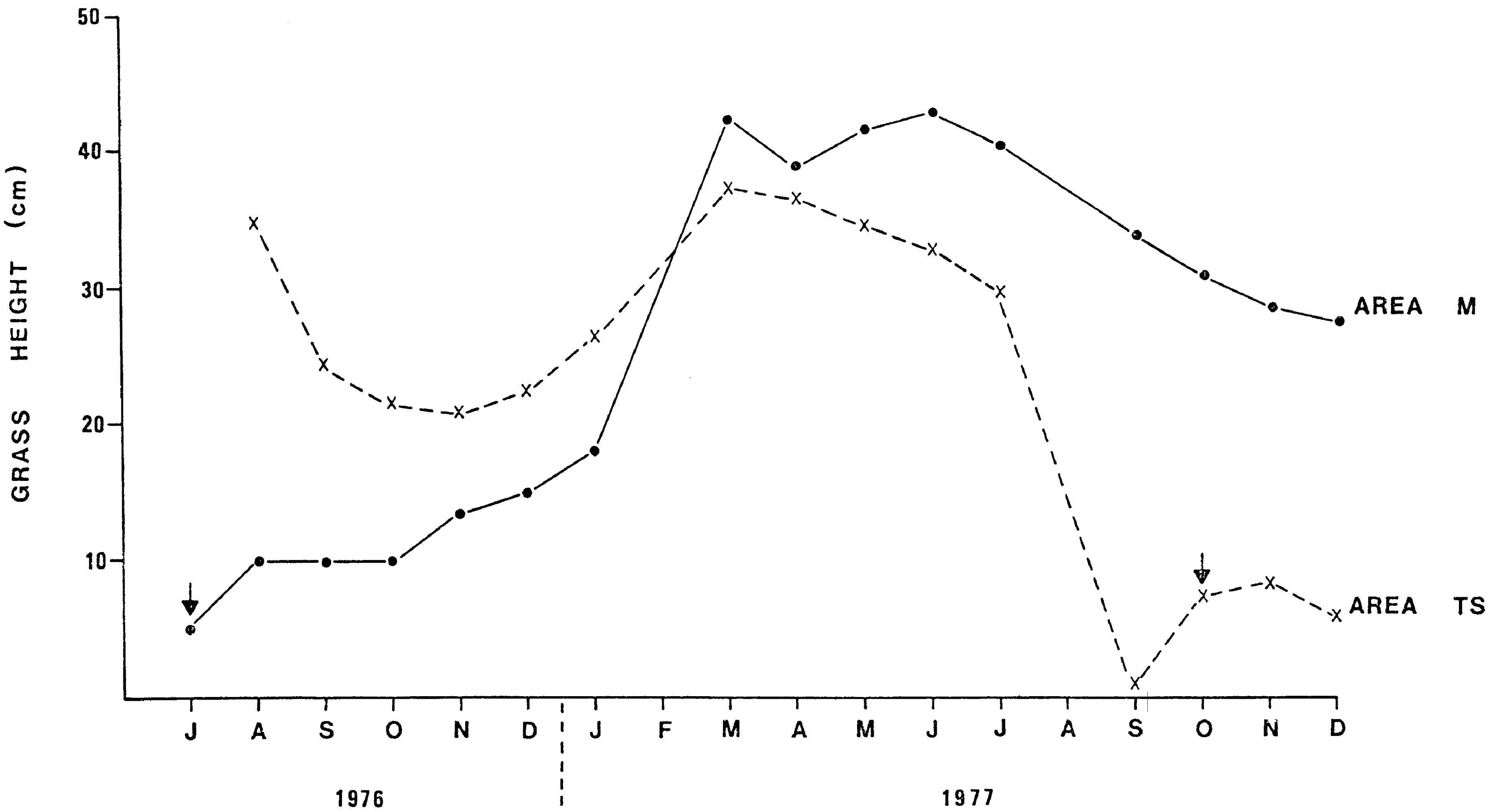


Figure 123. Monthly grass heights of area M, burnt in June 1976 and the rest of the main study area, area TS, burnt at the end of August 1977; an arrow denotes one month after a burn.

did show a small peak of 25 per cent attraction over this period. In November, zebra and wildebeest again moved onto the burn, but this time accompanied by buffalo, waterbuck and white rhino. By January the grass on the burn had reached a mean height of 18 cm and wildebeest began to show a strong negative association with the burn. Zebra, waterbuck, buffalo and to a lesser extent white rhino preferred the burn right through to the middle of the 1977 dry season when the grass was around 40 cm high, compared with a mean height of just over 30 cm away from the burn.

Warthog associated with the burn at random during wet months, but were negatively associated with it during both the first (1976) and second (1977) dry periods. Nyala showed a constant negative association. That these two species and also impala are avoiding the burn for reasons other than the grass condition will be seen from the results of the 1977 burn near the river.

The 1977 burn occurred in late August; because of this the July sampling is considered representative of conditions two months before burning. The July sample is included in the graphs (Figs. 120 to 122) to demonstrate animal distributions prior to the burn.

Impala were showing a near 100 per cent association with the near river area in July. This diminished during the first month after burning, but returned to higher values by December 1977. A similarly constant positive association is shown by warthog. Nyala are more variable. They were strongly associated with the area before it was burnt, which is expected, as DFA results have shown the use of densely shrubbed areas by nyala. They reduced their preference to random during the first month after the burn, then showed a strong positive association over the period of maximum height of the initial flush and then finally a random utilization during December. The mean grass height on the burn decreased in December to under 6 cm because of a lack of rain.

The shape of the association graph for waterbuck is similar to that for nyala, but waterbuck are preferring unburnt areas. They therefore appear to be more sensitive to the condition of the burn than other species. As before in 1976 zebra and wildebeest show an early positive preference for the burn, but they too move off in December. Buffalo, which were on the area before the burn, largely move off except for utilization of the 7,5 cm flush in October.

The conclusion is that the use of the initial flush after a burn by wildebeest and zebra is a constant feature in UGR, irrespective of burn location. Utilization by other species is affected by additional habitat constraints, particularly distance to water and in the case of nyala density of woody vegetation. As a rule if rains do not follow within a couple of months of a burn it is little used except by impala and warthog, and these only come on if water is present. This again points to the importance of leaving sufficient grazing away from burnt areas and also within burnt areas as patches untouched by the fire.

Waterbuck and the deterioration of grassland

Many results on the utilization of various types of grassland have already been given in this chapter. The only additional data presented here are mean grass heights of the areas occupied by each species, by month (Table 74).

Buffalo followed by zebra and waterbuck are associated with the longest grass, shorter grass areas only being utilized after a burn. This puts these three species into the most favourable category of not utilizing overgrazed areas.

The grazers of shorter grass can be split into two groups. The first is white rhino and wildebeest which, when there is a burn away from the river, move onto those burnt *Themeda* areas. The second is warthog, impala and nyala which under the same circumstances remain largely on short grass near the river. Therefore it is these last three that are the species which would persistantly graze overutilized areas during the dry season. Considering present biomass estimates (see Chapter 3) it is suggested that nyala and impala are the main species causing grassland deterioration. Should there be little burning away from the river wildebeest could become troublesome as DFA results indicate that they preferentially use overgrazed areas with *Sporobolus smutsii* and much scrub even when good quality medium height grasses are available.

The identification of nyala as important in grassland deterioration is particularly important for waterbuck because of habitat overlap. Nyala are often associated with dense woody vegetation and a *Panicum maximum* dominated herbaceous layer, near to the Black Umfolozi River. It is likely that mainly nyala are causing the low grass height, high percentage forbs and poor cover recorded in those areas. For example in July 1977 during the dry season two blocks, 8080c and 8478b, of *Panicum maximum* dominated closed woodland had mean grass heights of

Table 74. Monthly mean grass heights of the areas utilized by the eight main grazing species in the Umfolozi Game Reserve.

Month	Rainfall (mm)	Grass heights (cm)							
		Waterbuck	Buffalo	Zebra	Wildebeest	Warthog	Nyala	Impala	White rhino
1976									
Jul	14,3	30	40	13	28	22	32	29	25
Aug	7,5	30	28	31	19	23	32	27	28
Sep	7,8	23	30	19	14	21	18	15	17
Oct	145,6	15	33	30	12	17	19	15	14
Nov	43,8	16	14	13	14	15	17	14	15
Dec	130,5	18	17	18	15	18	19	20	17
1977									
Jan	155,7	18	27	18	17	22	21	19	20
Mar	99,9	38	60	35	35	36	33	37	38
Apr	16,4	33	50	33	22	34	29	28	30
May	31,5	40	45	40	29	29	31	30	30
Jun	8,0	30	53	31	28	26	31	25	29
Jul	0	33	34	28	25	25	26	21	26
Sep	90,5	18	32	3	18	4	7	5	13
Oct	39,8	13	7	7	7	10	10	10	13
Nov	18,0	16	15	8	11	13	11	10	14
Dec	63,7	14	15	15	12	10	10	9	10

10 cm and per cent forbs were 23,5 and 38,8 respectively. At this time the overall mean grass height near to the river was 30 cm (Fig. 123) and the mean per cent contribution to biomass of forbs was 2,9.

Impala are more catholic in their habitat associations than nyala and would be causing any overgrazing in more open habitats near to the Black Umfolozi River.

DISCUSSION AND CONCLUSIONS

The niche of waterbuck and competition

Most previous studies on habitat utilization by waterbuck have given their main requirement as proximity to water (Lamprey 1963, Hanks *et al.* 1969, Spinage 1970, Herbert 1972). Spinage (1970) suggested that this was because of the species' low tolerance of water loss (Taylor *et al.* 1969). DFA results have shown that nearness to water is often important in UGR, particularly for calves and females. No doubt much of this attraction is due to the water itself, but it is likely that a considerable amount of the attraction is also owing to the availability of good quality long grasses such as *Panicum maximum* being restricted to areas of denser woody vegetation near water. A similar conclusion was made by Hirst (1975) who included waterbuck in a multivariate habitat analysis in the Transvaal Lowveld. In contrast to this study he found waterbuck to be the most stenoecious of the five grazing species he examined. Their strict requirements were for a dense woody component, much tall grass and local water sources. As he pointed out, such conditions occur infrequently in semi-arid sub-tropical Africa; when they do occur it is along watercourses and the lush grassland attracts heavy utilization by many species. It is suggested that this niche is now occupied by nyala in UGR on a year round basis, the potentially long *Panicum* grassland being kept generally short. It is probable that the need for good quality longer grass can be adequately met in a wider range of habitats during summer months and that the strict habitat requirements refer mainly to winter. Lamprey (1963), Kutilek (1975), Elliott (1977) and Tomlinson (1978) all recorded variation in habitat usage by waterbuck between season, with swamp, lake shore or riverine habitats becoming important in the dry season. Kutilek (1975) emphasised how such movement could fit into a "grazing rotation system" with other ungulates, where various habitats were rested from grazing in a sequence. It is suggested that a more functionally realistic approach is to view such movement in relation to competition and the availability of suitable food. In UGR the finding of high flexibility in habitat usage even during winter and the overlap with both nyala and buffalo at that time, suggests that year-round utilization of the important waterbuck winter habitat by other species, particularly nyala, may result in depletion of acceptable food resources and direct competition for food during winter. Details of this possible competition will be discussed further after results on feeding ecology are presented in the next chapter.

Grazing successions in UGR

Porter (1975) suggested that a grazing succession similar in structure to that described by Bell (1971) may occur in UGR, with zebra, waterbuck and then wildebeest moving into long grass areas in sequence. Attwell (1977) believed that no definite succession into long grass occurred in UGR, the situation being more complex. Downing (1972) named buffalo and zebra as the only species using the long grassed upland areas of UGR, and Page (1977) demonstrated the association of buffalo and zebra with long grass areas and white rhino and wildebeest with short grassland in HGR.

The findings given here show that as suggested by Attwell (1977) a complex situation exists, the reason being that the utilization of grasslands of varying heights is greatly influenced by other habitat requirements for most species. It serves no purpose to try to generalise about successional use of long grass areas on a strict order basis. Rather species have been ranked in terms of their potential for contributing to the deterioration of the herbaceous layer. Buffalo, zebra, waterbuck and to a much lesser extent white rhino have been identified as the only species showing a preference for long grass areas. Therefore these, particularly the first three, are the species contributing least to overgrazing in UGR. At the other extreme impala, nyala and warthog are the most liable to contribute to overgrazing.

The succession of species onto burnt areas does follow a more regular pattern, with zebra and wildebeest the regular instigators. Once again, however, the species following on will depend on the location of the burn with respect to such variables as distance to water, the density of woody vegetation and the rainfall following the burn.

CHAPTER 9

FEEDING ECOLOGY

INTRODUCTION

In the last chapter waterbuck habitat utilization was viewed within the framework of all main grazer-habitat relationships in UGR. A similar holistic approach considering the other grazing species will be used to interpret the feeding ecology of waterbuck. The diet of waterbuck can then be assessed with respect to what other animals are eating, to grass species availability and to the nutrient content of grasses.

The need for a detailed investigation of feeding habits could be questioned in the light of Hairston, Smith and Slobodkins' (1960) hypothesis that the often observed superabundance of vegetation means that herbivores are not resource limited. Sinclair (1974c, 1975) has pointed out a flaw in this argument by demonstrating that quality of vegetation not quantity is a likely general limiting factor for herbivores.

Studies of mixed ungulate communities in Africa have emphasised mainly ecological separation of species (Lamprey 1963) and the facultative aspects of feeding interactions (Gwynne and Bell 1968, Bell 1971, Owaga 1975, McNaughton 1976). This has meant that the possibility of competition and the problems involved with defining competition have been largely neglected. When competition for food has been examined a static approach has usually been adopted where overlap of diet has been tentatively used as an index of competition (Casebeer and Koss 1970, Field 1972). The term static is used since the dynamics of possible competitive interactions have not been considered; separation of diet may in fact be the outcome of recent competition, whereas overlap may concern a superabundant resource, which precludes the possibility of competition. It is hoped that the broad base to this project, particularly with respect to studies of species abundance and habitat usage, will allow a more effective approach to assessing competition for food between waterbuck and other grazers.

Examination of diets

Composition of the diet of a large herbivore can be estimated during ingestion, during passage through the gut or after defecation.

It was not possible to consider fistulation for this study, so the main methods available were direct observation, stomach analysis and faecal analysis. Direct observation is difficult under field conditions and is restricted to a short percentage of the feeding time of an animal. Faecal and stomach analyses of plant species based on epidermal fragments overcome one of these problems since food eaten over the range utilized becomes mixed during digestion; however, differential digestion of plant species can occur. This is likely more important in faeces, but even here only species eaten infrequently and in small quantities are completely missed (Stewart 1967). The declining status of the waterbuck population meant that shooting to obtain stomach samples was undesirable, thus restricting this technique to fresh carcass finds.

It was decided to examine the diet of all main grazers in UGR by using faecal analysis, but to assess the reliability of the method by stomach analyses and direct feeding observations.

Nutrient content of grasses

Downing (1972) found that grasses from eluviated upland soils in UGR had lower nutrient content than the same species sampled from illuviated bottomland soils. He also found that *Panicum* species were of higher quality than the common *Themeda triandra*. These results suggest that it is necessary to sample both high ground and valley bottoms in order to describe adequately seasonal variation in the availability of nutrients. *Themeda triandra* and a *Panicum* species were the species chosen to be sampled. Not only do they represent contrasting quality, but these genera also constitute over 50 per cent of grass biomass in the main study area (see Chapter 2) and they typify upland and bottomland grass communities respectively. They also both figured prominantly in the diet of waterbuck as judged from direct observation during the first few months of the study.

Availability of grasses

One problem in feeding studies is how to define preferences. Here the results of discriminant function analysis used in Chapter 8 provide an estimate of availability, since one of the output matrices gives mean values of each original parameter for each animal. Thus the mean percentage contributions to biomass of all the main grasses encountered by a grazer can be retrieved and used to indicate proportionate availability in the specific habitat occupied by a herbivore in any month or season.

METHODS

Nutrient content of grasses

Sampling of grasses to examine the yearly cycle of nutrient availability was carried out between June 1976 and May 1977. Monthly samples of *Themeda triandra* and *Panicum coloratum* were collected from a rocky ridge and a valley bottom near Thobothi. Each sample consisted of 50 to 100 g of grass cut off at ground level; *Themeda triandra* samples were further divided into leaf and stem portions. The samples were placed in pre-weighed paper bags and immediately weighed to the nearest 0,1 g on a mechanical balance. They were dried in an oven at approximately 110 °C to constant weight. Water content was expressed as a percentage of the fresh weight. Dried samples were sent to Cedara Agricultural College for routine analysis of fat, crude fibre, ash, crude protein, phosphorus, calcium, magnesium, potassium and sodium.

A second study of grass quality examined the effects of burning. The grass sampling area near Thobothi had not been burnt for nine months in June 1976 and was not burned during the one year sampling period. However, as described in Chapter 2 the part of the main study area away from the river was burnt in June 1976. Grass samples were collected monthly from this *Themeda triandra* dominated upland area from July 1976 to November 1976. Samples were treated as described above.

A third examination of grass quality was connected with the movement of female waterbuck away from the study area during winter months (see Chapter 7). Samples of *Panicum coloratum* and *Themeda triandra* were collected in May 1977 at Mpila, near where a marked animal had been sighted the previous winter. Two samples of each species were taken, one from a ridge and one from a valley and analysed as described above to see if any obvious increase in macro-elements could be detected. Similar control samples were collected at the same time from the main study area.

The diet of waterbuck from direct observation

Waterbuck were regularly watched throughout the study period using a x 20 to x 60 spotting scope mounted on a Landrover. No attempt was made to cover the various grasslands equally but animals were observed wherever they were mainly feeding during any one month. Even so the results are probably biased towards observations in open habitats where viewing was easier. An item identified in the mouth of an animal was recorded as one observation. Grass species were individually recorded but forbs and other woody vegetation were all recorded as dicotyledons.

Faecal analysis

Plant leaf epidermis is largely indigestible and can be used as a specific diagnostic characteristic (Prat 1932, Storr 1961). The epidermis of some plants show little intraspecific variation but others vary considerably between different habitats (Stewart 1965). For this reason a reference collection of epidermis from the grass species found in the study area was prepared using fresh material and either the maceration method of Storr (1961) or by scraping the epidermis (Metcalfe 1960). Permanent slides were made as described by Stewart (1965).

Faecal analysis followed the basic method of Stewart (1967). Fresh faecal samples of up to 50 g were stored in formalin acetic alcohol (FAA - 85 parts 70 per cent alcohol, 10 parts 40 per cent formaldehyde, 5 parts glacial acetic acid). An approximately 1 g sub-sample was placed in 4,0 ml of concentrated nitric acid in a round bottomed flask and heated for two to three minutes over a boiling water bath. This treatment clears the epidermal fragments and allows their identification. The sub-sample was then made up to 100 ml with water and the fragments allowed to settle. The supernatant liquid was removed and the fragments stored in FAA for microscopic analysis.

Cleared fragments were viewed under x 400 magnification using a Zeiss binocular microscope. One hundred identifiable grass fragments were recorded per original sample; this is the number found sufficient to reveal species comprising more than five per cent of the diet (Stewart 1967). Dicotyledon fragments were noted during the scanning needed to record the 100 grass fragments. Fragments were observed along parallel transects one microscope field apart. Some grasses could be identified by a single cell or silica body while others needed larger fragments. Instead of setting a size limit, fragments were considered identifiable if a silica body and a section of intercostal zone were present. Dicotyledons were considered identifiable as such if a stoma and a number of surrounding cells were present. Thirty-nine species of grass and one reed could be recognised using the reference collection, while dicotyledons were not differentiated further. If a fragment of identifiable size could not be classified it was recorded as unidentified.

Ninety-one samples from adult waterbuck were analysed covering the one year period October 1976 to September 1977. Fresh samples were collected during foot coverage of the main study area. Between five and 10 wet and dry season samples were analysed for each of the other seven main grazers, making another 125 samples.

Rumen analysis

Ingested matter in rumens was well mixed and a sub-sample taken and stored in FAA. The analysis conducted subsequently was for plant parts using the method described by Gwynne and Bell (1968). The sub-sample was washed, spread in a shallow tray and covered with a wire grid consisting of 100 intersections spaced at 1,0 cm intervals. The material was viewed through a low power Zeiss dissecting microscope and the plant parts immediately below each intersection classified as grass leaf, grass sheath, grass stem, dicotyledon leaf or dicotyledon stem.

Seven waterbuck samples were analysed from animals dying in UGR during the study period. Nine samples from nyala and impala were also examined as these species had been implicated in competitive interactions with waterbuck.

Faecal analyses and rumen analyses for grass species were carried out on samples from two waterbuck carcasses in order to help assess the accuracy of the faecal method.

Grass species availability

The mean percentage contributions to biomass of the grasses included in DFA were extracted from computer outputs on a monthly and seasonal basis for waterbuck and seasonally for the other grazers. These figures were unique for each herbivore and can be thought of as describing conditions at their respective niche centres. These data were used in two ways. First, grass species preference indices were calculated as per cent in diet from faecal analysis/per cent available at the niche centre. Second, they were used to provide an index of area selection for grass species calculated as per cent available at the niche centre/mean per cent available in the whole study area.

RESULTS AND DISCUSSION

The nutrient content of grasses

Upland-bottomland variation

The nutrient content of *Themeda triandra* and *Panicum coloratum* grass samples taken from upland and bottomland sites are compared in Tables 75 and 76. The only significant difference ($0{,}01 < P < 0{,}05$) out of 30 comparisons is for increased calcium content in *Panicum coloratum* upland samples. The ranges of calcium content involved still overlapped considerably and no importance is placed on this result. The lack of an increase in quality of bottomland samples is probably because mineral rich dolerite rock was dominant through most of the main study area, including both plant sampling sites. Downing's bottomland sites were also overlying dolerite but his upland sites were on less mineral rich soil derived from older sedimentary rocks (Downing 1972). These results suggest that distribution of game in the study area with respect to altitude cannot be explained in terms of variation in the quality of individual grass species.

Seasonal variation in nutrient availability

The results of nutrient analyses of *Panicum coloratum* whole plant, *Themeda triandra* leaf, *Themeda triandra* stem and grass from a recent burn are shown in Figs. 124 to 126. In agreement with many studies (du Toit, Louw and Malan 1940, Bredon and Wilson 1963, Field 1968, Sinclair 1974c) grass quality is seen to decline during winter, particularly in terms of crude protein. A number of studies have shown that the digestibility of crude protein is very similar for most ruminants and that the minimum level for maintenance is near five per cent (French 1957, French, Glover and Duthie 1957, Bredon and Wilson 1963, Agricultural Research Council 1965, Milford and Minson 1966). The results given here suggest that if *Themeda triandra* was the main grass eaten and even if leaves were selected, this minimum dietary requirement for protein would not be realised for six months of the year. *Themeda triandra* stem protein content only

Table 75. A comparison of the nutrient content of a) *Themeda triandra* leaf and b) *Themeda triandra* stem from upland and bottomland sites in the Umfolozi Game Reserve using the Student's t test for paired variates.

	Water (per cent wet mass)	Per cent dry matter								
		Fat	Crude fibre	Ash	Crude protein	Phosphorus	Calcium	Magnesium	Potassium	Sodium
a) Upland	36,5	1,43	35,5	14,3	4,5	0,06	0,32	0,13	0,40	0,12
Bottomland	38,1	1,21	31,3	14,8	4,9	0,06	0,31	0,14	0,42	0,12
t	-1,99	1,85	1,58	-1,05	-1,56	-0,69	0,46	-1,32	-0,7	0,17
df	10	11	11	11	11	11	11	11	11	11
Significance	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
b) Upland	35,9	1,1	40,8	11,3	3,1	0,04	0,17	0,10	0,33	0,24
Bottomland	34,9	0,9	41,3	11,6	2,9	0,03	0,16	0,10	0,38	0,10
t	1,00	1,64	-0,49	-0,57	0,29	2,06	0,49	0,41	-2,1	0,47
df	9	10	10	10	10	10	10	10	10	10
Significance	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

NS = P>0,05

Table 76. A comparison of the nutrient content of *Panicum coloratum* whole plant from upland and bottomland sites in the Umfolozi Game Reserve using the Student's t test for paired variates.

	Water (per cent wet mass)	Per cent dry matter								
		Fat	Crude fibre	Ash	Crude protein	Phosphorus	Calcium	Magnesium	Potassium	Sodium
Upland	46,9	1,5	34,9	10,7	6,1	0,08	0,38	0,22	0,74	1,69
Bottomland	52,1	1,4	36,4	11,6	6,0	0,07	0,32	0,26	0,90	0,92
t	-1,46	0,73	-0,64	-0,09	0,09	0,30	2,3	-0,86	-1,52	1,53
df	10	11	11	11	11	11	11	11	11	11
Significance	NS	NS	NS	NS	NS	NS	$P < 0,05$	NS	NS	NS

NS = $P > 0,05$

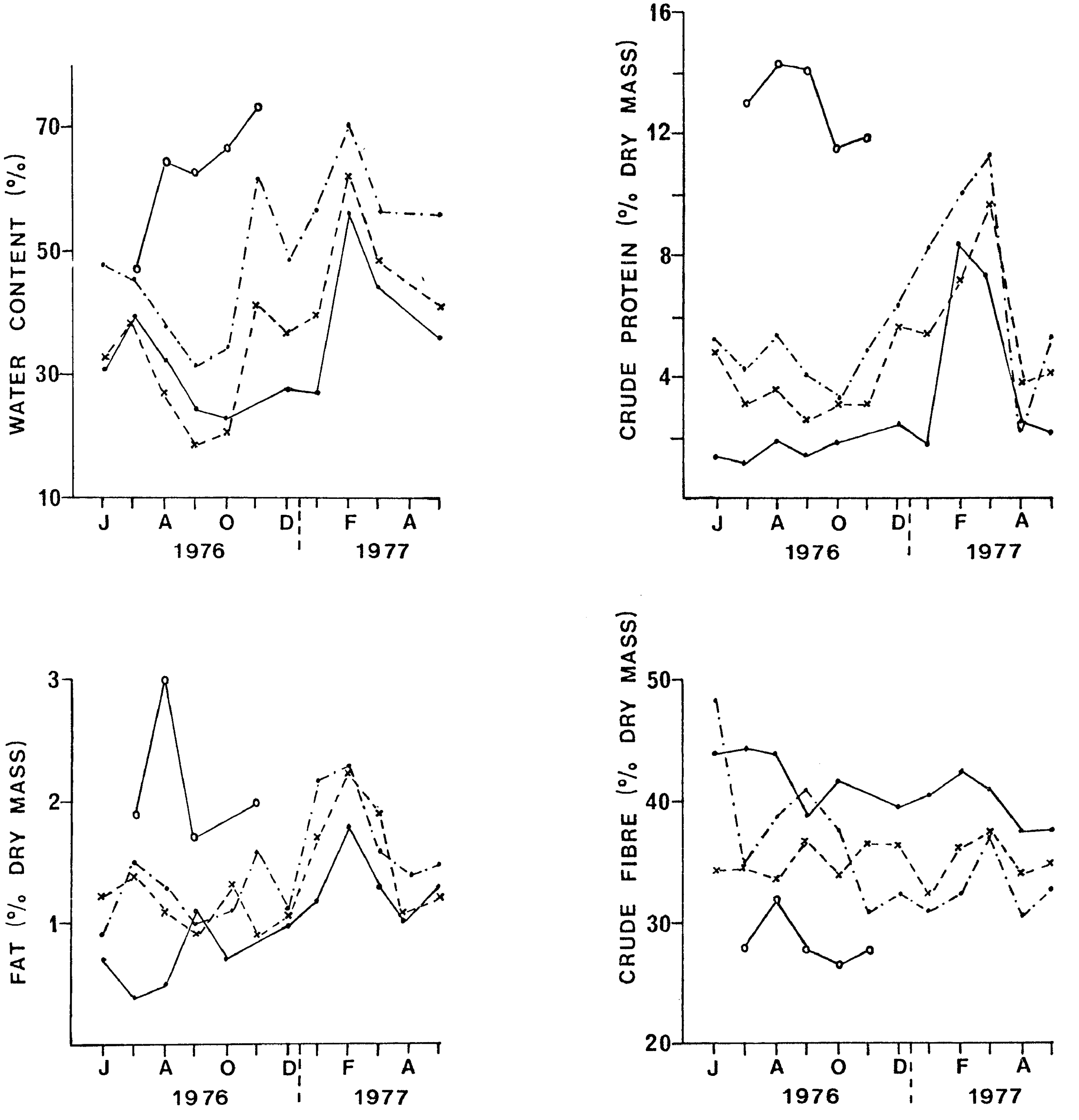


Figure 124. Results of four chemical analyses for *Themeda triandra* leaf (–x–), *Themeda triandra* stem (—•—), *Panicum coloratum* whole plant (·—•—) and grass on an area burnt in June 1976 (—o—). Samples were collected between June 1976 and May 1977 in the main study area.

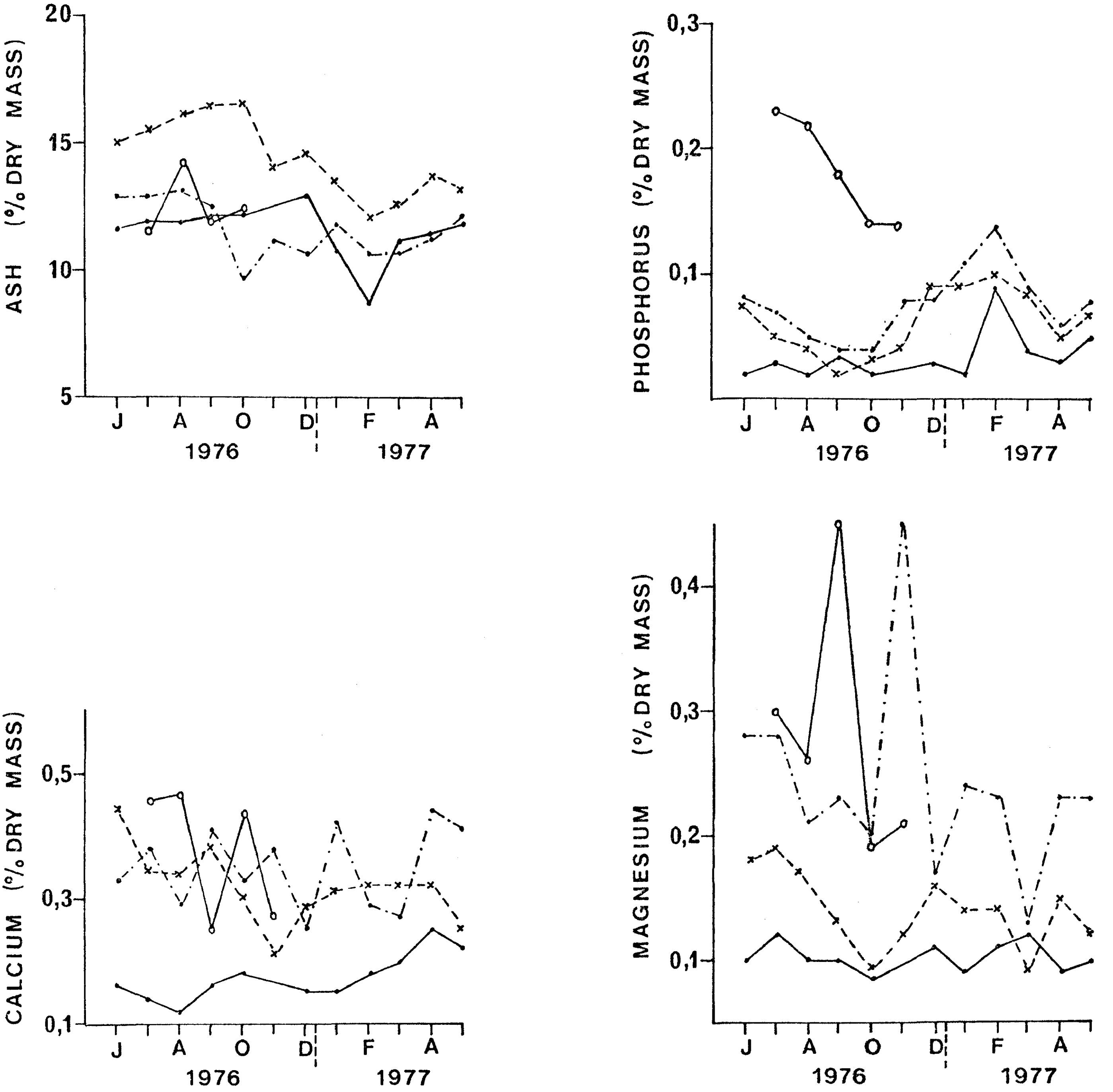
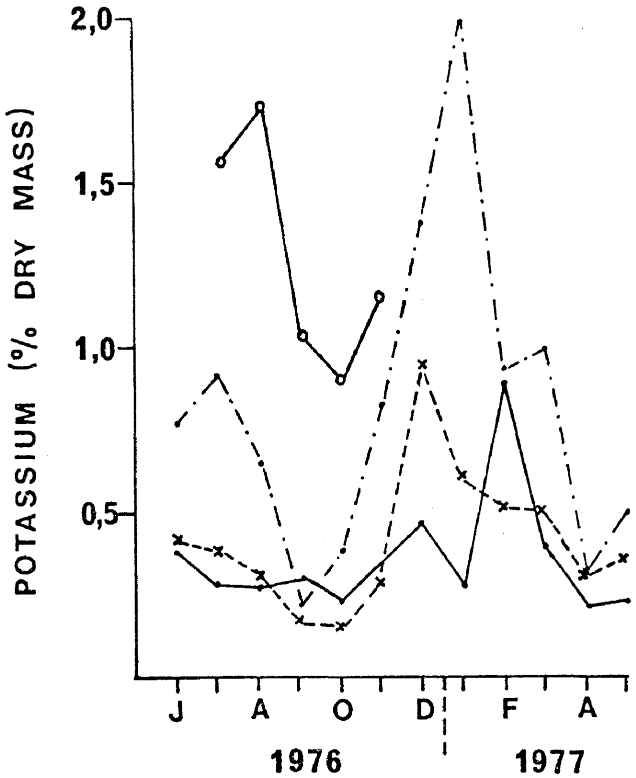


Figure 125. Results of four chemical analyses for *Themeda triandra* leaf (–x–), *Themeda triandra* stem (—•—), *Panicum coloratum* whole plant (·–•–·) and grass on an area burnt in June 1976 (—o—). Samples were collected between June 1976 and May 1977 in the main study area.



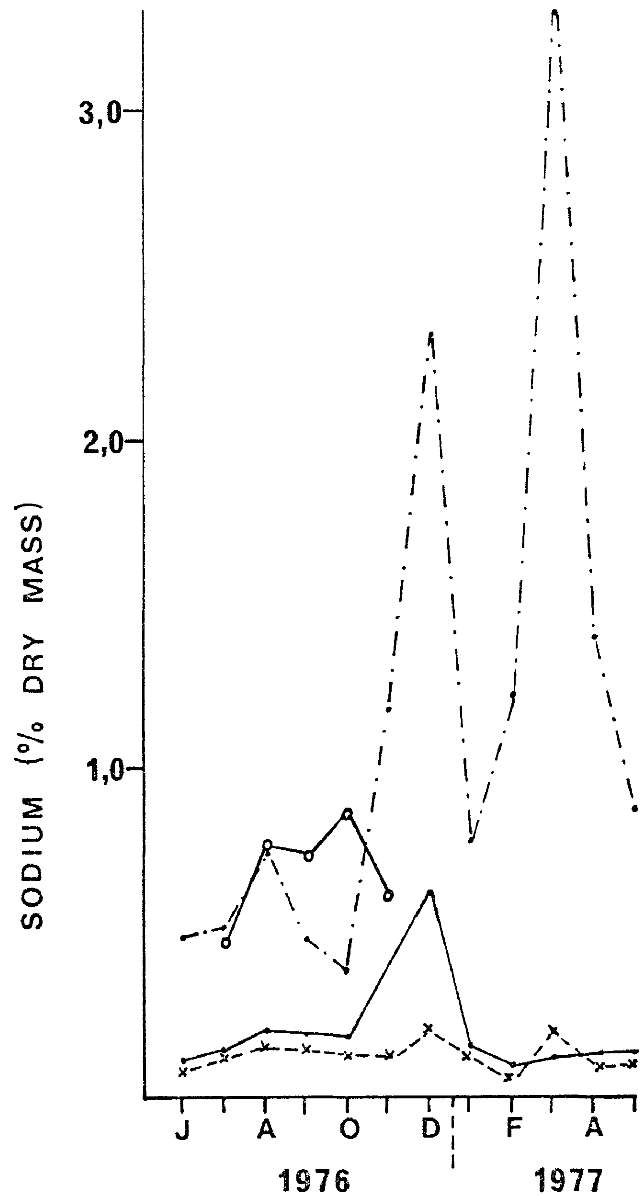


Figure 126. Results of two chemical analyses for *Themeda triandra* leaf (–x–), *Themeda triandra* stem (—•—), *Panicum coloratum* whole plant (·—•—·) and grass on an area burnt in June 1976 (—o—). Samples were collected between June 1976 and May 1977 in the main study area.

rises above three per cent for two months of the year. Whole plant samples of *Panicum coloratum* have generally higher protein levels, but even these fall below five per cent for three winter months. Although not analysed separately it is likely that *Panicum coloratum* leaf protein stays above the minimum level throughout the year. Taken along with previous findings (Long, Thornton and Marshall 1969, Downing 1972), these results suggest that *Panicum* species in UGR provide better food value than *Themeda triandra*, particularly during winter.

Like crude protein, fat content and water content are also highest during summer for both grasses. Crude fibre varies little, as expected for structural material. The measurement of crude fibre is of little value since although high values are considered undesirable in the ruminant diet, this parameter actually includes both indigestible lignin and digestible structural carbohydrates (Van Soest 1967). Samples containing higher crude protein content generally have higher mineral content, a trend also recorded by Long, Ndyanabo, Marshall and Thornton (1969). Phosphorus levels are low in all samples, only reaching the minimum maintainance level of cattle (0,1 per cent) at the end of summer. Du Toit *et al.* (1940) found low levels of phosphorus in vegetation throughout South Africa but suggested that low protein during winter was a greater limiting factor for grazers. The values recorded here for calcium, magnesium, potassium and sodium are all above the minimum requirements set for beef cattle maintainance (Agricultural Research Council 1965).

Figures 124 to 126 show that grass growth after winter burning offers a rich supply of nutrients during the dry season, with crude protein levels over twice those found in other samples collected at the same time.

The results given here indicate the range of nutrients available to grazers in UGR and will form a background for assessing feeding patterns described below. They emphasise the need for herbivores to select plant species, certain plant parts and certain growth stages if they are to meet their dietary requirements, particularly during winter.

Nutrients and waterbuck movement

The quality of grasses collected from near Mpila was not found to be significantly different from those collected at Thobothi (Table

77). The sample size was very low though and all that can be said is that no obvious macro-nutrient incentive was found to account for the movement of waterbuck during winter. The possibility of such attraction was shown recently by Kreulen (1974) who linked movement of lactating wildebeest to the presence of calcium rich grassland.

The diet of waterbuck

Table 78 lists all monocotyledon species identified in the diet of waterbuck in UGR by faecal analysis or rumen analysis and direct observation. Before considering the results of faecal analysis in detail it is necessary to see the extent to which differential digestion of taxa may be affecting this method. A first check is given by comparison of faecal and rumen analyses (Table 79). In carcass 15 the reed *Phragmites australis* was not observed in faeces but occurred as 10 per cent of fragments in the rumen; apart from this all other measurements were similar. For carcass 40 there were no significant differences ($P > 0,05$) in the amounts of grass species recorded by the two methods and the main grass species were all estimated to very similar proportions. Casebeer and Koss (1970) also found the two methods to be comparable for herbivores in Kenya. Owaga (1977) working with zebra recorded a somewhat poorer fit although the same 10 grass species were dominant in both rumen and faecal samples. A second check on the faecal method comes from the results of direct feeding observation on waterbuck (Table 80). The three main grasses observed eaten, *Themeda triandra*, *Panicum maximum* and *Panicum coloratum* are also the main three identified from faecal analysis. These two sets of results suggest that faecal analysis does reflect the main items eaten and can be used for seasonal and interspecific comparisons of diet. Unidentified fragments need not be taken into account as they never made up more than five per cent of samples from any herbivore examined.

Figure 127 shows the diet of waterbuck by month as indicated by faecal analysis for those grasses which made up over 10 per cent of grass fragments in any one month. The percentage contributions to biomass of these grasses at the niche centre of waterbuck are also shown as are preference indices for each species in terms of amount eaten/amount available. *Themeda triandra*, *Panicum maximum*, *Panicum coloratum* and *Eragrostis superba* always made up over 70 per cent of the diet. Although making up much of the diet throughout

Table 77. A comparison of the nutrient content of *Themeda triandra* leaf and *Panicum coloratum* whole plant sampled at Mpila and in the main study area during May 1977.

	Water (per cent wet mass)	Per cent dry matter								
		Fat	Crude fibre	Ash	Crude protein	Phosphorus	Calcium	Magnesium	Potassium	Sodium
Themeda triandra leaf										
Mpila	43,6	0,8	33,7	11,1	4,6	0,07	0,44	0,14	0,31	0,12
Study area	45,5	1,1	35,5	12,2	5,1	0,08	0,35	0,13	0,40	0,14
				$\chi^2 = 0,08$		$P > 0,9$				
Panicum coloratum										
Mpila	57,6	1,1	35,8	8,8	3,6	0,09	0,34	0,17	0,51	1,06
Study area	53,6	1,0	35,9	9,7	5,2	0,09	0,39	0,18	0,56	1,13
				$\chi^2 = 0,48$		$P > 0,9$				

Table 78. Monocotyledon species identified in the diet of waterbuck in the Umfolozi Game Reserve by faecal analysis or rumen analysis and direct observation.

Species	Faecal or rumen analysis	Direct observation
Aristida congesta barbicollis	+	+
Bothirochloa insculpta	+	+
Cenchrus ciliaris	+	+
Chloris virgata	+	
Cynodon dactylon	+	+
Dactyloctenium australe	+	
Digitaria argyrograpta	+	
Digitaria cf. macroglossa	+	+
Diplachne eleusine	+	+
Enteropogon monostachyos	+	
Eragrostis curvula	+	
Eragrostis sp.	+	
Eragrostis superba	+	+
Heteropogon contortus	+	
Phragmites australis	+	+
Panicum coloratum	+	+
Panicum maximum	+	+
Rhyncheletrum repens	+	
Setaria sphacelata	+	
Sporobolus smutsii	+	
Themeda triandra	+	+
Urochloa mosambicensis	+	+

Table 79. Comparison of waterbuck diet in the Umfolozi Game Reserve as shown by faecal and rumen analysis; figures are the number of fragments observed. Significance of differences are calculated only for species occurring as five fragments per 100 or more.

	Panicum maximum	*Cynodon dactylon*	*Sporobolus smutsii*	*Panicum deustum*	*Dactyloctenium australe*	*Eragrostis* sp.	*Panicum coloratum*	*Themeda triandra*	*Phragmites australis*	*Eragrostis superba*	*Digitaria* cf. *macroglossa*	Unknown 2	*Heteropogon contortus*	*Chloris virgata*	*Aristida* spp.	Unidentified	Dicotyledons	Total
Carcass 15																		
Faeces																		
Observed	59	17	6	5	3	3	1	1	0	0	0	0	0	0	0	5	0	100
Expected	54,5	18,5	6	2,5	1,5	1,5	2	0,5	5	2,5	0,5	1,5	0	0	0	3,5	1	
Rumen																		
Observed	50	20	6	0	0	0	3	0	10	5	1	3	0	0	0	2	2	102
Expected	54,5	18,5	6	2,5	1,5	1,5	2	0,5	5	2,5	0,5	1,5	0	0	0	3,5	1	
Total	109	37	12	5	3	3	4	1	10	5	1	3	0	0	0	7	2	202
χ^2	0,74	0,24	0	5	-	-	-	-	10,0	5	-	-	-	-	-	-	-	20,98
Carcass 40																		
Faeces																		
Observed	20	2	0	0	0	5	6	55	0	0	3	1	3	3	0	2	1	101
Expected	20,5	2,5	0	0	0	7,5	4	54	0	0	4	1	2,5	1,5	0,5	2	0,5	
Rumen																		
Observed	21	3	0	0	0	10	2	53	0	0	5	1	2	0	1	2	0	100
Expected	20,5	2,5	0	0	0	7,5	4	54	0	0	4	1	2,5	1,5	0,5	2	0,5	
Total	41	5	0	0	0	15	8	108	0	0	8	2	5	3	1	4	1	201
χ^2	0,24	-	-	-	-	1,67	2,00	0,04	-	-	0,50	-	-	-	-	-	-	4,45

Carcass 15: $\chi^2 = 20{,}98$, df = 5, $P < 0{,}001$

Carcass 40: $\chi^2 = 4{,}45$, df = 4, $P > 0{,}3$

Table 80. Direct feeding observations on waterbuck in the main study area during 1976 and 1977.

Species	Number of observations
Panicum maximum	169
Themeda triandra	164
Panicum coloratum	152
Bothriochloa insculpta	15
Digitaria cf. macroglossa	12
Urochloa mosambicensis	10
Eragrostis superba	8
Aristida sp.	7
Cynodon dactylon	3
Diplachne eleusine	1
Cenchrus ciliaris	1
Phragmites australis	4
Dicotyledons	9

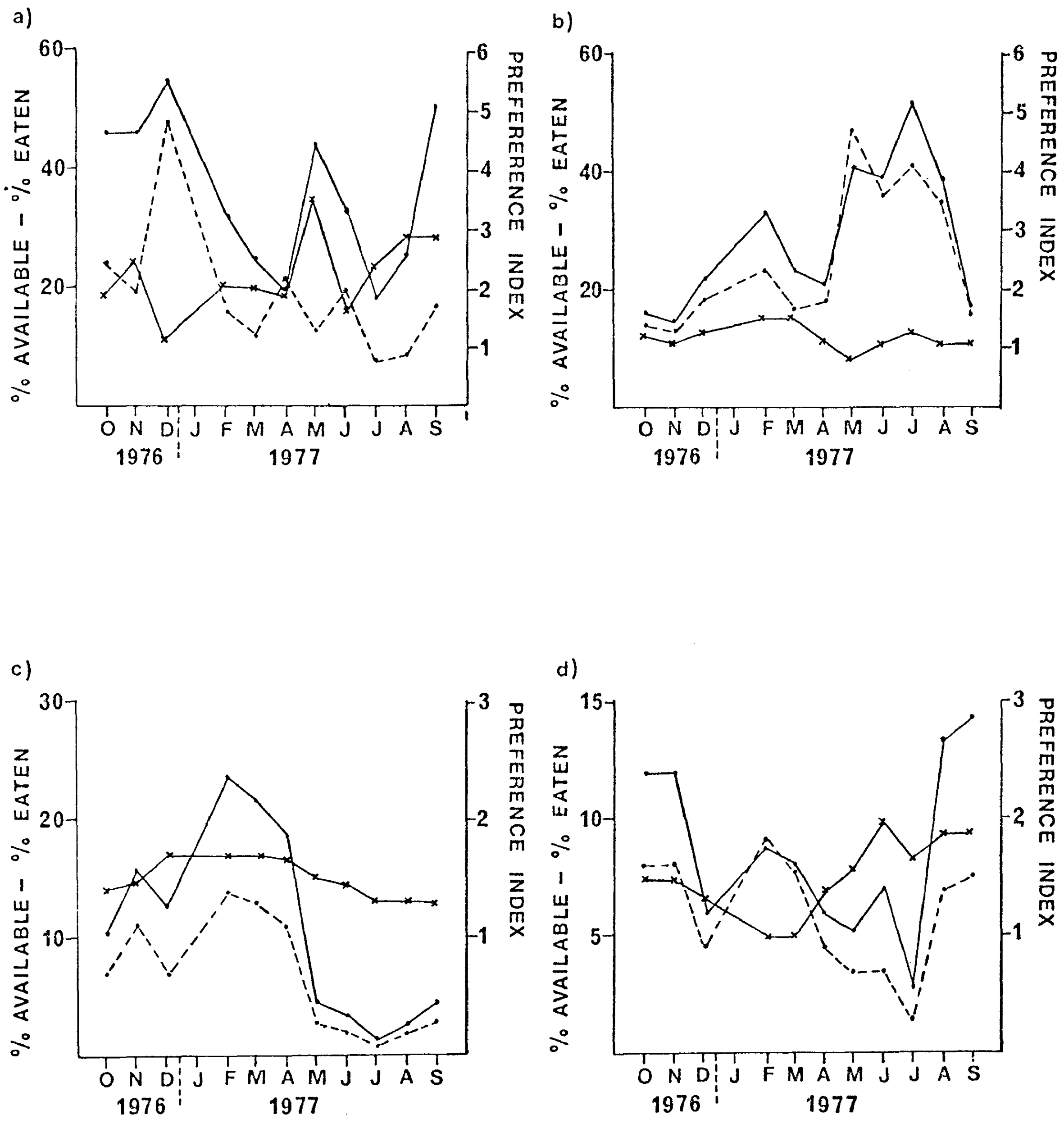


Figure 127. Percentage grasses available to waterbuck (—x—), percentages eaten by waterbuck (—•—) and preference indices (--•--), for a) *Themeda triandra*, b) *Panicum maximum*, c) *Panicum coloratum* and d) *Eragrostis superba*.

the year, *Themeda triandra* is only selected for during wet summer months. *Panicum coloratum* is also preferred only during summer, but it is also mainly eaten at this time. It appears that *Panicum coloratum* is favoured over *Themeda triandra* during the latter part of summer, since when the level of *Panicum coloratum* falls that of *Themeda triandra* rises again. During winter *Panicum maximum* assumes the role of the main grass eaten and is strongly selected for until the end of winter when *Themeda triandra* is again dominant.

A likely explanation for this grazing pattern centres on the opposing requirements of bulk food for energy, but also good quality of vegetation. This conflict of needs has already been implied in the last chapter where waterbuck were classified to an intermediate position between short grass grazers and long grass grazers. The abundant, tall, poorer quality *Themeda triandra* is only preferred when actively growing during summer. The more nutritious shorter *Panicum coloratum* assumes a main place in the diet only during late summer, presumably because that is the only period when this species increases in height in spite of heavy utilization by short grass grazers. During winter the nutritious *Panicum maximum* is mainly eaten even though its availability declines slightly while that of *Themeda triandra* generally increases. Even without considering what other herbivores are eating, it appears that waterbuck in UGR may be in an unfavourable position during winter since the species of grass upon which they apparently rely occurs little in the habitat they utilize and in an even lower proportion than in their summer habitat. This argument will be examined further after the diets of the other main grazers have been given.

Table 81 gives the results of waterbuck rumen analyses for plant parts. Although the sample size is small it is again seen that waterbuck graze almost exclusively in UGR and that leaves are strongly selected. Selection of leaves by waterbuck was seen often during direct feeding observations. The proportion of grass stem in the diet increases only during late winter, which no doubt reflects lowered availability of leaf rather than a preference for stem.

The majority of previous reports of waterbuck feeding habits have been species lists from direct observations (Brynard and Pienaar 1960, Child and von Richter 1969, Hanks *et al.* 1969, Herbert 1972, Elliott 1977). These studies have all found waterbuck to be predominantly grazers but have added little to an understanding of their

Table 81. Waterbuck rumen analyses for plant parts; figures refer to the number of fragments observed.

Carcass number	40	5	7	14	16	15	26	30
Month	Mar	Apr	Jun	Jun	Jun	Jul	Sep	Nov
Monocotyledon								
leaf	96	95	93	93	94	84	88	95
Stem	2	5	4	4	3	14	11	3
sheath	2	0	1	3	3	2	1	2
Dicotyledon								
leaf	0	0	2	0	0	0	0	0
stem	0	0	0	0	0	0	0	0

feeding ecology. All the authors just cited, apart from Hanks *et al.* (1969), record *Cynodon dactylon* as a main species eaten. This species occurred little in the main study area and was mainly eaten during dry months, reaching 4,6 per cent of fragments in faeces in July. Since *Cynodon dactylon* is, like *Panicum* species, a high quality food plant (Field 1968, Long *et al.* 1969), it is possible to suggest that waterbuck select for good quality grazing throughout the year. This is in accordance with the observed trends in nutrients available in UGR and with the findings of Taylor *et al.* (1969) that waterbuck require a particularly high protein diet. Kiley (1966), using faecal analysis in Kenya and Uganda, concluded exactly the opposite. She suggested that low quality species such as *Aristida* sp. and *Heteropogon contortus* were preferred and that waterbuck was possibly a species adapted to poor quality grassland. This certainly seems erroneous. Her brief descriptions of the habitats sampled show them to have either been recently burnt or in very dry poor condition, either of which could explain why a wide range of plants were being eaten including poor species. This interpretation is supported by her finding of up to 30 per cent browsing in samples from the dry unburnt areas. Lamprey (1963) recorded 95 per cent grazing by waterbuck and Field (1972) found a maximum of 3,9 per cent dicotyledons in the diet during dry months. Tomlinson (1978) noted an increase in browsing during dry months, but the maximum percentage of feeding activity taken up by browsing was still only 1,8 per cent at that time. He also recorded increased grazing of *Panicum maximum* by waterbuck during dry months, which he attributed to the higher nutrient content of this grass. Faecal analysis in UGR indicated a figure of 1,1 per cent dicotyledons during summer and 3,2 per cent during winter (see below). Hofmann and Stewart (1972) and Hofmann (1973) used mainly morphological features of the stomach to define waterbuck as a grazing species requiring fresh grass growth and being dependent on water. They did, however, consider the ruminal mucosa able to cope with a more rapidly fermenting diet. It seems likely that any quantity of browse is only taken under conditions of extremely poor grazing.

<u>Seasonal variation in the diets of the eight main grazers in UGR</u>

Table 82 gives the results of faecal analysis for grass species composition of the diet of all eight main grazers in UGR for wet and dry seasons. The percentage contributions to biomass of the main

Table 82. Grasses in the diets of the main grazers in the Umfolozi Game Reserve by season, as shown by faecal analysis. Only grasses occurring as over five per cent of fragments are considered; significance of seasonal differences for these grasses are calculated using the Student's t test.

	Panicum maximum	*Themeda triandra*	*Panicum coloratum*	*Eragrostis superba*	*Eragrostis* sp.	*Cynodon dactylon*	*Digitaria* cf. *macroglossa*	*Heteropogon contortus*	*Sporobolus smutsii*	Unknown 2	*Enteropogon monostachyos*	*Dactyloctenium australe*	*Panicum deustum*
Waterbuck													
summer	21,3	40,2	17,1	8,8	0	0,4	4,9	1,4	0,2	0	0,1	0	0
winter	41,9	24,8	2,5	7,4	1,6	3,6	1,4	4,4	0,1	3,9	0,1	0,03	0,1
	t=4,62	t=1,96	t=7,88	t=1,33									
	P<0,001	P>0,05	P<0,001	P>0,1									
Nyala													
summer	36,7	14,0	25,0	8,7	0	0	2,9	0,3	4,0	2,7	0,9	0	0
winter	59,5	5,5	2,5	4,3	7,6	6,6	0,7	0,6	3,1	0	4,2	0	1,0
	t=1,59	t=-2,10	t=-4,88	t=-1,41	t=2,15	t=1,82							
	P>0,1	P=0,05	P<0,001	P>0,1	P<0,05	P>0,05							
Impala													
summer	59,7	7,4	13,1	9,1	0,1	0	4,8	0,4	0,1	0,1	0,3	0,8	0,3
winter	58,1	1,3	15,3	3,2	4,4	3,2	0,8	0	1,9	4,6	1,2	3,1	0,1
	t=-0,21	t=2,01	t=0,39	t=-2,24									
	P>0,1	P>0,05	P>0,1	P<0,05									
Buffalo													
summer	23,4	49,9	10,1	3,3	0	0,3	5,9	2,8	2,3	0,8	0,2	0	0
winter	26,8	53,9	2,5	1,5	0,4	2,0	2,3	2,0	1,7	3,0	0,4	0	0
	t=0,64	t=0,62	t=-4,18				t=-1,49						
	P>0,1	P>0,1	P<0,001				P>0,1						
Wildebeest													
summer	9,5	26,6	21,2	10,9	0	1,6	9,9	6,7	10,0	0,7	0	0	0
winter	9,0	7,9	7,2	19,2	0,3	0	7,9	7,2	35,4	2,3	1,3	0	0
	t=0,22	t=-4,57	t=-4,10	t=2,69			t=-1,06	t=0,23	t=11,61				
	P>0,1	P<0,001	P<0,001	P<0,05			P>0,1	P>0,1	P<0,001				

continued

Table 82, continued.

	Panicum maximum	*Themeda triandra*	*Panicum coloratum*	*Eragrostis superba*	*Eragrostis* sp.	*Cynodon dactylon*	*Digitaria cf. macroglossa*	*Heteropogon contortus*	*Sporobolus smutsii*	Unknown 2	*Enteropogon monostachyos*	*Dactyloctenium australe*	*Panicum deustum*
Zebra													
summer	10,0	65,8	4,6	0	0	0,2	2,2	13,2	3,2	0	0,4	0	0
winter	51,2	9,9	2,3	6,3	3,0	0,7	0,9	7,5	6,0	8,5	0,4	1,6	0
	t=5,27	t=-5,42		t=1,98				t=0,97	t=0,8	t=2,72			
	P<0,001	P<0,001		P>0,05				P>0,1	P>0,1	P<0,05			
White rhino													
summer	45,2	16,3	6,5	0,5	0,2	6,7	5,7	1,0	7,7	0	4,5	2,7	0,7
winter	32,5	22,7	5,9	4,4	1,0	1,7	3,6	4,2	5,1	3,9	8,9	2,5	0,1
	t=-1,65	t=0,77	t=-0,19			t=-1,42	t=-0,93		t=-0,98		t=1,02		
	P>0,1	P>0,1	P>0,1			P>0,1	P>0,1		P>0,1		P>0,1		
Warthog													
summer	59,4	1,0	8,4	0,3	2,3	0,3	0,1	0	7,2	0	3,0	5,9	10,2
winter	32,9	9,7	6,2	3,4	10,8	2,7	4,3	0,1	4,5	2,1	3,0	14,4	3,2
	t=-2,80	t=1,97	t=-0,76		t=1,35				t=-0,70			t=0,97	t=-2,08
	P<0,05	P>0,05	P>0,1		P>0,1				P>0,1			P>0,1	P>0,05

grasses at the niche centre of each herbivore are recorded in Table 83 and the preference indices of grasses eaten are shown in Table 84. Only grasses comprising over five per cent of the diet or over five per cent availability for at least one grazer are included in these three tables. For waterbuck wet season samples cover the period October to March and dry season samples are from June to August.

As predicted above, the main seasonal differences for waterbuck are a significant increase ($P<0{,}001$) in the amount of *Panicum maximum* taken during winter and a significant increase in the amount of *Panicum coloratum* eaten during summer. In contrast to the amounts eaten, the availability of *Panicum maximum* declines during the winter and that of *Themeda triandra* increases. However, *Themeda triandra* is not preferred at this time while *Panicum maximum* is strongly preferred (Tables 83 and 84).

Nyala and impala are the species eating the most *Panicum maximum* during the dry season. Impala eat it to the same degree during summer whereas nyala show a decline in *Panicum maximum* and an increase in *Panicum coloratum*, as recorded for waterbuck. Impala and nyala also have the highest availability of *Panicum maximum* of all grazers in their habitats during winter (Table 83).

Zebra is another species for which *Panicum maximum* forms the bulk of the diet during winter, but this grass is taken significantly less ($P<0{,}001$) during summer. Of the remaining four grazers, white rhino and warthog eat mainly *Panicum maximum* in both seasons, but during winter many other grasses are consumed in reasonable quantities. Although *Panicum maximum* does not form the bulk of the diet of buffalo in either season, it is strongly preferred during winter (Table 84). Wildebeest is the only grazer both eating *Panicum maximum* in small quantity and showing a low preference for it. *Sporobolus smutsii* is the main grass eaten by wildebeest in winter, which agrees with an attraction for this grass noted in the last chapter.

Table 85 gives seasonal selection indices for grass species; only grasses which occurred at five per cent or over at the niche centre of at least one herbivore are included. These results show that most grazers are selecting areas in which the grasses that make up the bulk of their diet commonly occur. Thus impala and nyala show the strongest preference of all grazers during winter for *Panicum maximum* dominated areas; buffalo show the highest preference for *Themeda triandra* grassland in both seasons and wildebeest show the highest area selection

Table 83. The percentage contributions to biomass of grasses at the niche centres of the main grazers in the Umfolozi Game Reserve by season. Only grasses accounting for at least five per cent of the biomass at the niche centre of at least one herbivore are considered.

	Panicum maximum	*Themeda triandra*	*Panicum coloratum*	*Eragrostis superba*	*Bothriochloa insculpta*	*Urochloa mosambicensis*	*Enteropogon monostachyos*	*Sporobolus smutsii*
Waterbuck								
summer	12,2	19,6	16,0	6,9	4,4	18,8	2,8	3,9
winter	10,3	24,9	14,6	8,5	5,1	12,9	2,7	2,3
Nyala								
summer	16,6	19,7	13,1	4,6	3,1	19,3	3,7	3,9
winter	16,3	16,5	13,3	4,1	3,1	21,7	4,5	3,4
Impala								
summer	11,3	22,8	14,2	5,8	4,4	17,2	4,5	4,1
winter	15,6	15,7	13,6	7,4	3,3	20,1	5,4	4,1
Buffalo								
summer	8,7	31,7	14,5	10,2	3,7	8,8	0,8	2,1
winter	3,4	45,7	10,7	8,2	5,9	4,1	2,9	1,0
Wildebeest								
summer	10,6	22,5	14,9	6,4	3,9	18,7	1,9	5,0
winter	12,4	15,4	15,2	6,6	5,9	21,1	4,1	4,6
Zebra								
summer	7,6	20,4	17,3	6,0	10,5	11,8	1,9	1,3
winter	13,2	21,7	16,8	5,5	4,8	18,3	1,4	2,3
White rhino								
summer	10,1	24,6	13,6	6,2	3,7	16,9	3,7	3,5
winter	10,6	17,3	14,2	6,0	3,6	19,7	6,0	4,8
Warthog								
summer	13,5	18,2	14,6	4,8	3,0	18,4	6,9	3,2
winter	12,5	17,1	14,8	4,1	4,3	21,4	4,6	3,6

Table 84. Preference indices* for grasses eaten by the main grazers in the Umfolozi Game Reserve, by season. Only grasses comprising at least five per cent in the diet or at the niche centre of a herbivore are considered.

	Panicum maximum	*Themeda triandra*	*Panicum coloratum*	*Eragrostis superba*	*Eragrostis* sp.	*Cynodon dactylon*	*Digitaria* cf. *macroglossa*	*Heteropogon contortus*	*Sporobolus smutsii*	Unknown 2	*Enteropogon monostachyos*	*Dactyloctenium australe*	*Panicum deustum*	*Bothriochloa insculpta*	*Urochloa mosambicensis*
Waterbuck															
summer	1,75	2,05	1,07	1,28	-	-	-	-	-	-	-	-	-	-	0,02
winter	4,07	1,00	0,17	0,87	-	-	-	-	-	-	-	-	-	0,08	-
Nyala															
summer	2,21	0,71	1,91	1,89	-	-	-	-	-	-	-	-	-	-	0,01
winter	3,65	0,33	0,19	-	+	+	-	-	-	-	-	-	-	-	-
Impala															
summer	5,28	0,32	0,92	1,57	-	-	-	-	-	-	-	-	-	-	0
winter	3,72	0,08	1,13	0,43	-	-	-	-	-	-	0,22	-	-	-	0
Buffalo															
summer	2,69	1,57	0,70	0,32	-	-	2,19	-	1,10	-	-	-	-	-	0
winter	7,88	1,18	0,23	0,18	-	-	-	-	-	-	-	-	-	0,02	-
Wildebeest															
summer	0,90	1,18	1,42	1,70	-	-	4,95	1,76	2,00	-	-	-	-	-	0
winter	0,73	0,51	0,47	2,91	-	-	3,59	3,00	7,70	-	-	-	-	0,10	-
Zebra															
summer	1,32	2,20	0,26	-	-	-	1,10	3,56	-	-	-	-	-	0	0
winter	3,88	0,46	0,14	1,15	-	-	-	2,42	2,61	+	-	-	-	-	0
White rhino															
summer	4,48	0,66	0,46	0,08	-	+	2,85	-	2,20	-	-	-	-	-	0
winter	3,07	1,31	0,42	0,73	-	-	-	-	1,06	-	1,48	-	-	-	0

continued

* Preference index = per cent in diet/per cent at niche centre.
\- Occurs as <5 per cent in diet and at niche centre.
\+ Present as >5 per cent in diet but not recorded at niche centre.

Table 84, continued.

	Panicum maximum	*Themeda triandra*	*Panicum coloratum*	*Eragrostis superba*	*Eragrostis* sp.	*Cynodon dactylon*	*Digitaria* cf. *macroglossa*	*Heteropogon contortus*	*Sporobolus smutsii*	Unknown 2	*Enteropogon monostachyos*	*Dactyloctenium australe*	*Panicum deustum*	*Bothriochloa insculpta*	*Urochloa mosambicensis*
Warthog															
summer	4,40	0,05	0,57	-	-	-	-	-	2,25	-	0,43	1,90	6,80	-	0
winter	2,63	0,57	0,42	-	+	-	-	-	-	-	-	4,65	-	-	0

Table 85. Area selection for grass species by the eight main grazers in the Umfolozi Game Reserve as shown by preference indices (PI)*: all grass species contributing over five per cent to total grass biomass at the niche centre of any grazer are considered.

	Panicum maximum	*Themeda triandra*	*Panicum coloratum*	*Eragrostis superba*	*Bothriochloa insculpta*	*Urochloa mosambicensis*	*Enteropogon monostachyos*	*Sporobolus smutsii*
Availability (per cent)+	12,8	26,6	12,6	5,0	4,4	13,5	5,3	3,0
Waterbuck								
summer	1,0	0,7	1,3	1,4	1,0	1,4	0,5	1,3
winter	0,8	0,9	1,2	1,7	1,1	1,0	0,5	0,8
Nyala								
summer	1,3	0,7	1,0	0,9	0,7	1,4	0,7	1,3
winter	1,3	0,6	1,1	0,8	0,7	1,6	0,8	1,1
Impala								
summer	0,9	0,9	1,1	1,2	1,0	1,3	0,8	1,4
winter	1,2	0,6	1,1	1,5	0,8	1,5	1,0	1,4
Buffalo								
summer	0,7	1,2	1,2	2,0	0,8	0,7	0,2	0,7
winter	0,3	1,7	0,8	1,6	1,3	0,3	0,5	0,3
Wildebeest								
summer	0,8	0,8	1,2	1,3	0,9	1,4	0,4	1,7
winter	1,0	0,6	1,2	1,3	1,3	1,6	0,8	1,5
Zebra								
summer	0,6	1,1	1,4	1,2	2,4	0,9	0,4	0,4
winter	1,0	0,8	1,3	1,1	1,1	1,4	0,3	0,8
White rhino								
summer	0,8	0,9	1,1	1,2	0,8	1,3	0,7	1,2
winter	0,8	0,7	1,1	1,2	0,8	1,5	1,1	1,6
Warthog								
summer	1,1	0,7	1,2	1,0	0,7	1,4	1,3	1,1
winter	1,0	0,6	1,2	0,8	1,0	1,6	0,9	1,2

* PI = per cent contribution to biomass at niche centre/mean per cent contribution to biomass in the study area (availability+).

for *Sporobolus smutsii*. Waterbuck, however, show a decline in preference for *Panicum maximum* areas during winter, so that this preferred grass is encountered less than would be expected if the study area were utilized randomly. At the same time *Themeda triandra* areas are less strongly selected against, although this grass decreases in the diet during winter. Waterbuck is the only species for which a significant increase in the amount of a grass eaten during winter is accompanied by a change to area selection against the grass.

These results have shown that all the main grazers apart from wildebeest show a preference for *Panicum maximum*, especially during winter. Good quality food as offered by *Panicum* species is believed to be a limited resource in UGR during winter for which competition takes place. Waterbuck particularly appear to rate poorly in these competitive interactions. Nyala is considered a main competitor since the competition with waterbuck described in the last chapter is now seen to be important in terms of the trophic niche. The other herbivores eating much *Panicum maximum* during winter are impala and zebra. Zebra are considered of low competitive importance because of their low percentage contribution to metabolic biomass (see Chapter 3) and because they drastically diversify their diet during summer. In contrast impala are considered a prime competitor with waterbuck because of their persistant grazing of *Panicum maximum* throughout the year and their high density. That impala are successful competitors is further shown by their ability to maintain a high level of *Panicum coloratum* in their diet during winter, the only species to do so.

The results of rumen analyses for nyala and impala are given in Table 86. The data, although few, suggest that as found for waterbuck, both species select leaf over stem, the latter only rising slightly in winter. There is no hint of a facultative feeding association between these species and waterbuck. The increase in stem is likely to reflect a decrease of available leaf, with leaves still strongly selected, as found by Sinclair (1974c) for buffalo. The rumen analyses also show that both nyala and impala consume appreciable amounts of browse during winter. This is shown more clearly by the results of faecal analysis (Table 87). Nyala and impala take dicotyledon material as up to 50 per cent of their diet during dry months. This agrees with reports that impala prefer grass but can browse extensively during dry months (Talbot 1962, Azavedo and Agnew 1968, Stewart 1971, Hofmann and Stewart 1972). Nyala have generally been regarded as a

Table 86. Nyala and impala rumen analyses for plant parts, by season; figures refer to the mean number of fragments observed.

	Monocotyledon			Dicotyledon	
	Leaf	Stem	Sheath	Leaf	Stem
Nyala					
summer (n=2)	70,5	7,0	3,5	17,5	1,5
winter (n=1)	43,0	12,0	1,0	39,0	5,0
Impala					
summer (n=5)	86,0	1,8	1,2	9,6	1,6
winter (n=1)	65,0	9,0	2,0	23,0	1,0

Table 87. The percentage of dicotyledons eaten by the main grazers in the Umfolozi Game Reserve, by season; figures refer to the number of dicotyledon fragments observed per 100 fragments. The significance of seasonal differences was calculated using the Student's t test on the original data.

	Waterbuck	Nyala	Impala	Buffalo	Wilde-beest	Zebra	White rhino	Warthog
Summer	1,1	0,9	7,3	0,5	0,3	0	1,2	0,2
Winter	3,2	51,2	50,4	3,8	2,0	4,8	2,4	0,9
t	1,93	3,70	5,66	2,93	3,80	2,80	1,30	1,88
df	71	15	17	18	17	13	14	17
Significance	0,05<P< 0,1	P<0,01	P<0,001	P<0,01	P<0,01	P<0,05	P>0,1	0,05<P< 0,1

browser (Dorst and Dandelot 1970), but recent work has shown them to eat mainly grass during wet periods in a manner similar to impala (Anderson 1978). The high densities of nyala and impala in UGR mean that their browsing does not detract from their roles as competitive grazers. Indeed this browsing indicates low levels of good quality grass available during winter to even these small selective feeders, which emphasises the lack for larger animals such as waterbuck.

Field (1972) studied the diets of waterbuck and five other ungulates in Uganda using stomach analyses for plant species. Significant seasonal differences were found in the diet of waterbuck, but the interpretation of these results was unclear. He used a multivariate analysis of variance to compare the numbers of grass species fragments both between seasons and between animals and suggested that waterbuck could have been competing with buffalo for *Chloris gayana, Heteropogon contortus* and *Themeda triandra* and with hippopotamus for *Sporobolus pyramidalis* and *Heteropogon contortus*. It is worth explaining why this statistical approach is considered misleading and has not been adopted here to study feeding competition. First, estimation of diet using proportions of grass species fragments in rumens or faeces is crude and only main trends can be expected to be followed. Second, and most important, the finding that two sets of samples differ significantly in amount of a grass does not mean that the two animals are not competing for that grass. For example the 41,9 per cent *Panicum maximum* eaten by waterbuck in winter (Table 82) differs significantly ($t = 2,68$, $P < 0,05$) from the 59,5 per cent eaten by nyala, but this does not mean that the two ungulates are not competing for a limiting resource. Casebeer and Koss (1970) went to the trouble of using analyses of variance to compare the diets of four herbivores only to conclude: "In comparing the selectivity shown for the three dominant grasses there is a high similarity even though statistical differences were demonstrated."

CONCLUSION

It is concluded that good quality food for herbivores represents a limited resource in UGR during winter, for which waterbuck may be largely outcompeted. Although a number of species are implicated, nyala and impala are believed to play the main role. This conclusion is supported by results presented in Chapters 3 and 8, where waterbuck were found to be poorly competitive and impala and nyala were the suggested main competitors because of their recent increases in percentage contributions to metabolic biomass, their central roles in overgrazing in UGR and, in the case of nyala, direct habitat overlap.

CHAPTER 10

CONCLUSION

THE NATURAL REGULATION OF WATERBUCK DENSITY IN UGR

Waterbuck appear to have strict habitat requirements for the maintainance of a healthy population. The main factor determining habitat suitability is believed to be the availability of grass of a certain minimum height and minimum quality throughout the winter period, such as is found in riverine communities. Since these habitats usually occur as a low percentage of any wildlife area in Africa, and since they are also favoured by many other species including highly competitive short grass grazers such as impala, waterbuck cannot be expected usually to make a high contribution to total grazing biomass.

The density of between 700 and 900 waterbuck in UGR is close to the maximum which can be expected at the present stocking rate of 63,3 kg/ha for all grazers which is probably near the ecological carrying capacity for the area. The waterbuck population is, however, declining and the age-specific reason for this is a 80,7 per cent juvenile mortality rate. It is suggested that the main proximate cause of death of calves is associated with severe infestations of engorged female brown ear ticks and subsequent condition loss. Results from this and other studies all point to these high tick infestations on young animals and adults as being symptomatic of poor condition of the whole waterbuck population in UGR, which means that the ultimate cause of juvenile mortality must be sought elsewhere.

The hypothesis that the waterbuck population is in a stressed condition is supported by examinations of their habitat utilization patterns, their feeding ecology and aspects of their behaviour. The dynamics of the grazing associations defined by habitat utilization studies suggest that the primary habitat of waterbuck is that now occupied year round by nyala and what have been recorded are the results of competition with nyala pushing waterbuck into an unfavourable habitat. Quantification of feeding habits and food availability have shown that competition between nyala and waterbuck extends to the trophic niche and that true competition is possible because good quality grass represents a limited resource in winter. Impala are also implicated as a main competitor with waterbuck because of their feeding habits, their prime potential for causing overgrazing and their recent increase in abundance. The general applicability of this classification of competitive ability is shown by the significant inverse relationship which exists between waterbuck and impala when their abundance is compared over many areas of Africa.

It is concluded that the cause of the present decline in waterbuck numbers in UGR is high calf mortality attributable mainly to severe tick infestations, but that this high loss rate of young would not have occurred without the ultimate predisposing factor of interspecific competition. These findings support the suggestions that herbivores may often be resource limited (Sinclair 1975) and that it is juvenile mortality which is first affected by an increase in environmental stress (Caughley 1977, Eberhardt 1977).

It is possible that interspecific competition, acting through the food supply, may often be the mechanism whereby large herbivore populations are regulated. Such mechanisms need not be detected easily by habitat monitoring since, as stated by Sinclair (1974c), there is no need for overutilization or damage to occur as a consequence of regulation through food. It is suggested that a logical progression from the work of Jarman (1974) would be to place large African herbivores on a scale of competitive ability under various habitat conditions, where the position of a species would be ultimately related to its morphology and physiology. This approach represents a method whereby the important relationship between proportional faunal composition and grassland condition can be quantified. Relative changes in the density of animal species could then be meaningfully appraised as potential indices of stress in a grazing community, just as changes in grass species abundance can be used to define pasture condition.

MANAGEMENT IMPLICATIONS

It is suggested that the abundance of both nyala and impala needs to be reduced if the decline of waterbuck in UGR is to be arrested. As discussed below such a move is also considered desirable in terms of the overall functioning of the reserve. Removals should be organised initially on an experimental basis so that grassland condition and animal utilization patterns can be monitored both before and after removals, particularly during winter. The impact of this management action on waterbuck should be assessed further by monitoring the age structure of the population during November-December. A figure of approximately 30 juveniles per 100 adult females needs to be recorded before the population can be expected to have stopped declining.

At least four separate bottomland areas should be used, one where nyala are removed, one where impala are removed, one where both species are removed and one as a control area. This system would help to clarify the relative effects of these two species on lowlying grassland. This study has shown that impala and nyala have the closest habitat associations of any pair of species in UGR during the limiting winter period and that they both graze mainly *Panicum maximum* at that time. Impala are, however, believed to have a competitive advantage over nyala as they also concentrate on the important winter grass species *Panicum maximum* through the summer and are able to maintain a high level of the short palatable species *Panicum coloratum* in their diet during winter. This viewpoint is not contradicted by the findings of Keep (1973) who documented a crash in the nyala population in the Ndumu Game Reserve which resulted ultimately from a lack of food, whereas no decline was seen in the abundant impala population. It is possible that impala have a greater overall detrimental effect on the reserve and ultimately a greater competitive effect on waterbuck, even though the habitat overlap between nyala and waterbuck is more pronounced.

On a broader scale the decline of waterbuck has been interpreted as being symptomatic of an overall imbalance in the grazing community of UGR as quantified by the proportional abundance of species. Thus the decision whether to remove impala and nyala is really part of a larger question of how the whole grazing community should be managed. The present management aims for UGR (Anon. 1978) do not form a detailed enough framework on which these types of decisions can be made. This lack of specificity can be justified by arguing that enough is not known of the functioning of plant and animal communities to allow precise ecosystem management. This is true for UGR and NPB staff are at present restructuring their research activities using a systems approach to define priorities in order to produce results that will enable more effective management. However, reserves need to be managed now and decisions have to be made continuously on many subjects including the offtake of animals. The results of this study suggest that the proportionate abundance of large herbivore species represents a useful basis for setting interim management goals for the grazing community. Obviously any formalised approach to the managing of large herbivores must also form part of an integrated system of management for the whole reserve. For this reason it is suggested that a top priority should be the setting of specific interim goals for both the animal and plant communities in UGR. These aims can then be refined as more data become available from ongoing research and monitoring of both the large mammals and the vegetation of the reserve.

SUMMARY

Between 1970 and 1975 Natal Parks Board helicopter counts of waterbuck in the Umfolozi Game Reserve (UGR) declined from 1 098 to 494. The purpose of this project was to study the ecology of waterbuck with an emphasis on population regulating mechanisms, so that the reality and significance of this decline could be assessed.

Corrected helicopter counts and stratified fixed wing estimates gave totals of between 700 and 900 waterbuck in UGR during 1976-1977, but the population was shown to be declining. The ecological density of waterbuck represented 11,9 per cent of the metabolic biomass of grazers, which compared well with data from other areas. However, the other species' proportionate contributions to biomass were considered far from optimal, with an excess of selective short grass feeders.

Field age classification of individuals and age determination of skulls allowed the population structure of Umfolozi waterbuck to be investigated. High juvenile mortality (80,7 per cent) was the cause of the present decline of waterbuck and this would have to be reduced to 60 per cent before the population could be expected to stop declining. Adult mortality data indicated an annual loss rate of between four and nine per cent given this poor calf survival. Severe infestations of the tick *Rhipicephalus appendiculatus* were the probable main cause of death in young waterbuck, but poor condition likely preceded severe infestations and therefore the ultimate cause of juvenile mortality must be sought elsewhere.

Social organisation, movement and activity patterns of Umfolozi waterbuck were similar to populations studied elsewhere. Territory size, home range size and group size were all considered functions of resource abundance and dispersion. The fragmentation of groups and reduction of home range during winter suggested that acceptable food was limited and scattered during this season.

Waterbuck stood out as a species showing preferences for a wide range of habitat types in UGR. The primary habitat of waterbuck was believed to be that now occupied year round by nyala and what have been recorded are the results of competition pushing waterbuck into an unfavourable environment. Waterbuck were placed with buffalo and zebra in the most favourable category of not utilizing overgrazed areas, while impala, nyala and warthog were shown to persistantly graze overutilized grassland during the dry season.

Feeding studies indicated that nutritious food for herbivores represents a limited resource in UGR during winter, for which waterbuck may be largely outcompeted and that nyala and impala are the main competitors.

It was concluded that the cause of the decline of waterbuck in UGR was high calf mortality attributable mainly to severe tick infestations; however, this high loss of young would not have occurred without the predisposing factor of interspecific competition for food. A removal program of nyala and impala has been recommended, but it was emphasised that this must be integrated into a more precise management plan for UGR than exists at present.

SAMEVATTING

Tussen 1970 en 1975 het Natalse Parkeraad helikopter waterboktellings in die Umfolozi Wildtuin (UWT) van 1098 tot 494 gedaal. Die doel van hierdie projek was om die ekologie van waterbokke te bestudeer met die klem op bevolkingsregulerendemeganismes om aldus die werklikheid en betekenisvolheid van hierdie afname te kan bepaal.

Gekorrigeerde helikopter tellings en vastevlerk vliegtuig skattings verkry deur gestratifiseerde monstering het getalle van tussen 700 en 900 waterbokke in UWT tussen 1976 - 1977 gegee, maar dit is bewys dat die bevolking besig was om af te neem. Die ekologiese digtheid van waterbokke het 11,9 persent van die metaboliese biomassa van grasvreters verteenwoordig, wat goed vergelyk met data van ander gebiede. Aan die anderkant egter was die proporsionele bydraes van die ander spesies tot die biomassa as ver van optimaal beskou, met 'n oormate van selektiewe kortgras weiers.

Ouderdomsbepaling van indiwidue in die veld en deur middel van skedels het die ondersoek van die bevolkingstruktuur van Umfolozi waterbokke moontlik gemaak. 'n Hoë mortaliteit (80,7 persent) onder jong bokke is verantwoordelik vir die huidige daling in die getal waterbokke en dit sal tot 60 persent beperk moet word voordat daar verwag kan word dat die bevolkingsafname sal ophou.

Mortaliteitsgegewens vir volwasse bokke het 'n jaarlikse verlies tempo van tussen vier en nege persent getoon as die swak kalfoorlewingsyfer aanvaar word. Ernstige besmetting deur die bosluis *Rhipicephalus appendiculatus* word as die mees waarskynlike oorsaak van dood in jong waterbokke beskou, maar swak kondisie het swaar besmettings waarskynlik voorafgegaan en die eintlike oorsaak van mortaliteit onder jong bokke moet derhalwe elders gesoek word.

Sosiale gedrag, bewegings en aktiwiteitspatrone van Umfolozi waterbokke is soortgelyk aan die van bevolkings elders bestudeer. Grootte van territoriums, tuisgebiede en groepe is almal as funksies van voedselbeskikbaarheid en verspreiding beskou. Die opbreking van groepe en vermindering in tuisgebiedoppervlaktes gedurende Winter het aangedui dat aanneembare voedsel beperk en versprei was gedurende dië seisoen.

Waterbokke het uitgestaan as verbruikers wat voorkeur gegee het aan 'n wye reeks habitat-tipes in UWT. Die primêre habitat van waterbokke is in alle waarskynlikheid dié wat nou dwarsdeur die jaar deur njalas gebruik word; wat dus nou waargeneem word is die gevolg van kompetisie wat die waterbokke in 'n meer ongunstige omgewing druk. Waterbokke is saam met buffels en kwaggas in die mees gunstigste kategorie, d.w.s. dié wat nie oorbeweide gebiede verbruik nie gegroepeer, terwyl dit bewys is dat rooibokke, njalas en vlakvarke deurgaans oorbeweide gebiede gedurende die droë seisoen gebruik.

Voedingstudies het aangedui dat voedsame kos vir herbivore beperk in UWT gedurende Winter is, dat waterbokke nie hiervoor kan meeding nie en dat njalas en rooibokke die hoof kompeteerders is.

Die gevolgtrekking is gemaak dat die afname in waterbokgetalle in UWT aan 'n hoë kalfmortaliteit te wyte is, hoofsaaklik as gevolg van ernstige bosluisbesmetting; hierdie hoë verliese sou nietemin nie plaasgevind het nie sonder die nadelige invloed van interspesifieke kompetisie vir voedsel. 'n Verwyderingsprogram vir rooibokke en njalas is aanbeveel maar dit is beklemtoon dat dit moet inpas in 'n meer presiese bestuursplan vir UWT as wat tans bestaan.

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APPENDIX 1

The preparation of thin tooth sections for cementum line counts, after Ludbrook (1977)

1. Trim the tooth to a suitable size in the desired root area, approximately 2,0 cm x 0,5 cm x 0,5 cm.

2. Fix in buffered neutral formalin for four days.

3. Decalcify in five per cent nitric acid for four to six days at room temperature in plastic containers. The proportion of acid to tooth should be 20:1. It is not necessary to agitate.

4. Store in buffered neutral formalin.

5. Infiltrate according to the following scheme; a to 1 can be carried out on an autotechnician:

   a) Agitate in 70 per cent alcohol for two hours.
   b) Agitate in 96 per cent alcohol for two hours.
   c) Agitate in absolute alcohol for two hours.
   d) Agitate in absolute alcohol for two hours.
   e) Agitate in absolute alcohol for two hours.
   f) Agitate in absolute alcohol for two hours.
   g) Agitate in chloroform for two hours.
   h) Agitate in chloroform for two hours.
   i) Agitate in chloroform for two hours.
   j) Agitate in chloroform for two hours.
   k) Leave in a wax bath for two hours.
   l) Transfer to another wax bath for two hours.
   m) Vacuum infiltrate specimens for 20 minutes.

6. Cut sections of 7,0 μm thickness.

7. Stain according to the following schedule:

   a) Dewax in xylene for five minutes.
   b) Absolute alcohol for five minutes.
   c) Absolute alcohol for five minutes.
   d) 96 per cent alcohol for five minutes.
   e) 96 per cent alcohol for five minutes.
   f) 70 per cent alcohol for five minutes.
   g) Wash in tap water.
   h) Stain for approximately 2,5 hours in Erlich's Haematoxylin.
   i) Wash in tap water.
   j) Dip in acid alcohol (one per cent solution HCL/absolute alcohol) to differentiate.
   k) Wash in tap water to "blue".
   l) 70 per cent alcohol for five minutes.
   m) 96 per cent alcohol for five minutes.
   n) 96 per cent alcohol for five minutes.
   o) Absolute alcohol for five minutes.
   p) Absolute alcohol for five minutes.
   q) Xylene for five minutes.

8. Mount on a microslide using a synthetic resin.

APPENDIX 2

Details of all waterbuck captures in the Umfolozi Game Reserve during 1976 and 1977.

Date	Time	Animal number	Sex	Age class	Boma drive method		All methods	Immobilising drug doses			Time under drugs (darting to antidote, min)	Antidote	Waterbuck successfully released	Waterbuck subsequently resighted
					Period of chase to boma (min)	Time in boma before darting (min)	Time from darting to collapse (min)	Narcotic	Tranquiliser	Parasympatholytic				
19/5/76	09h40	1	F	A	-	-	Landrover Found after 35 min	50 mg Fentanyl	300 mg Azaparone	-	75	50 mg Lethidrone	yes	yes
21/5/76	07h36	2	M	A	-	-	Landrover 15 min	50 mg Fentanyl	350 mg Azaparone	-	120	150 mg Lethidrone	yes	yes
5/6/76	08h15	3	F	A	5	35	7	1 mg M99 +30 mg Fentanyl	25 mg Phenergan	-	50	100 mg Lethidrone	yes	no
5/6/76	08h15	4	M	A	5	50	5	"	"	-	56	"	yes	yes
5/6/76	08h15	5	M	J	5	Restrained by hand after 50 min in boma, no drugs used.					-	-	yes	yes
5/6/76	10h30	6	F	A	5	4	3	1 mg M99 +30 mg Fentanyl	25 mg Phenergan	-	51	100 mg Lethidrone	yes	yes
5/6/76	10h30	7	F	A	5	4	4	"	"	-	51	"	yes	yes
5/6/76	14h43	8	M	A	-	-	Helicopter 10 min	"	"	-	42	"	yes	yes
5/6/76	15h30	9	M	SA	-	-	Helicopter 4 min	2 mg M99 +30 mg Fentanyl	"	-	54	"	yes	yes
6/6/76	10h44	10	F	A	5	10	5	"	"	-	60	"	yes	died
6/6/76	10h44	11	M	J	5	Restrained by hand after 10 min in boma, no drugs used.					-	-	yes	yes
6/6/76	10h44	12	M	J	5	Restrained by hand after 10 min in boma, no drugs used.					-	-	died	-
6/6/76	10h44	13	F	J	5	Restrained by hand after 10 min in boma, no drugs used.					-	-	yes	yes
6/6/76	12h15	14	F	A	5	20	6	45 mg Fentanyl	25 mg Phenergan	-	60	100 mg Lethidrone	died	-
6/6/76	12h15	15	F	A	5	25	10	"	"	-	55	"	yes	died
6/6/76	12h15	16	F	A	5	25	10	20 mg Fentanyl +1 mg M99	"	-	55	"	died	-

M = male, F = female, A = adult, SA = 2 yr, J = 1 yr.

continued

Appendix 2, continued.

Date	Time	Animal number	Sex	Age class	Boma drive method: Period of chase to boma (min)	Boma drive method: Time in boma before darting (min)	All methods: Time from darting to collapse (min)	Immobilising drug doses: Narcotic	Immobilising drug doses: Tranquiliser	Immobilising drug doses: Parasympatho-	Time under drugs (darting to antidote, min)	Antidote	Waterbuck successfully released	Waterbuck subsequently resighted
7/6/76	08h25	17	M	J	15	Restrained by hand after 8 min in boma, no drugs used.					-	-	yes	yes
7/6/76	08h25	18	F	A	15	2	6	1 mg M99 + 20 mg Fentanyl	-	-	30	75 mg Lethidrone	yes	yes
7/6/76	08h25	19	F	A	15	30	6	"	-	-	25	"	yes	no
7/7/76	09h45	20	F	A	5	6	9	"	-	-	25	"	yes	yes
7/6/76	09h45	21	F	A	5	30	7	2 mg M99	-	-	28	"	yes	no
7/6/76	09h45	22	M	J	5	Restrained by hand after 62 min in boma, no drugs used.					-	-	yes	no
7/6/76	11h31	23	M	SA	-	-	Helicopter 15 min	1,5 mg M99 +30 mg Fentanyl	50 mg Phenergan	-	38	100 mg Lethidrone	yes	yes
7/6/76	15h41	24	M	A	-	-	Helicopter 9 min	"	"	-	44	"	yes	died
17/6/76	08h17	25	M	A	-	-	Helicopter 16 min	2,5 mg M99	-	10 mg Hyoscine	42	"	yes	yes
17/6/76	10h26	26	M	A	-	-	Helicopter 6 min	"	-	"	29	"	yes	no
17/6/76	14h06	27	M	SA	-	-	Helicopter -	"	-	"	19	"	yes	yes
17/6/76	15h35	28	M	A	-	-	Helicopter 9 min	"	-	"	15	"	yes	yes
25/7/77	09h01	29	M	SA	-	-	Helicopter 5 min	1 mg M99 +30 mg Fentanyl	250 mg Azaparone	-	54	"	yes	no
25/7/77	11h07	30	F	A	-	-	Helicopter 5 min	"	"	-	53	9 mg M285	yes	yes
26/7/77	08h16	1	F	A	-	-	Helicopter 10 min	"	150 mg Azaparone	-	55	"	yes	yes
26/7/77	14h15	2	M	A	-	-	Helicopter 30 min	"	250 mg Azaparone	-	64	"	yes	yes