KILIAN, JAN WERNER

THE SPATIAL AND TEMPORAL UTILIZATION OF RESOURCES BY THE RED HARTEBEEST (*ALCELAPHUS BUSELAPHUS CAAMA*)

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THE SPATIAL AND TEMPORAL UTILIZATION OF RESOURCES BY THE RED HARTEBEEST (*Alcelaphus buselaphus caama*)

by

JAN WERNER KILIAN

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THE SPATIAL AND TEMPORAL UTILIZATION OF RESOURCES BY THE RED HARTEBEEST (Alcelaphus buselaphus caama)

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Jan Werner Kilian

Supervisor: Professor J.D. Skinner
Mammal Research Institute
University of Pretoria
Pretoria

ABSTRACT

This study on red hartebeest was conducted on the S.A. Lombard Nature Reserve (SALNR), location of one of the largest remaining examples of the Cymbopogon - Themeda grassland. The grassland on the SALNR was characterized by high quantitative and qualitative fluctuations, which elicited spatial and temporal responses from the red hartebeest population. Hartebeest responded to the dry and most limiting period by selecting plant communities of relatively high biomass, including dicotyledenous material in their diet and the tendency to disperse into small groups to minimise intraspecific competition for food. In contrast, hartebeest responded to high rainfall periods by selecting plant communities with the highest nutrient content and forming large herds, which facilitated defence of neonates. During this period of food abundance, their diet consisted almost exclusively of grass. The adaptations to the fluctuating conditions on the western Transvaal Highveld ensured that optimal use of available resources was achieved by the red hartebeest breeding herd on the SALNR.

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CHAPTER 1

INTRODUCTION

Hartebeest belong to the Tribe Tragelaphini and the genus Alcelaphus. Two species, Alcelaphus lichtensteinii (of which no subspecies are recognized) and Alcelaphus buselaphus occur in the southern African subregion (Ansell 1972). Dorst & Dandelot (1970) mentioned the puzzling systematics of hartebeest, which led to the group being split up into several forms with specific rank. For practical reasons it is wise to consider the groups of form as geographic representatives of the same species.

Information regarding studies on red hartebeest (Alcelaphus buselaphus caama) in South Africa, has up to date been surprisingly scant, which made the red hartebeest population under study a good choice for enhancing our knowledge on large herbivores.

The Poaceae and mammals with hypsodont dentition first appeared in the Eocene and simultaneously underwent adaptive radiations from the Miocene to the Pleistocene (Stebbins, 1981). Mack & Thompson (1982) illustrated that the properties of grasses in grazing ecosystems differ markedly from those in grasslands lacking large herbivores. McNaughton (1985) pointed out that traits of both the plants and animals in the Serengeti ecosystem suggested that co- evolution took place among the trophic web members. In contrast to a well- defined, functional unit such as the Serengeti National Park in Tanzania (Pennycuick 1975), most of the nature reserves in South Africa are far smaller and many have been proclaimed without a knowledge of the movement patterns and nutritional requirements of the large herbivores they were designed to conserve. Fears have been expressed by Soule, Wilcox & Holtby

(1979) that many such smaller nature reserves will become ecological islands and lose a large proportion of their existing mammalian fauna.

The severity of the latter situation, with specific reference to red hartebeest populations in the Transvaal is illustrated in Table 1 (Van Rensburg, pers comm. 1990). The reserves under consideration fall under the jurisdiction of the Transvaal Provincial Administration.

Table 1: Estimated numbers of red hartebeest on nature reserves in the Transvaal

Nature Reserve	Area (ha)	Numbers
Boskop Dam	23 000	97
Abe Bailey	1 888	57
Rustenburg	4 257	80
Wolvespruit	2 333	43
SA Lombard	3 600	101
Bloemhof Dam	3 800	93
	3 500	72
Roodeplaat dam	1 200	27
Hartebeespoort Dam	135	7
Suikerbosrand	13 337	270
Langjan	5 000	30
Nyala	8 000	15
Atherstone	13 500	350

The SA Lombard Nature Reserve (SALNR) site of the present study, is a textbook example of an ecological island surrounded by a monoculture created as a result of farming practises.

It was proposed in this study to investigate certain aspects of red hartebeest ecology, pertaining mainly to adaptations within the confines of the SALNR. The main objective was to determine which of a variety of physical factors or combination of factors are paramount in determining the feeding adaptations of red hartebeest, as well as the behavioural responses (temporal and spatial) to those factors. Proposals concerning red hartebeest management on the SALNR and the possible factors limiting their distribution on the Transvaal Highveld are expected to emanate from this project.

CHAPTER 2

STUDY AREA

The SA Lombard Nature Reserve, 3633 ha in extent, is situated approximately 20 km northwest of Bloemhof in the western Transvaal (25x30'E and 27x35'S) at an altitude of 1200 - 1600 m (Fig.1). Data, over 25 years, revealed a mean annual rainfall of 510,7 mm (248,7 - 965,3 mm) and precipitation is confined mainly to the period November to April (Weather Bureau 1990). The annual mean temperature is 17,6xC (range -8,7xC in winter to 40xC in summer) (Skinner, van Zyl & Oates 1974).

The region is open grassland with isolated patches of bush, classified as dry Cymbopogon-Themeda veld (Acocks 1975). The vegetation can broadly be divided into five types (Van Zyl 1965) .

1. Eastern alluvial area
2. Western dry Cymbopogon-Themeda veld
3. Pans
4. Bushveld
5. Abandoned alluvial diamond diggings

The SALNR is situated in a geological area classified as the Supergroup Ventersdorp (Transvaal Nature Conservation Report 1985). Glenrosa and Hutton soil types are prevalent in the western dry Cymbopogon-Themeda veld, whilst the Mispah and Swartland types are predominant and characteristic of the eastern alluvial floodplain (Fig.2). The plain is inundated to a depth of up to 50 mm during heavy rains and carries flood waters down to the Vaal river (Van Zyl 1965).

The history of the Reserve from 1947 to 1955 has been described by Van der Merwe (1955). Of importance for the present study was the fact that the game was confined to the eastern half of the Reserve (Meester 1955), whilst the western part was utilized for agricultural purposes.

FIG.1. THE LOCATION OF THE S.A. LOMBARD NATURE RESERVE.

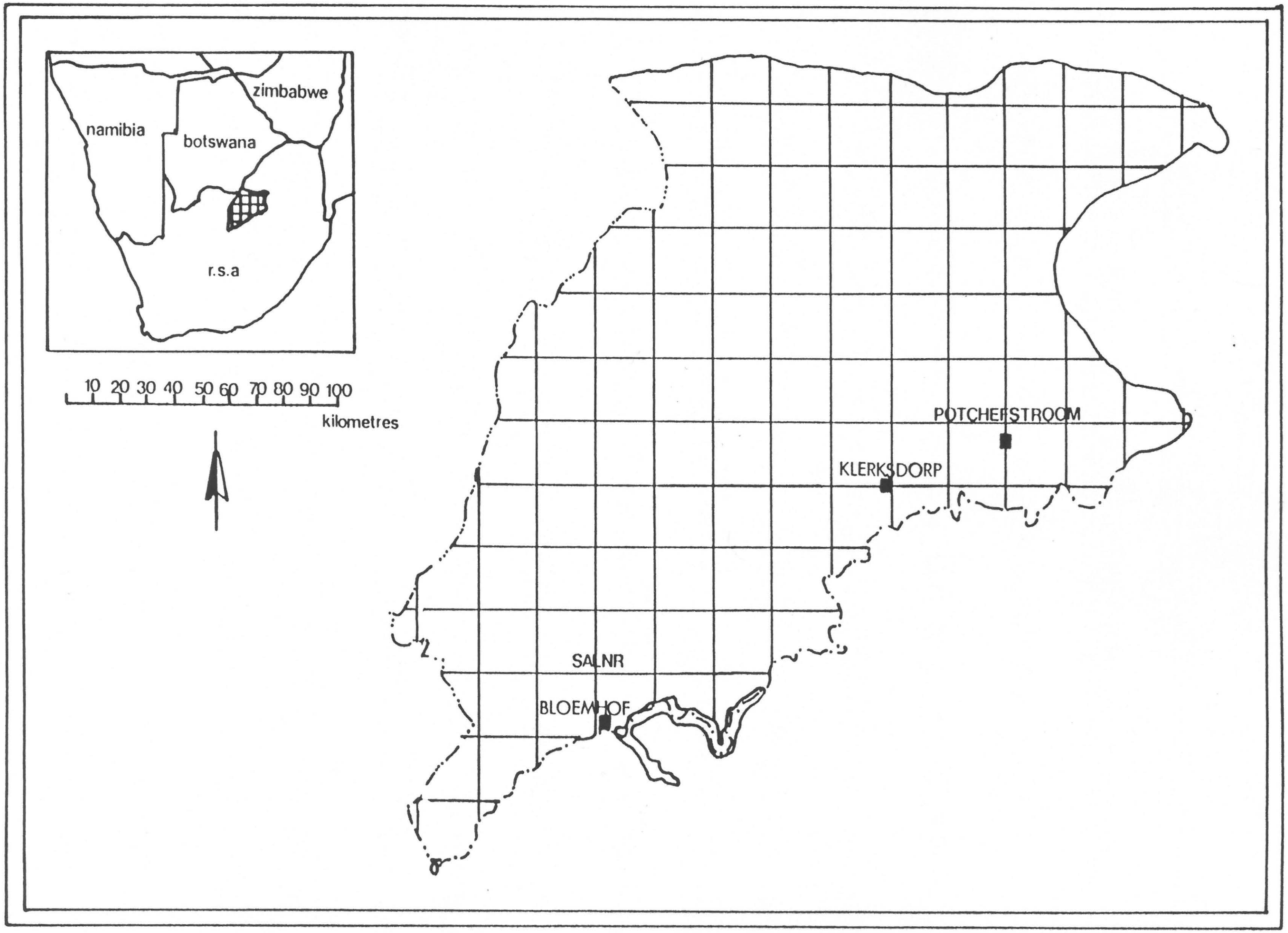
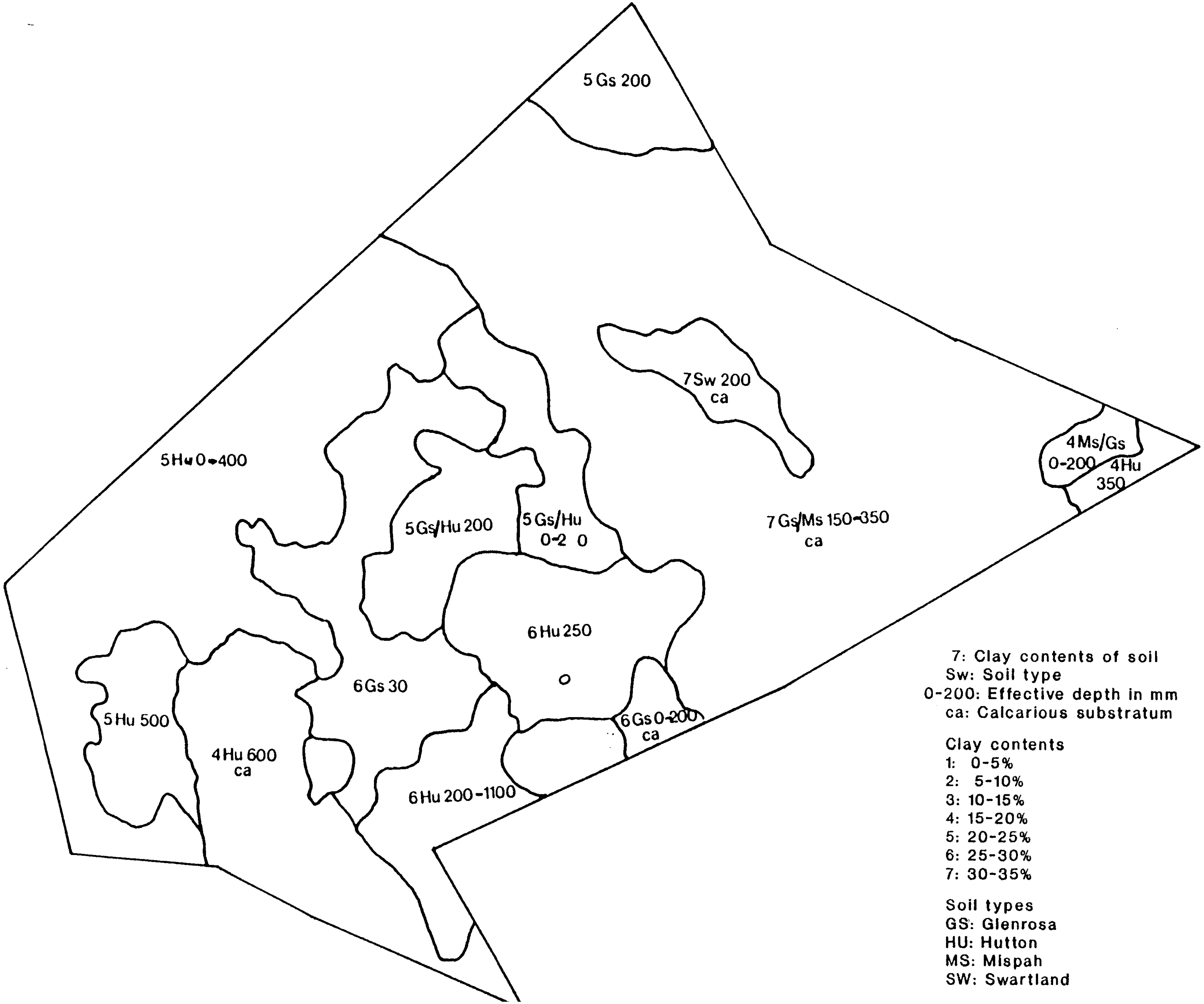


FIG.2. SOIL TYPES OF THE S.A. LOMBARD NATURE RESERVE.



7: Clay contents of soil
Sw: Soil type
0-200: Effective depth in mm
ca: Calcarious substratum

Clay contents
1: 0-5%
2: 5-10%
3: 10-15%
4: 15-20%
5: 20-25%
6: 25-30%
7: 30-35%

Soil types
GS: Glenrosa
HU: Hutton
MS: Mispah
SW: Swartland

CHAPTER 3

LITERATURE REVIEW

Red hartebeest occur in the Cape Province along the Botswana border, but have been re-introduced to several localities throughout South Africa (Skinner & Smithers 1990).

Physiological studies include the assessment of Etorphine (M-99) immobilization on red hartebeest (Kok 1973), physiological responses of red hartebeest to different capture methods (Ganhao, Hattingh, Pitts, Raath, de Klerk & de Vos 1988), seasonal trends in body condition, applying bone- marrow fat and kidney fat indices (Shackelton & Granger 1989), the effect of season on their breeding cycle (Skinner, van Zyl & Oates 1974), as well as thermoregulation and heat balance in Coke's hartebeest (Finch 1972). Digestive physiology studies have been undertaken by numerous authors (Arman & Hopcraft 1975; Stanley-Price 1977; Hoppe, Qvortrup & Woodford 1977; Clemens & Maloiy 1983; Clemens & Maloiy 1984; Clemens, Maloiy & Sutton 1983). Hofmann & Stewart (1972) classified hartebeest as roughage grazers, based on the distinctive morphological features of their digestive system.

Jarman (1974) considers hartebeest to be primarily grazers. This viewpoint is supported by the findings of several authors (Lamprey 1963; Blakenship & Field 1972; Kok 1975; Afolayan 1976; Henshaw 1979; Lewis & Wilson 1979; Booth 1980). Contrary to these findings, Van Zyl (1965) concluded that 44,4 percent of the diet of red hartebeest on the SALNR consisted of browse.

Ecological and behavioural studies include the assessment of feeding preferences (Van Zyl 1965; Kok 1975), habitat preferences, herd composition and territorial status (Kok & Opperman 1975), and a study on the life cycle of a red hartebeest population (Van der Walt, de Graaff & van Zyl 1976).

CHAPTER 4

RAINFALL AND REPRODUCTION

INTRODUCTION

In response to seasonal rainfall, the herb layer undergoes quantitative and qualitative changes (de Leeuw & Bakker, 1986; Boutton, Tiezen & Imbamba, 1988), which are important in determining feeding selectivity (McNaughton, 1983; Smits, 1986), movement patterns and habitat utilization (Pennycuick, 1975; Kutilek, 1979).

The optimal timing of parturition with respect to season may enhance the survival and growth of the offspring as well as the survival and future reproductive success of the mother (Rutberg 1987). The breeding season should therefore be initiated at such a time when environmental conditions are most favourable for the survival of the young after birth.

It is proposed in this chapter to address and interpret the adaptations of the red hartebeest breeding herd with regard to the rainfall patterns in the south western Transvaal.

METHODS

Rainfall

Rainfall figures for the SA Lombard Nature Reserve, as well as for Hertzogville, Christiana, Bloemhof, Schweizer-Reinecke and Wolmeranstad were obtained from the Weather Bureau (1990).

The latter five weather stations are in close proximity to the SALNR. The amount and variability of the rainfall were analysed for all the stations to derive an approximation of the rainfall regime in the entire region.

A climatogram, using the convention of Walther (1979), where 1°C equals 2mm of rain, effectively summarizes the rainfall and temperature data (Fig. 3). This climatogram (Skinner et al. 1974), was used as a benchmark for comparison with a climatogram drawn up for the SALNR during 1985. All observations on the red hartebeest herd were carried out during this period. The high coefficient of variance of rainfall (62% - 85%) (Appendix 1) in the peak rainy season (November to March) minimise the use of rainfall as a proximate cause in the timing of breeding by red hartebeest.

Population and reproduction

During the study period there was only one breeding herd on the reserve, exclusively utilizing the eastern alluvial floodplain, other breeding herds having been removed by capture operations prior to the onset of the present study. Five territorial bulls simultaneously occupied the floodplain whilst a group of 16 bachelors occupied the western dry Cymbopogon-Themeda veld.

Due to the extreme wariness of the breeding herd, three hides were constructed to facilitate intensive observations. This ensured that the distribution of births could be determined accurately. The method of observation is described in full in Chapter 6.

RESULTS

Rainfall

Measures like variance, standard deviation, standard deviation and coefficient of variation reflect the extremes of wetness and dryness with which organisms must contend. Generally, when the variance of an environmental variable is very small, organisms may evolve to "time" very closely to the variable even when it is extreme. On the other hand, the greater the range of variance the less dependable the value of any particular resource (Low 1979).

The coefficient of variation (variability) in the total amount of rainfall for the weather stations varies between 28% - 39%, an extent which is indicative of an erratic rainfall pattern. The variability of precipitation in the Namib, a true desert, exceeds 100% (Seely 1978).

According to the Koppen classification (Schulze & McGee 1978) the area is cool dry steppe with summer rains.

The rainfall data are presented in Appendix 1-6. The mean total rainfall varies from 470mm - 564mm. The rainfall measured at the SALNR during the study period totalled 414mm, which falls well within the range of 248,7 - 965,3mm. However, total rainfall during November, was 46,9% below the 25 year mean for the SALNR. The climatogram for the SALNR (Skinner et al. 1974) clearly indicates that a dry, arid period (May to September) prevails when the rainfall curve declines below the temperature curve and the prevalence of a wet, humid period (October to April) when the rainfall curve exceeds the temperature curve. The effect of the lower than average rainfall in November, is illustrated in Fig. 3. Lengthening of the dry period implies that increased demands are imposed on the red hartebeest population to meet their seasonal requirements, reproduce and maintain a viable population within the confines of the SALNR.

The high coefficient of variance of rainfall (62% - 85%) (Appendix 1) in the peak rainy season (November to March) minimize the use of rainfall as approximate cause in the timing of breeding by red hartebeest.

Population and Reproduction

In agreement with Skinner, van Zyl & van Heerden (1973), the bulk of the red hartebeest calves (82%) were born during the period September/ October (Fig 4). Extrapolating back using a gestation period of eight months, as given by Skinner et al. (1973) for red hartebeest, conception took place from the beginning of February to the end of March. The rut would have lasted longer as bulls start rutting prior to mating.

The breeding herd under study had a calving percentage of 75,3%. Up to the end of the study no calf mortalities were noted. Hence female red hartebeest appear to take advantage of greatest food availability to ensure maximum calf survival.

DISCUSSION

Red hartebeest on the SALNR show a distinctive pattern of being short-day seasonal breeders. The optimal mating season is determined primarily by daylength (Skinner et al. 1973), which is considered the proximate cause in the timing of breeding. The highly synchronous seasonal breeding pattern, exhibited by the red hartebeest may have several advantages. The first is that predation on neonates is greatly reduced as Estes (1976) illustrated. However, hartebeest are not preyed upon due to the absence of large predators on the SALNR, partly explaining the high survival rate of calves. The second is that resource availability (quantitative and qualitative) is at an optimum to enhance the survival of the young after birth.

FIG.3. THE CLIMATOGRAM FOR THE SALNR.

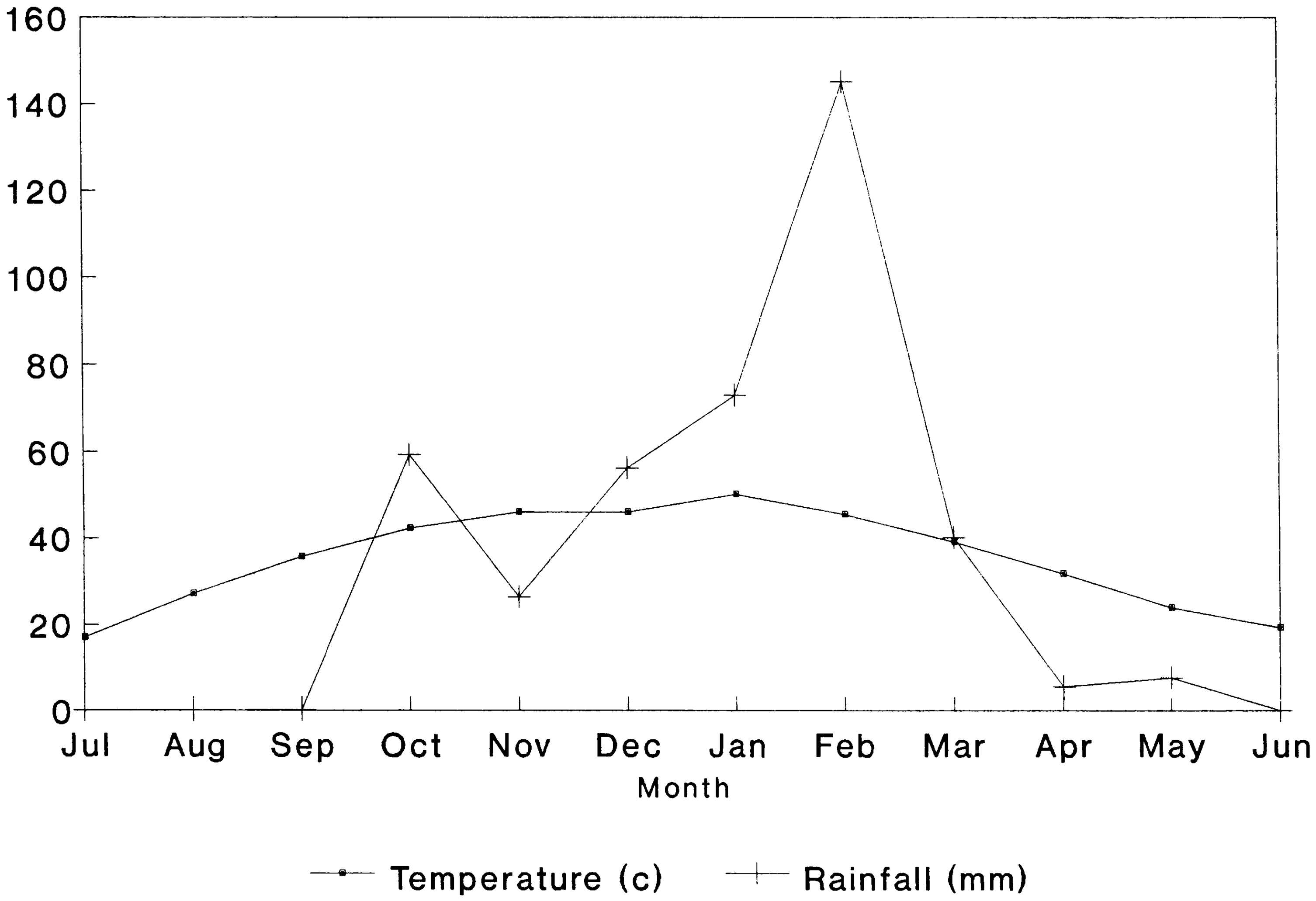
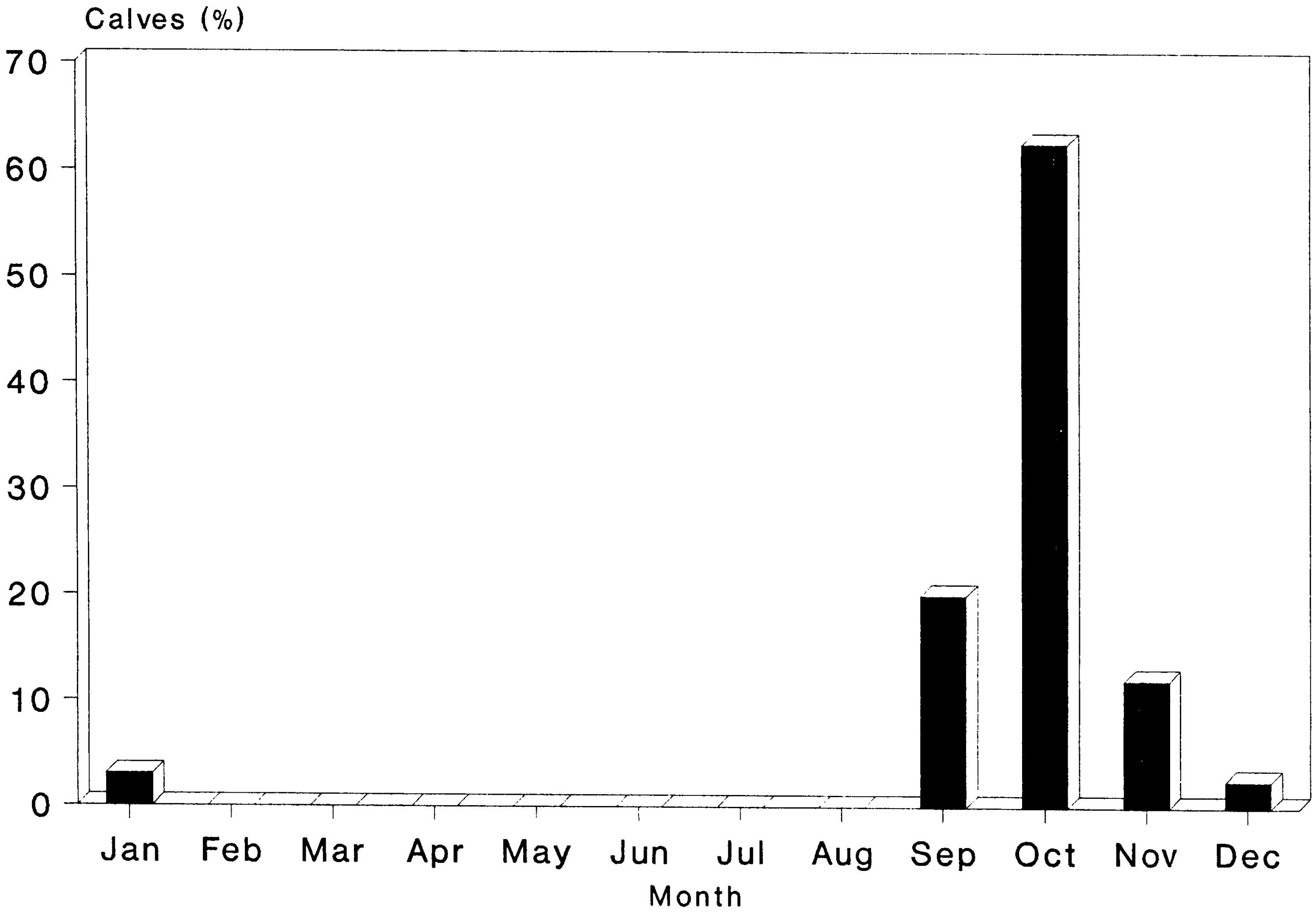


FIG.4. PERCENTAGE CALVES BORN DURING THE SEASONAL CYCLE.



CHAPTER 5

PLANT SURVEY

INTRODUCTION

The SALNR is one of the largest remaining examples of the Cymbopogon-Themeda grassland which once covered the region (Acocks 1975, Buys 1987). The importance of a sound plant survey in the description of habitat- ungulate relationships has been illustrated by several authors (Bell 1970, Hirst 1975, Osborne 1984, Sinclair 1985, Sodeinde 1989). Barnes (1976) remarked that a knowledge of the diet of grazing and browsing animals, combined with a knowledge of the composition of the vegetation available to them, is of basic importance in the management of vegetation, as well as the development of efficient systems of animal production.

The main objective of the plant survey was to identify, characterize and describe the plant communities on the SALNR. The results obtained should contribute to a better understanding of the impact of the grassland phytosociology on the temporal and spatial patterns exhibited by red hartebeest. Information on the characteristics of the woodland communities can be obtained from Buys (1987). These communities were either never or rarely utilized by the red hartebeest and were therefore excluded from the vegetational analyses.

METHODS

Classification

The Braun Blanquet method of sampling and classification followed in this study, is described by Mueller-Dombois & Ellenberg (1974) as well as Werger (1974).

The entire study area, comprising grassland, was stratified into relatively homogeneous physiognomic units determined by stereoscopic interpretation of 1:50 000 aerial photographs. Coetzee (1974) considered sample plots with a size of 16m/ to adequately represent the floristic composition of a temporate grassland community. A total of one hundred and ten (110) quadrats, each measuring 16m/ were randomly distributed throughout the study area. In each quadrat all grass species (= relevé), using the Braun-Blanquet cover abundance scale (Mueller- Dombois & Ellenberg 1974) were recorded, namely:

r: Very rare and with negligible cover (usually a single individual).

+: Present, but not abundant and with a small cover abundance value (less than 1% of the quadrat area).

1: Numerous, but covering less than 1% of the quadrat area, or not so abundant but covering 1-5% of the quadrat area.
2: Very numerous and covering less than 5% of the quadrat area, or covering >5-25% of the quadrat area independant of abundance.
3: Covering >25-50% of the quadrat area independant of abundance.
4: Covering >50-75% of the quadrat area independant of abundance.
5: Covering >75-100% of the quadrat area independant of abundance.

The raw data matrix, with columns representing relevés and rows species, was rearranged into an order that best reveals the intrinsic structure of the data. Compositionally similar samples are brought close together, as are distributionally similar species.

Two-way indicator species analysis (TWINSPAN) (Hill 1979a) is a polythetic divisive classifying technique which, due to its emphasis on indicator species, bears similarities to the approach of Braun-Blanquet. TWINSPAN was applied to the floristic data set to derive a first approximation of the vegetation types in the study area. The Braun-Blanquet method was used to refine the initial classification by TWINSPAN. The two classification methods supplemented each other to delineate the study area into the differentiating plant communities.

DECORANA

The floristic data set was ordinated by DETRENDED CORRESPONDENCE ANALYSIS (DECORANA). DECORANA determines similarity relationships among vegetation samples and among species and calculates axes scores for each sample (or species) (Hill & Gauch 1980). Ordination attempts to place each stand in relation to one or more axes in such a way that a statement of its position relative to the axes conveys the maximum information about its composition (Greig-Smith 1984). Ordination is also useful in the comparison of community patterns with environmental information (Gauch 1982).

Veld Condition

The method for veld condition assessment is based on allocating every recorded species to a species category (Decreaser, Increaser I, Increasers II or Increaser III). Foran, Tainton & Booysen (1978) defined the first three categories as follows:

Decreaser species decline in abundance with bad management practises
Increaser I species increase with under-utilization
Increaser II species increase with over-utilization
Increaser III species increase when grazing is selective (Vorster 1982).

Although no condition assessment was carried out, all grass species identified by means of the Braun Blanquet method, were allocated to their respective categories (Appendix 7). The classification of grass species in their respective ecological groups followed that of Janse van Rensburg (1987). This approach is based on the perceived responses of the grasses to degradation gradients. Due the similarities between the SALNR and van Rensburg's (1987) study area this approach is considered sound.

RESULTS

Classification

The analysis resulted in the recognition of nine plant communities (Table 2), which may be grouped into four major community types. The hierarchical classification of these communities is as follows:

1. The Echinochloa holubii - Panicum maximum Grassland on shallow pans with a high clay content.(40%-50%.)

2. The Sporobolus fimbriatus - Digitaria argyrograpta Grassland on the Glenrosa and Hutton soil types, representative of a continuum with its variants as follows:

2.1 *Aristida diffusa* - *Eragrostis chloromelas* variant.
2.2 *Eragrostis curvula* - *Heteropogon contortus* variant.
2.3 *Enneapogon scoparius* - *Heteropogon contortus* variant.
2.4 *Aristida curvata* - *Heteropogon contortus* variant.
2.5 *Digitaria eriantha* - *Panicum coloratum* variant.
2.6 *Sporobolus fimbriatus* - *Aristida barbicollis* variant.

3. The *Aristida meridionalis* - *Aristida uniplumis* Grassland on the sandy loam soils of the Hutton type with a low clay content.

4. The *Sporobolus ioclados* Grassland on the Glenrosa and Mispah soil types with a high clay content.

1. The *Echinochloa holubii* - *Panicum maximum* Grassland

The community occurs on shallow pans, most prevalent in the eastern alluvial floodplain, with a high clay content (40%-50%). This community is characterised by the diagnostic species in Species Group A. (Table 2). Characteristic of this community is its low species diversity.

2. The *Sporobolus fimbriatus* - *Digitaria argyrogrypta* Grassland

This community occurs on both the Glenrosa soil type in the eastern alluvial area, and the Hutton soil type, which predominate in the western part of the Dry *Cymbopogon* - *Themeda* veld (Acocks 1975). Species Group G is diagnostic for this community. This community is distiguished by the diagnostic species in Species Group G (Table 2). This community is distinguished by species group G with *Sporobolus fimbriatus* and *Digitaria argyrogrypta* conspicuous.

dominant. The presence (although low in cover-abundance) of pioneer species such as Cynodon dactylon and Aristida congesta subsp. barbicollis are indicative of overgrazing either as a result of farming practises or a heavy grazing regime. Several variants of this community type were identified:

2.1 The Aristida diffusa - Eragrostis chloromelas Grassland

This variant occurs on the Hutton soil type and is distinguished by species group B, dominated by Aristida diffusa and Eragrostis chloromelas (Table 2). The conspicuous presence of Aristida congesta subspecies barbicollis emphasizes the poor condition of this community. Other grasses which are often found include Digitaria argyrograpta and Eragrostis curvula.

2.2 The Eragrostis curvula - Heteropogon contortus Grassland

This variant occurs in the western part of the reserve,which had been subjected to farming practises to a greater or lesser extent. No diagnostic species group could be identified, but the community could be distinguished by the simultaneous presence of Species Groups B and C (Table 2). The community is dominated by Eragrostis curvula and Heteropogon contortus, whilst Eragrostis chloromelas and Aristida diffusa are locally prominent.

2.3 The Enneapogon scoparius - Heteropogon contortus Grassland

This variant occurs on Hutton soils with a relatively high clay content (20% - 25%). The community could be distinguished by the presence of Species Group C and the absence of Species Groups B and

D (Table 2). However, *Eragrostis chloromelas* from Species Group B are frequently present in this community. *Heteropogon contortus* and *Enneapogon scoparius* clearly dominate the community, with *Eragrostis chloromelas* and *Aristida curvata* less dominant.

2.4 The *Panicum laevifolium* - *Eragrostis pallens* Grassland

This variant also occurs on Hutton soils with a relatively high clay content and can be distinguished by the presence of Species Group D (Table 2).

2.5 The *Digitaria eriantha* - *Panicum colartum* Grassland.

This variant occurs on Hutton soils with a relatively high clay content, (30% - 35%) this variant can be distinguished by the diagnostic species in Species Group E (Table 2). The dominant grass species are *Digitaria eriantha* and *Themeda triandra* with *Panicum coloratum*, *Cynodon dactylon* and *Cympogon plurimodes* locally dominant. The presence of *Chloris virgata* is indicative of either heavy grazing and/or cultivation.

2.6 The *Sporobolus fimbriatus* - *Aristida congesta subsp. barbicollis* Grassland

This variant community occurs on Hutton soils with a relatively high clay content and can be distinguished by Species Group F (Table 2). Dominating in the community are *Sporobolus fimbriatus* and *Aristida congesta* subspecies *barbicollis*. *Cynodon dactylon*, indicative of overgrazing was also prevalent. The presence of *Digitaria argyrogrypta*, an increaser might be a benchmark as to how the community could develop under controlled management practices.

3. The Aristida meridionalis - Aristida uniplumis Grassland

The community occurs on the sandy loam soils of the Hutton type with a relatively low clay content (15%-25%). This community is characterized by Species Group H (Table 2) and the diagnostic species are Aristida meridionalis and Stipagrostis uniplumis and Aristida vestita. The infrequent occurrence of increasers, such as Themeda triandra, Cymbopogon plurinoides and Eragrostis lehmanniana seems to be indicative of a successional stage in this community. This community, which had been subjected to cultivation might again reach climax status following the discontinuation of farming practices.

4. The Sporobolus ioclados Grassland

This community occurs on the Glenrosa/Mispah soil type with a very high clay content (30% - 35%) and is almost entirely characterized by Sporobolus ioclados, creating a "grazing lawn" (Table 2). The presence of especially Chloris virgata and to a lesser extent Aristida congesta subspecies barbicollis gives an indication of the local intensity of grazing to which this community is subjected. Species group H, for the absence of respectively the pan areas (characterized by Echinochloa holubii) and the short grass area (characterized by Sporobolus ioclados) are present throughout the study area. Themeda triandra (with high cover-abundance values) and Eragrostis lehmanniana dominate this community. Cymbopogon plurinoides (high cover-abundance values) and Eragrostis superba often occur in this community, whilst the large extent to which Aristida congesta subspecies barbicollis appears, is yet again indicative of disruptive processes, either agricultural or overgrazing. Apart from the localized occurrence of Sporobolus ioclados, the remainder of the species in species group I are very patchily distributed throughout the study area. Their low cover-abundance values are prominant.

Detrended correspondence analysis (DCA)

The application of DECORANA to the floristic data set of the eastern portion on the SALNR resulted in the recognition of the four major plant community types.

The Braun Blanquet approach, TWINSPAN and DECORANA revealed a grassland continuum from east to west, which illustrated the need to further delineate the plant communities in the eastern alluvial area, to the extent where habitat use by the red hartebeest could better be interpreted.

The results are presented in Figure 5. The analysis resulted in the recognition of four plant communities. The hierarchical classification of the communities is as follows:

1. *Echinochloa holubii* - *Panicum maximum* Grassland on shallow pans with a high clay content (40% - 50%).
2. *Sporobolus ioclados* Grassland on the Glenrosa and Mispah soil types with a high clay content (30% - 40%).
3. *Themeda triandra* - *Eragrostis lehmanniana* Grassland on the Glenrosa, Mispah and Hutton soil types with a relatively high clay content (30% - 40%). Patches consisting almost entirely of *Sporobolus ioclados* occur frequently throughout the community, creating a mosaic of tall to short grassland.
4. *Themeda triandra* - *Aristida congesta* subsp. *barbicollis* Grassland on the Glenrosa, Mispah and Hutton soil types with a relatively low clay content

(20% - 25%). This plant community occurs in the extreme eastern alluvial floodplain area. This community is considered a variant of the Themeda triandra - Eragrostis lehmanniana community. The prominence of Increaser species such as Aristida congesta congesta and Aristida congesta barbicollis is the main distinctive feature separating the two communities.

A vegetation map, illustrating the different plant communities in the eastern alluvial floodplain, is shown in Figure 6. The woodland communities (after Buys 1987) are shown to be periferal to the eastern alluvial floodplain.

General Comments

The reserve was effectively divided into a dry western Cymbopogon-Themeda veld and the eastern alluvial floodplain. The higher complement of Decreasers in the eastern alluvial floodplain rendered this area highly suitable to herbivores. This is in contrast to the western area, which, due to the prominence of several increaser species, is considered unsuitable for sustained optimal use by herbivores.

The eastern alluvial floodplain is regarded as the climax state of vegetation on the SALNR, as opposed to the disturbed successional stages of the vegetation predominating the western area.

Table 2. A phytosociological table of the grasses on the S.A. Lombard nature reserve.

Community number	1					2			
Releves	0110000000011 7100746796900 8026781429139	00000000 53890295 84678642	00000 22268 01277	0000000000 5156789346 7890299598	0000100000 2469036736 5053613984	0000000100000010000000000001 0881144000134801355671472570 3143656029032385614659307537	00000000 08016955 70412060	000 892 289	0010000001000000000001000 4701724800122333338990105 1612137515748027985644 53
Species Group A									
Echinochloa holubii	+3123243 +								
Panicum maximum	1+3235434455								
Chloris virgata	+++ + +++2	R			2	+ + + 1++ R+R	+		R+R12+++ +
Species Group B									
Eragrostis chloromelas	2	1+++1+1	1 11+	1 11+	++	+			
Aristida diffusa		2++++++1	++1	1					
Eragrostis curvula	1	+ 1 +	+++2+	+	+			+	
Species Group C									
Aristida curvata			+ +	R +	+1+1 +11 2				
Enneapogon scoparius			+	+1 + 1+1	1+	+			
Heteropogon contortus			1 +++	+ ++ + 22	+R11 1+	+	+		
Species Group D									
Eragrostis pallens					R+ + +	+			
Eragrostis denudata					+ ++1				
Eragrostis homomalla					+R				
Eragrostis rotifer					1R			1	
Panicum laevifolium	+				11 +12	1			
Species Group E									
Panicum coloratum						+R R + + ++ RR+++1+1	+	+	R +
Digitaria eriantha						+R+ 2+4122344++++			
Fingerhuthia africana				2+	R	2+ R1 1 + R			
Eragrostis gummiflua						1 R+ 2			
Species Group F									
Sporobolus fimbriatus	1	+	+ +	+ 2 +	R +	22 22322+111+1++ R33	++1R2		R
Cynodon dactylon	4++ +	+		+	R 111	54312 2++3 + 1+ R+	1 1		+
Aristida congesta bar.	+ +	133 +	+	+ 1+1 +	+ +	RR+ + + + 1	31++ 2		+ R
Digitaria argyrograpta		R +1	1++	++ ++1	+ +22 +1	+ + + +	1+ +		
Elionurus muticus		R12R1	+ +	+ ++	+++1+	+ ++ R R R	1+		
Species Group G									
Aristida meridionalis			+	+				23+	
Aristida scabrivalvis								+	
Stipagrostis uniplumis								2	
Aristida vestita			+					+1	
Species Group H									
Themeda triandra		3222	11 21	1R1212+22	3 3122222+	+R3322332 3333233543	R2+ R	R	
Eragrostis lehmanniana		++++ 1 +	+++	+ 1++1+ +	+ 1+1 +	+ 1+11 1+R1111111 ++2 2	++ 3112	+ 1	2
Aristida congesta con	+ 1	3 1+ +	+	+ +++R+1	1 111++	2 21+ + +R +R++ +1 + +	+2+2+1	2	R
Cymbopogon plurinodis		+ ++1	2++	R 1++11 +	1 1 + 2	3 2222331331 + +	1+ 3	+	
Eragrostis superba		+RR+	1+++R	R +++ R+	+R++ +	R + RR+ + +	+ +R+1+	R+	
Eragrostis obtusa		+	+	+ R 1+3	+R++R 1+2	R R + + 1R R	+ +1 1	++	
Species Group I									
Sporobolus ioclados						13234	3		3333433233343433433433333
Species Group J									
Trichoneura grandiglumis		1					1		
Eragrostis bicolor					+	+	R		
Brachiaria eruciformis			+			R			
Eragrostis cilianensis			+	+		1			
Pogonarthria squarrosa						R			
Setaria flabellata						R			
Eragrostis rigidior	1 +								

FIG.5. DETRENDED CORRESPONDENCE ANALYSIS OF THE GRASSLAND COMMUNITIES OF THE EASTERN ALLUVIAL FLOODPLAIN.

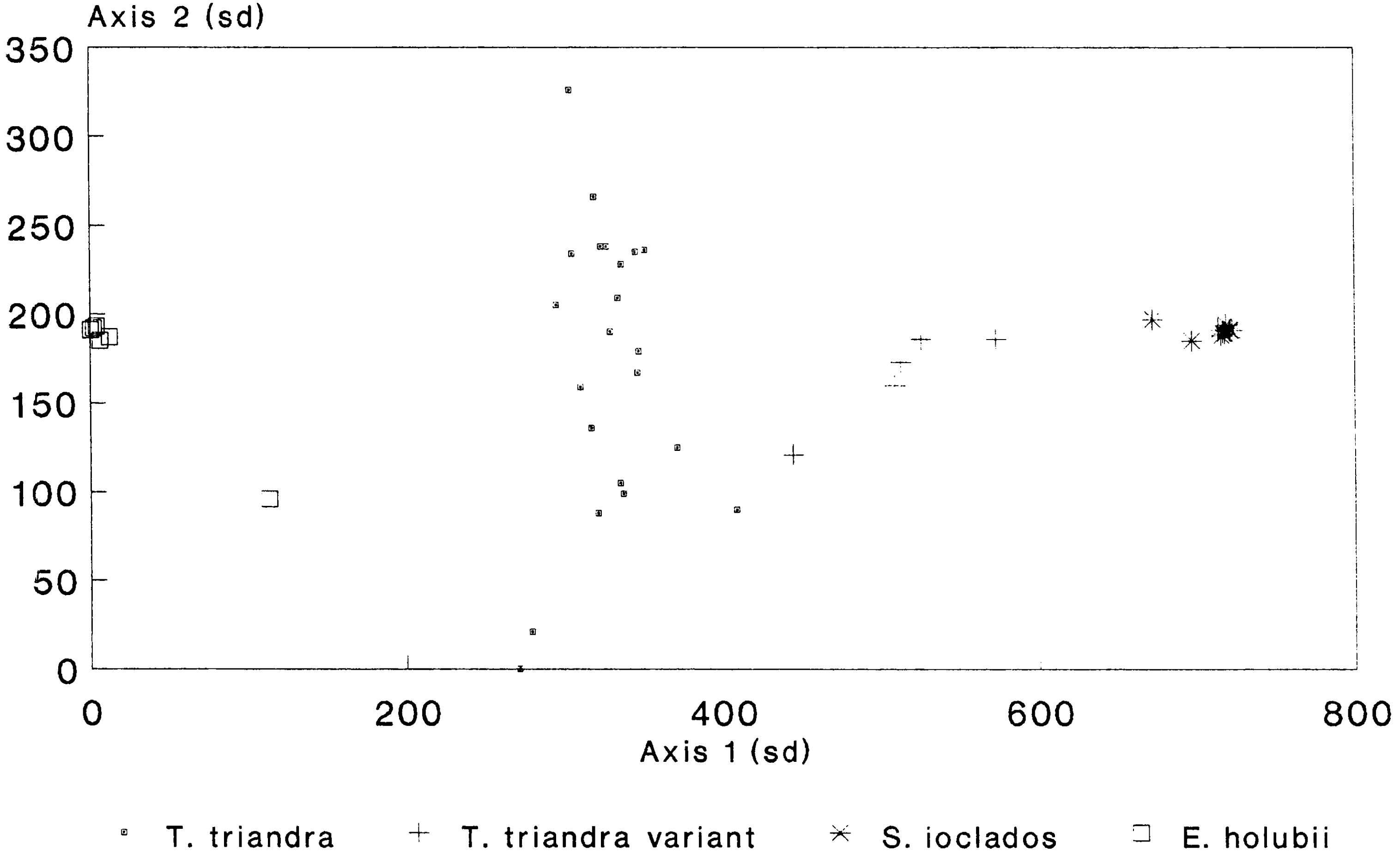
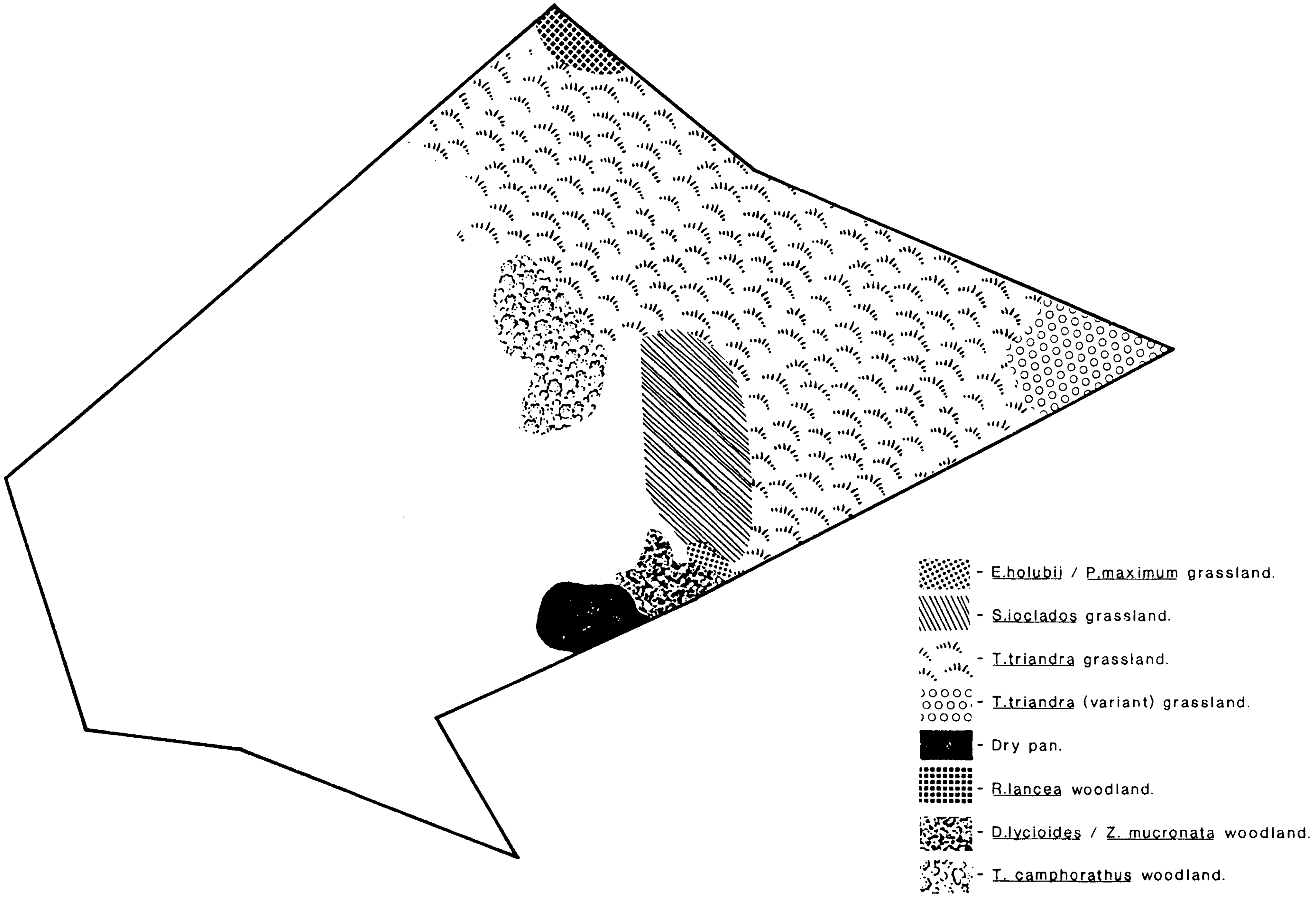


FIG.6. PLANT COMMUNITIES OF THE EASTERN ALLUVIAL FLOODPLAIN.



CHAPTER 6

HABITAT SELECTION

INTRODUCTION

Ungulates seldom range randomnly. The nature of a random distribution implies that the probability of finding an individual at a point in the area is the same for all points (Greig-Smith 1983). Several statistical methods such as Cole's coefficient of association (Cole 1949) and selection/ preference studies (Hillman 1979, Beardall, Joubert & Retief 1984) have been employed to illustrate deviation from randomness or not. The null hypothesis to be tested in the analysis of ungulate/habitat relationships is that the distribution of animals is random over all community types. This implies that the expected occurrence of animals would be in proportion to the relative occurrence of the different communities in the study area.

Red hartebeest are predominately associated with open country and, according to Kok (1975), ecotonal areas are preferred. They occur in open woodland (Ben-Shahar 1984) but avoid closed woodland (Skinner & Smithers 1990). In terms of habitat selection Van der Walt _et_ _al_. (1976) considers red hartebeest to be one of southern Africa's most adaptable ungulates.

A knowledge of habitat selection by red hartebeest on the SALNR is considered essential for effective future management.

The objective of this chapter was to assess the preference for the different community types by red hartebeest and the interpretation thereof in terms of qualitative and quantitative changes in the herb layer.

METHODS

Biomass

Quadrats, 1 m⌡ in size were randomnly placed out in each of the four grassland communities (eastern alluvial floodplain). The herbaceous layer was subsequently clipped at ca. 50 mm above ground level, ensuring that the stubble which is supposedly not utilized by animals is left behind. Clipping was continued until a standard deviation of ca. 15% was reached. The harvest samples were not sorted into different grass components, such as leaves and stems, as selection at this level was not carried out during the present study. The clipped material was air dried for two days, then oven dried to a constant mass at 50xC. Biomass per community type was measured and calculated as g/m⌡.

The clippings were repeated for six periods over time to assess the impact of biomass change in the grassland community preference by red hartebeest over time.

Dietary quality

The results obtained by Buys (1987) were used to derive an estimation of grass quality differences between the short and tall grassland communities in the eastern alluvial floodplain. This is justifiable as the observational period corresponded with the period of grass quality determination. The collection of grasses was done in the same location to minimise differences in nutritive quality due to different soil types.

The impact of seasonal dietary quality in combination with biomass change on the plant community selection and use by the red hartebeest, was assessed in this chapter.

Distribution

The entire reserve was divided into grid squares, each measuring 250m X 250m (Fig. 7). Stakes were errected to form a 250 m X 250 m grid pattern, which ensured accurate plotting of the position of individual herd members relative to the major plant communities at any given time. Unlimited visibility of the herd was possible due to the plainslike nature of the eastern area. This facilitated plotting the spatial distribution of the breeding herd. The use of space by red hartebeest was studied from the erected hides,which ensured that the herd was under observation from dawn until twilight. The position of the herd was plotted at 30 min intervals. The breeding herd was not always spatially distributed as a cohesive unit. Consequently, plottings of the splinter groups had to be done in the same manner. Distance moved per time interval was calculated from subsequent plottings of the estimated herd centre.

Simultaneous confidence intervals

Bonferroni simultaneous confidence intervals (BSCI) involve count (enumeration) data. One needs to find the observed number of instances of use and the expected number of occurrences based upon the known availability of vegetation types in the veld (Byers, Steinhorst & Krausman 1984).

When examining a set of vegetation types BSCI are calculated as follows:

$$p_i - \frac{Z}{2k}\sqrt{p_i(1-p_i)/N} \le p_i \le p_i + \frac{Z}{2k}\sqrt{p_i(1-p_i)/N}$$

Where k = the number of categories (8 in the present study).

With k = 8 and = 0,05 , $Z_{0,0031} = 2,73$.

The expected proportion of use (p_io) is equal to the relative proportion of category i. If p_io lies outside the confidence interval, expected use and actual use are significantly different at the stated level of significance, equalling 0,05 in the present study. When p_io lies within the interval, chance use of the vegetation type by red hartebeest is implied. BSCI were calculated for six time periods.

To facilitate the discussion on habitat selection, the time periods were allocated to an estimated seasonal category, bearing in mind the rainfall pattern during the study period:

January/February	(late summmer)
March/April	(autumn)
May - August	(winter)
September	(spring)
October	(early summer)
December	(summer)

RESULTS

Biomass

The change in biomass on the eastern alluvial floodplain is illustrated in Fig. 8. The peak biomass is generally attained during late summer and autumn. Biomass declined during the winter period, reaching lowest levels during spring and early summer, before the onset of the first rains. An increase in biomass was apparent after the commencement of the first rains in late October.

A significant decrease in the biomass of the *E*, *holubii*/*P*. *maximum* grassland was observed for the period autumn to winter ($t_{26}=11,8p\leq0,05$).

The biomass of the *S*.*ioclados* short grassland peaked during autumn, preceding the winter, spring and early summer periods, when the biomass declined substantially. The increase in biomass, following the first rains was significant, although not to the same extent as in the medium tall *E*.*holubii* community.

The *T*. *triandra* community was also characterized by peaks in biomass during autumn and early spring and pronounced depressions preceding the commencement of the hot, wet summer period. The seasonal fluctuations in biomass of the *T*. *triandra* (variant) grassland followed the same trend as the *T*. *triandra* grassland, albeit to a lesser extent.

Nutrient quality

The protein content of selected grass species characteristic to medium-tall and short grasslands is presented in Figures 9 to 10. The selected grass species of the short grassland had consistently higher protein values than those of the medium-tall grasslands. During the cold, dry and warm dry periods, the protein content declined to levels below 5%. In contrast, the species occurring on short grassland, maintained higher levels of protein during the corresponding period.

Community selection

The probable reasons for the breeding herd avoiding the western dry *Cymbopogon* communities, were mentioned in Chapter 4. In contrast, the bachelor herd avoided the eastern alluvial floodplain area during all seasons.

The preference/avoidance of the eight vegetation communities in the eastern alluvial floodplain is summarized in Table 3 and shown in Appendix 8-13. The peripheral woodland areas were avoided during all seasons. Occasionally, and then only for short periods, members of the harem herd penetrated the *Tarchonanthus camphoratus* woodland. The herd preferred the *E. holubii*/*P. maximum* and *S.ioclados* commmunities during the hot, wet summer months, as opposed to avoidance of these communities during both the dry, cold and warm dry periods. Except in late summer, hartebeest showed a preference for the *T. triandra* (variant) grassland which was utilized only during the late summer and winter periods.

Table 3: Seasonal preference (*) or avoidence (-) for the different community types during the seasonal cycle

Community type	**Late summer**	**Autumn**	**Winter**	**Spring**	**Early summer**	**Summer**
Echinochloa holubii *Panicum maximum* grassland	*	-	-	*	*	*
Sporobolus ioclados grassland	*	*	-	-	-	*

Themeda triandra grassland	*	*	*	*	-	-
Themeda triandra (variant) grassland	*	-	*	-	-	-
Dry pan	-	-	-	-	-	-
Rhus lancea woodland	-	-	-	-	-	-
Diospyros lycioides/ *Ziziphus mucronata* woodland	-	-	-	-	-	-
Tarchonanthus camphoratus woodland	-	-	-	-	-	-

Group size

Although a single harem herd occurred on the SALNR at the commencement of the observations, this herd showed a tendency to disperse and form "splinter" groups. The reverse tendency was also evident, and Prins (1989) referred to the splitting and coalescing of groups as fusion-fission respectively. The nul hypothesis to be tested is that group size is independent of season. A Chi-square statistic on the percentage occurrence of group sizes during all season, was highly significant.χ^2 = 803.17 d.f. = 40 $p<0.05$). The nul hypothesis is therefore rejected, indicating the influence of season on fusion-fission pattern within the red harte breeding herd. Fusion could best be illustrated by plotting the frequency occurrence of the splinter groups against the seasonal occurrence (Figures 11 to 13). The tendency for fusion (notably the 49+ interval) amongst herd members was observed to be greatest during the late summer as well as autumn (Table 4). The degree of fusion after the commencement of the first rains (= summer), was less noticeable than expected (Table 4). Alternatively, fission was most noticeable during the warm, dry periods. Both small and high group sizes are associated with the winter period (Table 4). Fusion-fission could occur several times daily within a season. Recording whether a group had split off temporarily, is admittedly, a subjective assessment. Although prone to some error, the influence of season on fusion- fission patterns within the harem herd, was well illustrated. Single animals were regarded as groups throughout all seasons.

Table 4: Percentage occurrence of group sizes during all seasons on the SALNR.

	SEASON					
Group sizes	**Late summer**	**Autumn**	**Winter**	**Spring**	**Early summer**	**Summer**
1	0.0	0.5	1.7	3.4	9.9	2.7
2	0.9	1.7	5.0	8.5	15.3	5.9
3	1.5	5.3	5.5	5.4	7.0	7.3
4	1.8	2.6	4.9	5.2	5.9	5.3
5 - 6	3.3	5.8	6.4	7.2	4.0	12.3
7 - 12	10.7	12.0	18.8	26.1	19.7	20.9
13 - 24	18.0	15.6	13.4	17.1	17.8	14.3
25 - 48	22.2	27.7	27.0	25.8	20.4	16.3
49 +	41.7	28.9	17.3	1.3	0.0	15.1

The influence of season on mean splinter group size is illustrated in Fig. 14. Groups of larger size predetermined the hot, wet season, whilst groups observed during the dry, cold and warm dry periods were smaller. Seasonal variations in mean group size (MGS) of several herbivores were found to be positively correlated with rainfall (Rogers 1977). The relationship between rainfall and MGS of red hartebeest was determined by means of linear regression, although weakly correlated coefficients. To compensate for the lag period between rainfall and the subsequent response of the vegetation, preceding rainfall (one and 2 months earlier) was used. A stronger correlation resulted from the 2-month preceding rainfall (r = 0.612) as opposed to one-month preceding rainfall (r = 0.469).

DISCUSSION

The results confirmed those of Kok (1975) that harem herds occupy the most favourable grazing areas at the expense of bachelor herds. The extent of seasonal fluctuations in the biomass of the S. ioclados grassland was minimal, contrary to the fluctuations recorded in the medium-tall T. triandra community (Fig.8). During the hot, wet summer months, the short grassland was subjected to heavy grazing by both red hartebeest and black wildebeest, resulting in the maintenance of a "grazing lawn".

This implied that red hartebeest could not sustain themselves on short grassland swards, due to low plant biomass restricting adequate food intake. The presence of C virgata, an unpalatable increaser grass, in the short grassland, could be likened to a defence mechanism, operating through a negative feedback system, against overgrazing. The T. triandra community was characterised by maintaining the highest biomass levels, which could support red hartebeest through the most limiting periods. Fig. 15 illustrates the strong negative correlation (r = -0,95) between the utilization of the medium-tall T. triandra and short S. ioclados grassland.

The grasses characteristic of the E. holubii/P. maximum responded rapidly to rainfall, which attracted both red hartebeest and black wildebeest. The resultant heavy grazing led to severe reduction in plant biomass, which initiated the dispersal of red hartebeest to the T. triandra grassland.

The nul hypothesis, implicating a random distribution of animals, is therefore rejected. Hartebeest responded to fluctuations in the herb layer by adopting a pasture rotation pattern similar to herbivores in the Serengeti National Park (McNaughton 1985).

The tendency and degree of the fusion-fission patterns within the harem herd, could be related to both dynamical changes in the herb layer as well as social factors. During late summer, the abundance of the food resources and the strong female-calf bond resulted in the strong cohesiveness of the harem herd (Table 4) (Fig. 11). Due to the high incidence of rutting during this period, the cohesiveness facilitated the task of the herd bull in defending the females against both territorial and bachelor bulls.

The fact that fusion was associated with an abundance of food, suggested that minimal intraspecific competition amongst herd members occurred. In contrast, declining food resources stimulated a pattern of fission amongst hartebeest, possibly through an increase in intraspecific competition. The fact that fission peaked during the most limiting season (early summer) (Table 4) (Fig. 13), was contrary to expectations. Intuitively, one would expect a tendency for cohesiveness so as to protect the neonates. However, fusion only became apparent after the onset of the summer rains. Moreover, the magnitude of cohesion was not as large as expected (Table 4) (Fig. 13). It seems plausible that the the harem herd had become too large to operate as a social unit. This viewpoint is substantiated by the relatively low MGS of the summer period. MGS is also a good measure of the degree of cohesion amongst the herd members (Fig. 14).

The degree of cohesion seemed to be primarily dependent on the temporal variations in rainfall (Fig. 14), which affect the productivity of the herb layer. Social factors, however, contained the extent of the fusion-fission patterns. This is well illustrated in Fig. 14 where the influence of rainfall on the MGS at its upper range started levelling off.

FIG.7. GRID SYSTEM APPLIED ON THE S.A. LOMBARD NATURE RESERVE.

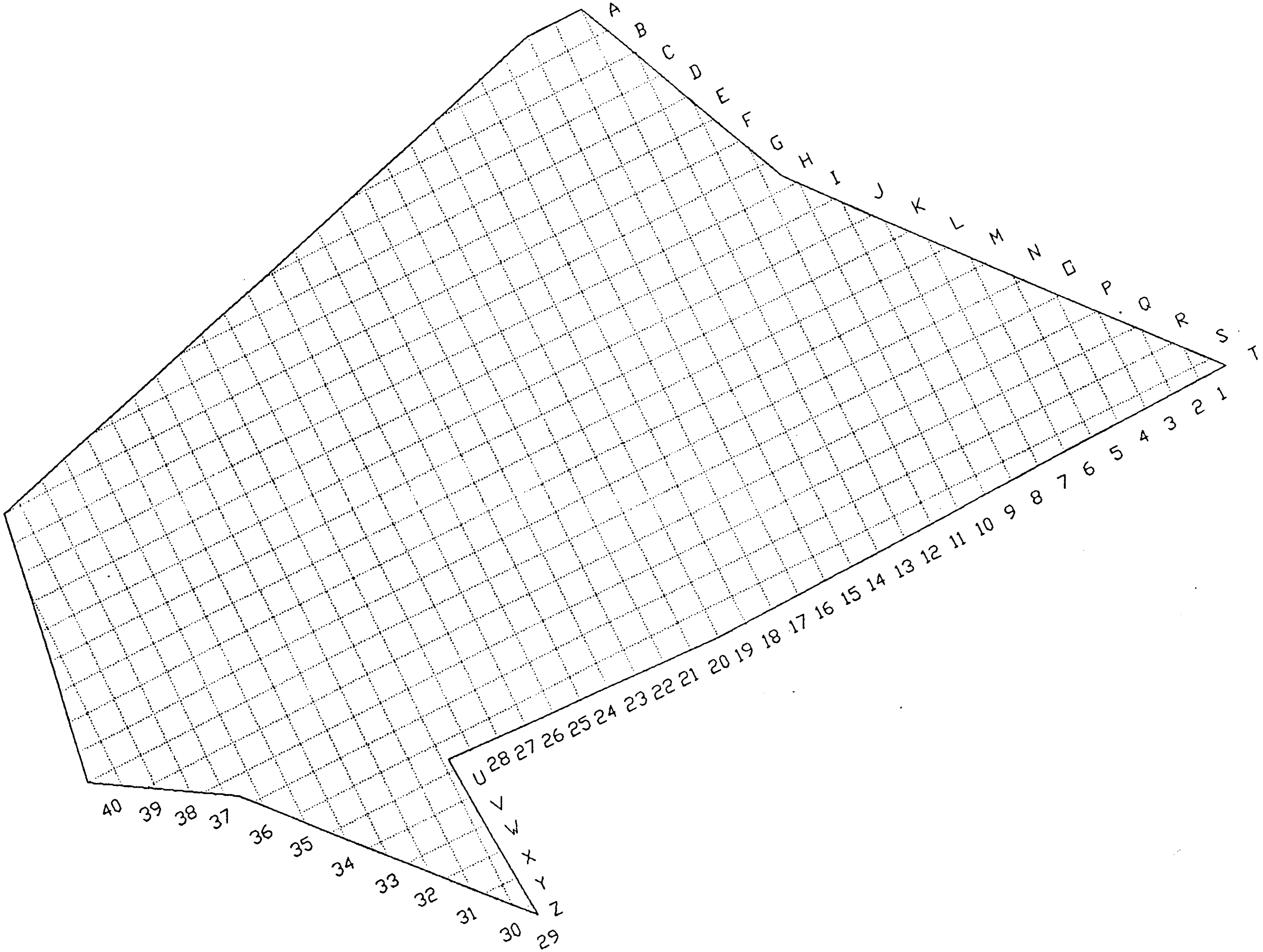


FIG.8. BIOMASS CHANGES IN THE GRASSLAND COMMUNITIES OF THE EASTERN ALLUVIAL FLOODPLAIN.

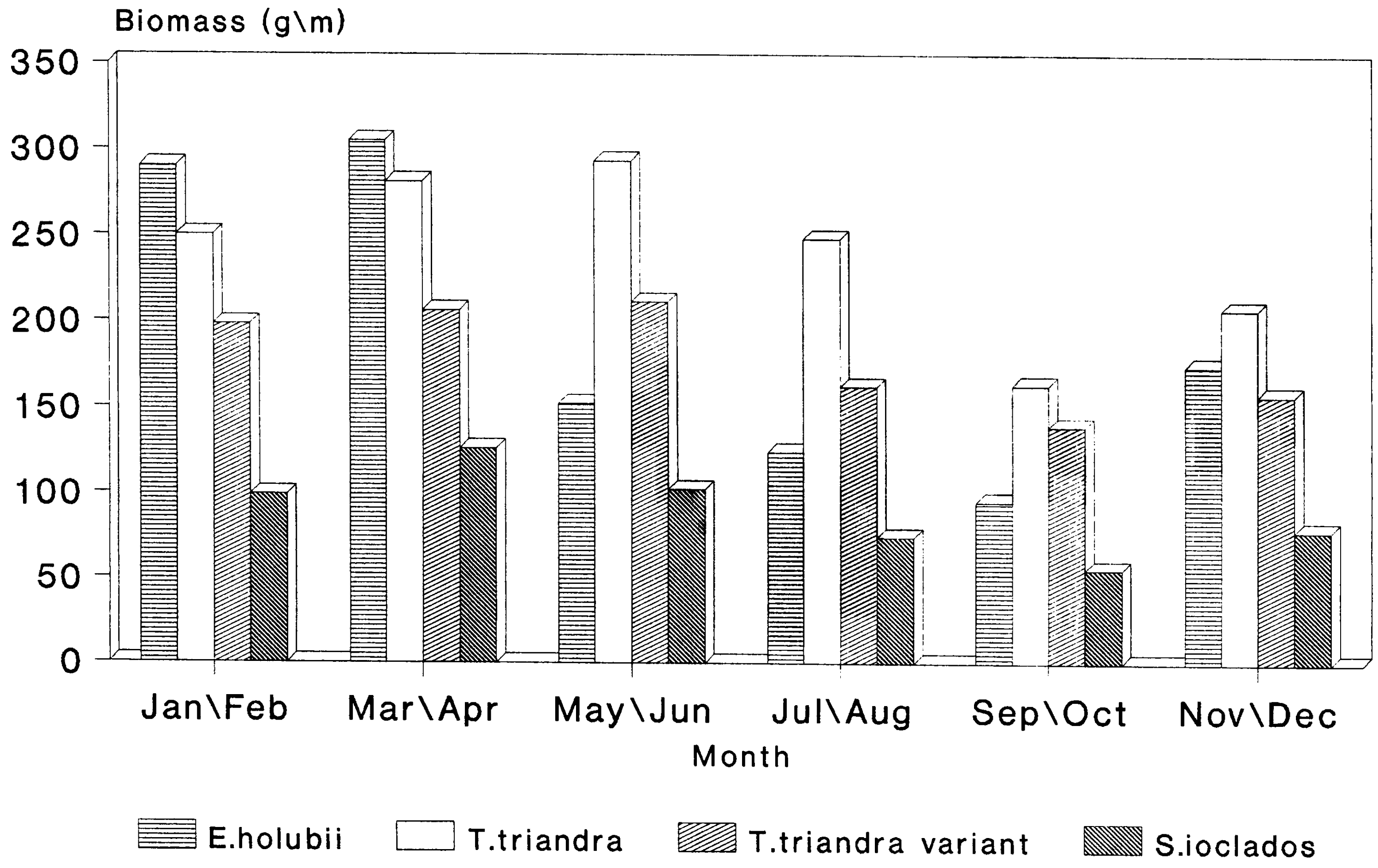


FIG.9. SEASONAL CHANGES IN THE PROTEIN CONTENT OF SELECTED MEDIUM-TALL GRASSES OF THE EASTERN ALLUVIAL FLOODPLAIN.

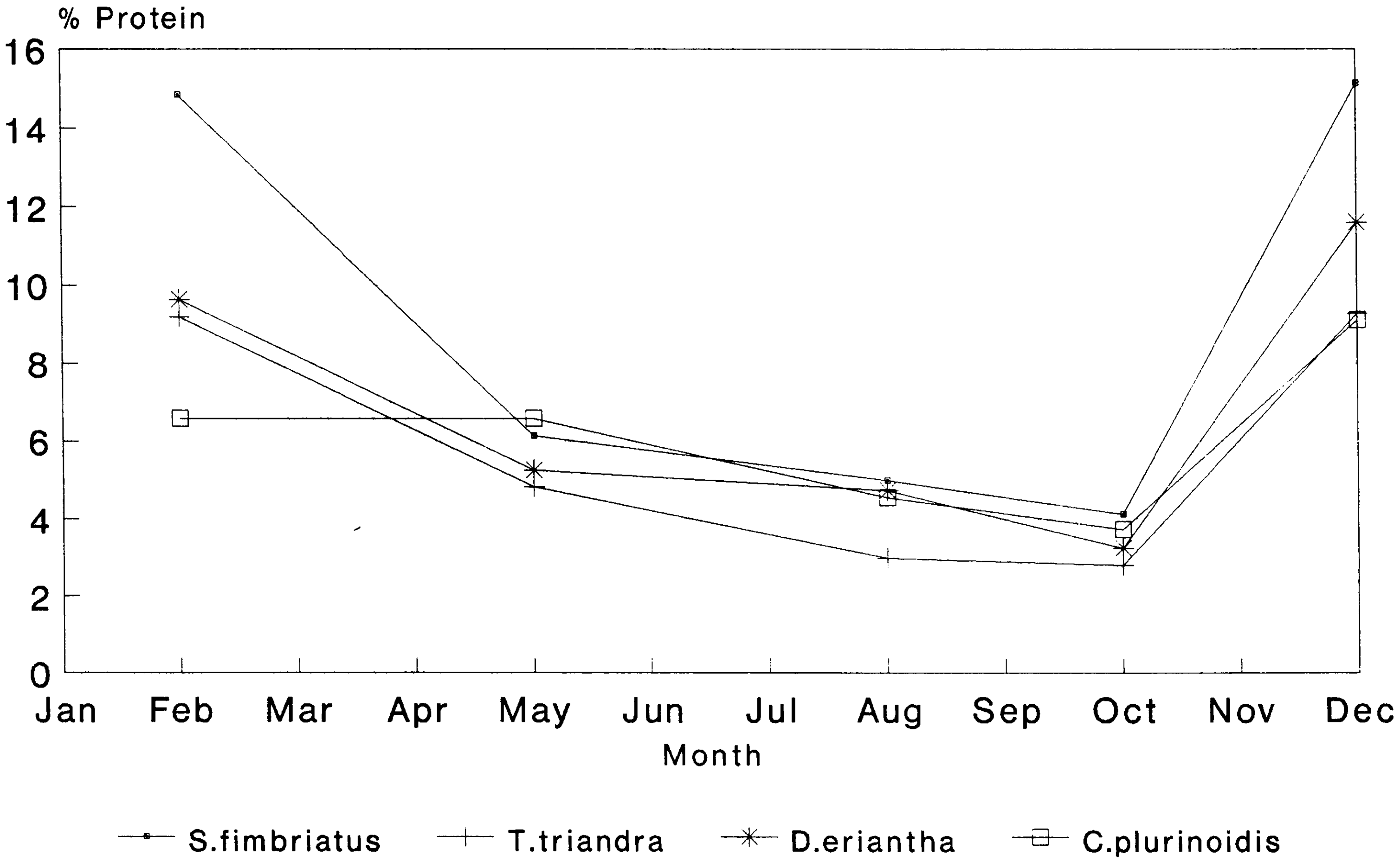


FIG.10. SEASONAL CHANGES IN THE PROTEIN CONTENT OF SELECTED SHORT-GRASS SPECIES OF THE EASTERN ALLUVIAL FLOODPLAIN.

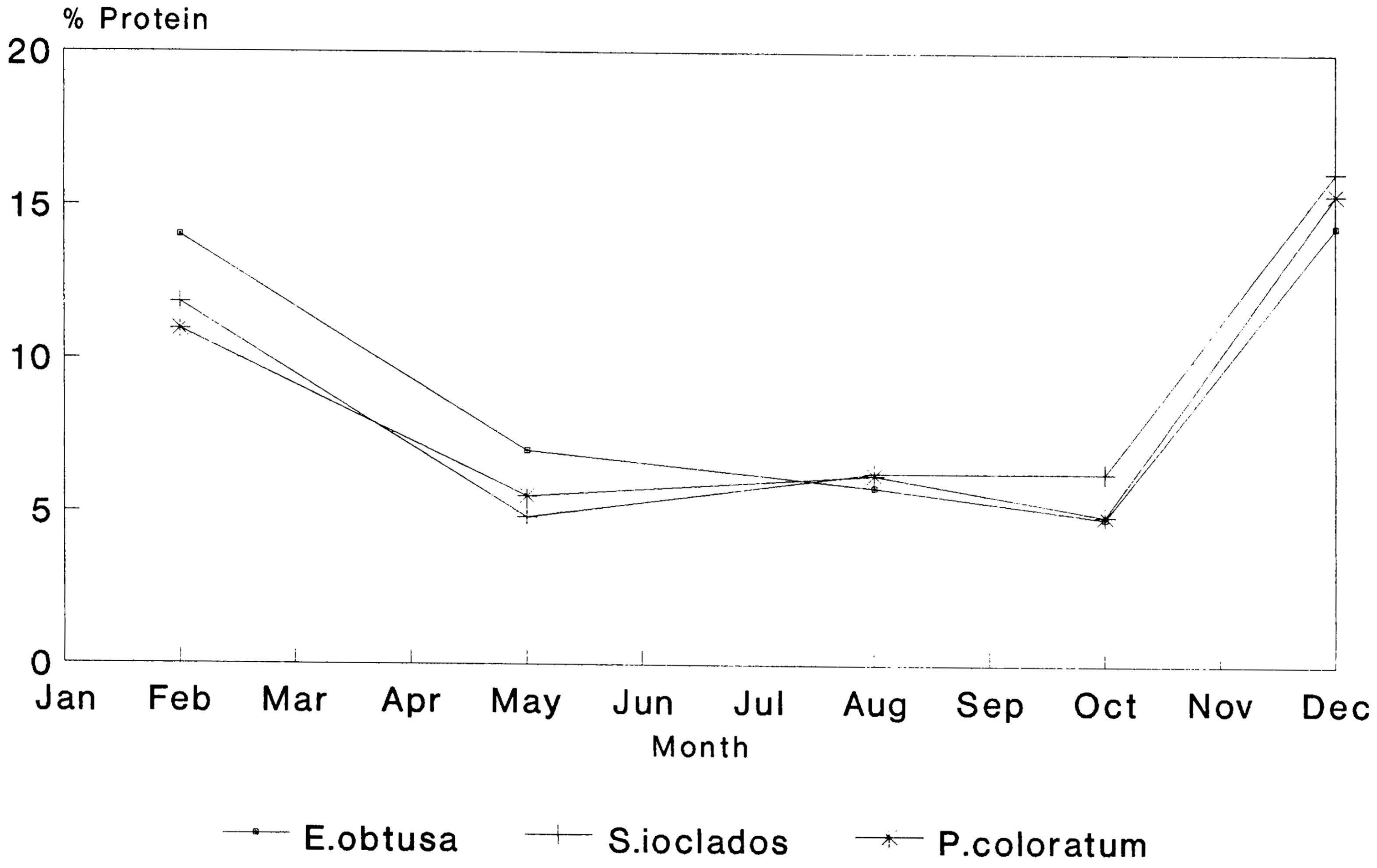


FIG.11. FREQUENCY OCCURRENCE OF SPLINTER GROUPS ON THE EASTERN ALLUVIAL FLOOD-PLAIN DURING LATE SUMMER AND AUTUMN.

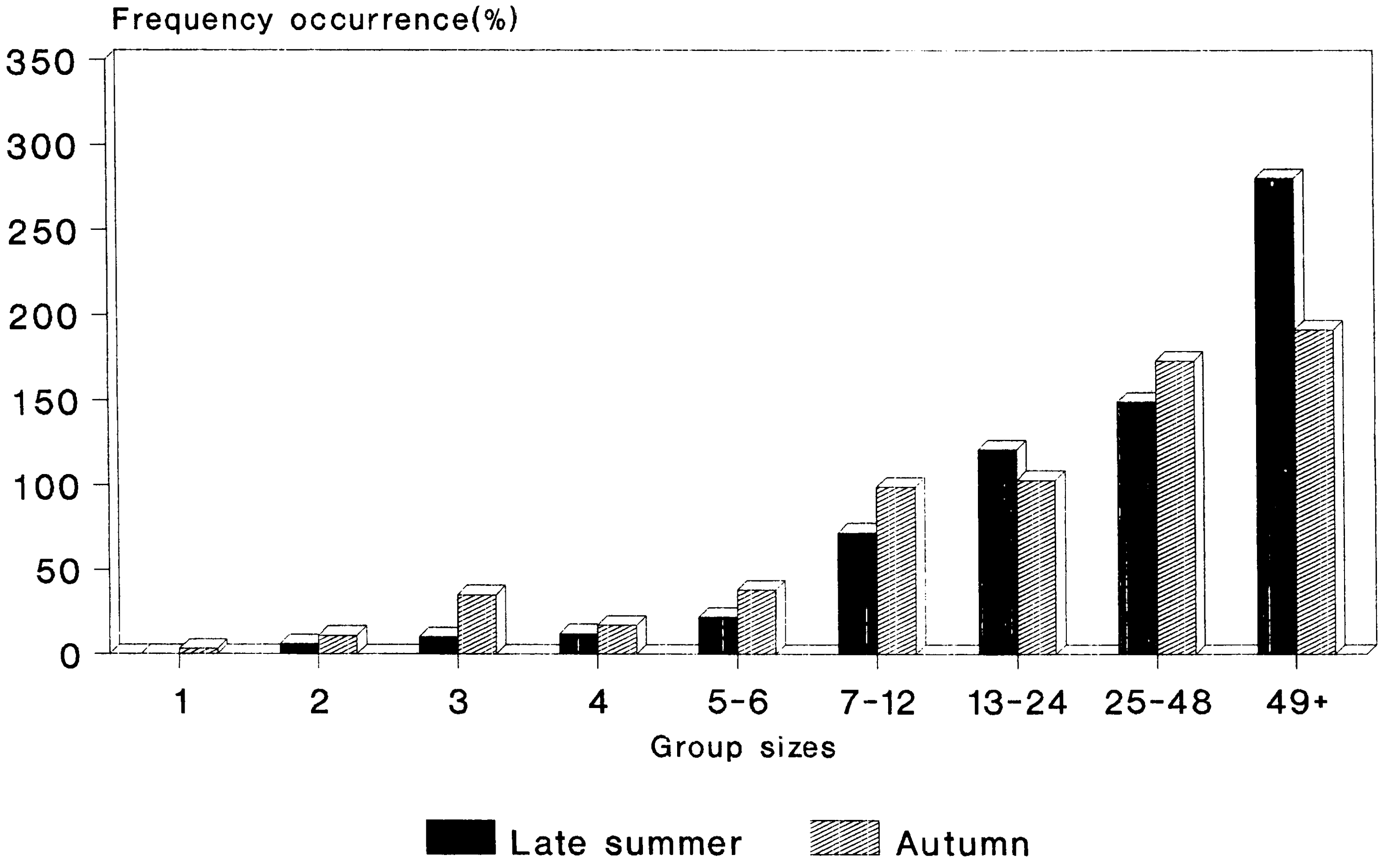


FIG.12. FREQUENCY OCCURRENCE OF SPLINTER GROUPS ON THE EASTERN ALLUVIAL FLOODPLAIN DURING WINTER AND SPRING.

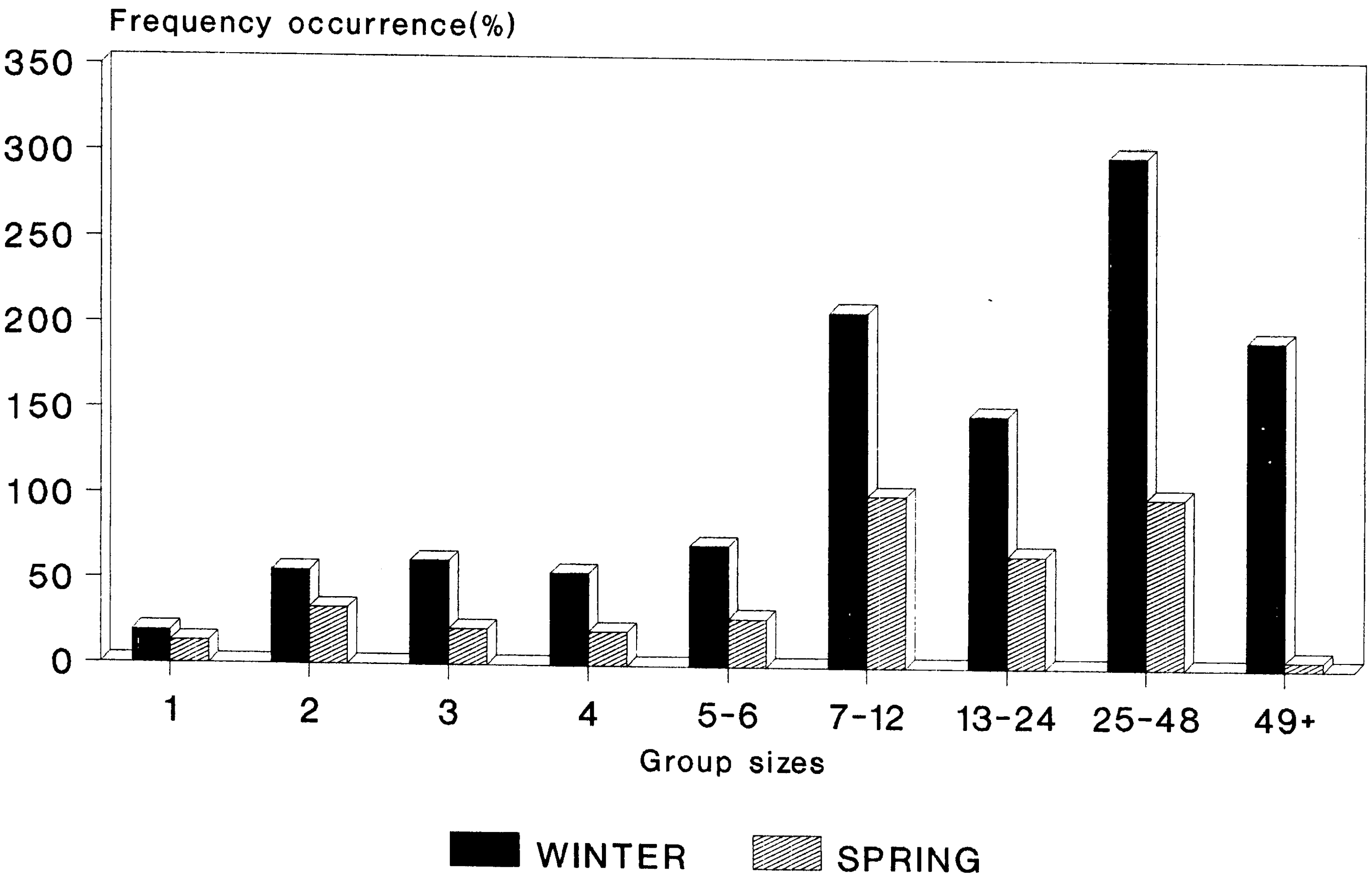


FIG.13. FREQUENCY OCCURRENCE OF SPLINTER GROUPS ON THE EASTERN ALLUVIAL FLOODPLAIN DURING EARLY SUMMER AND SUMMER.

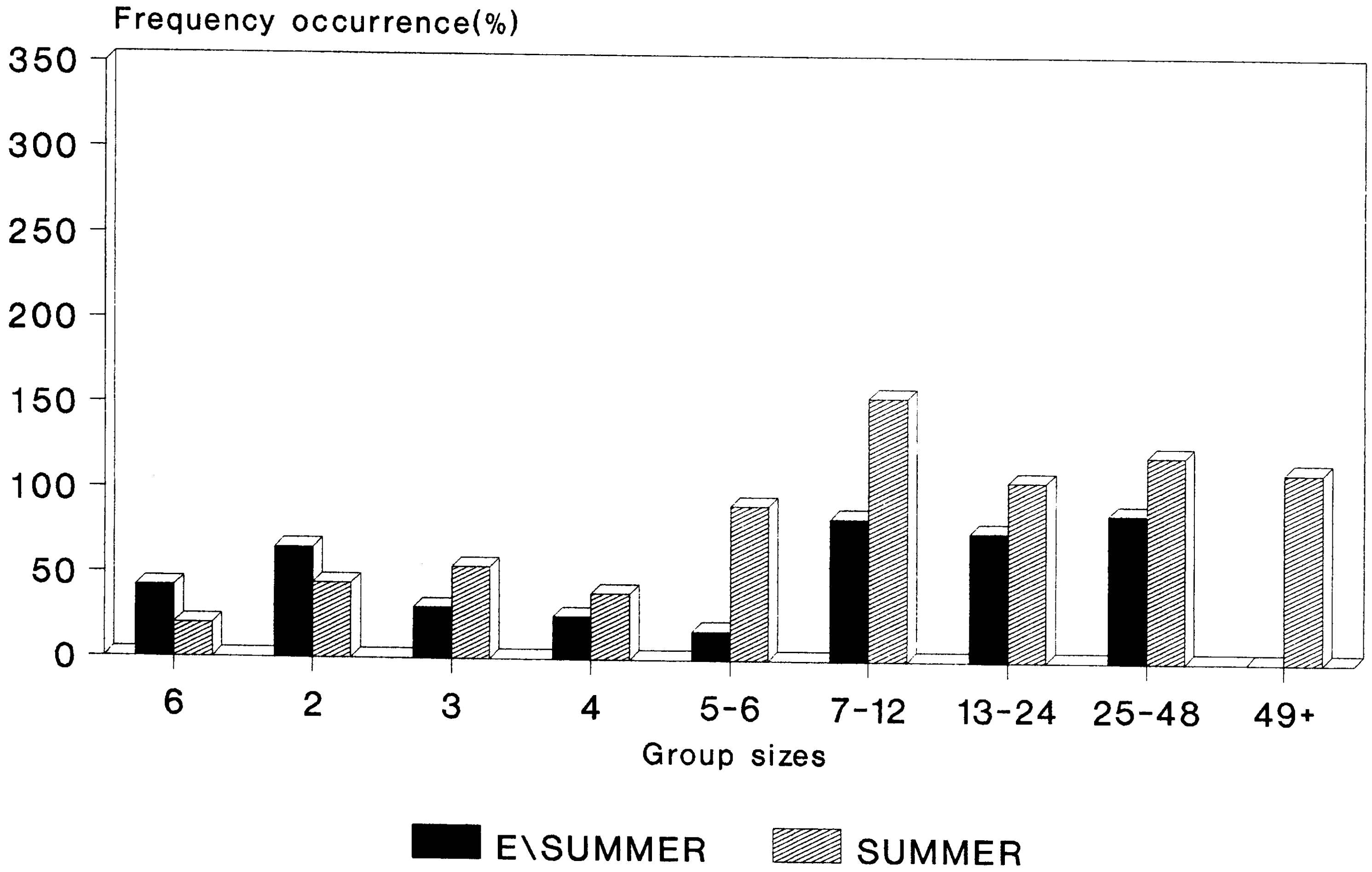


FIG.14. SEASONAL MEAN GROUP SIZE OF RED HARTEBEEST SPLINTER GROUPS.

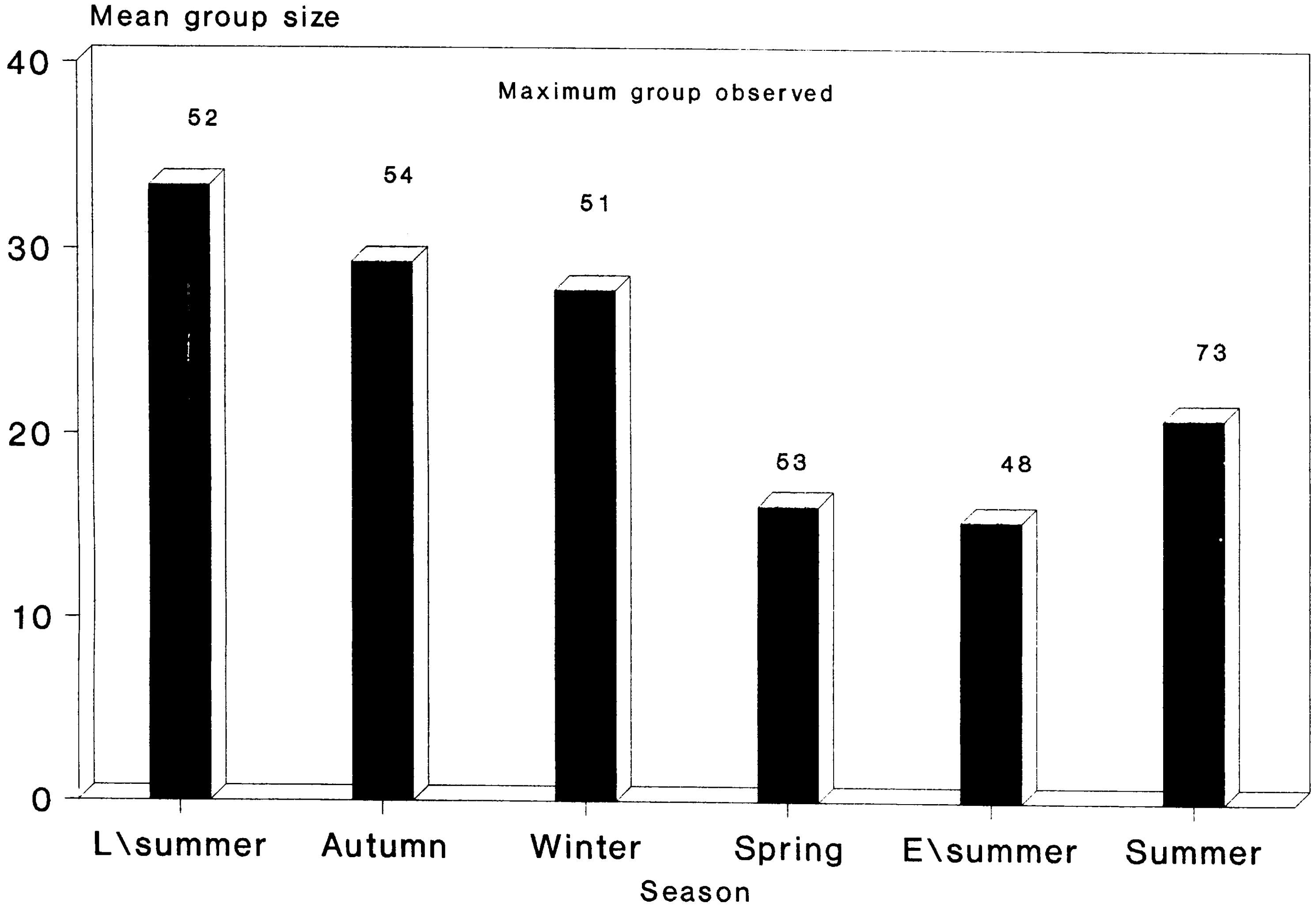
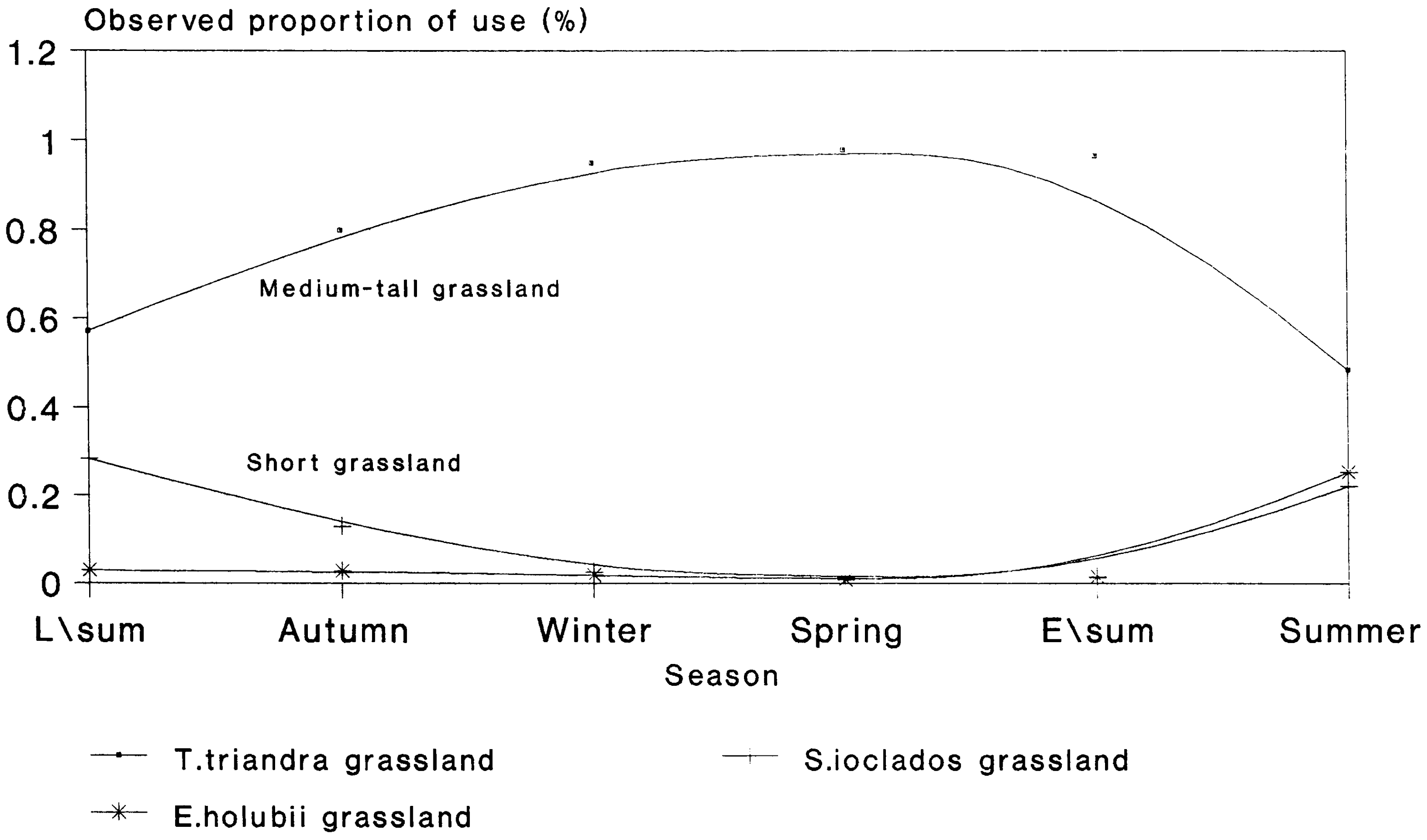


FIG.15. SEASONAL UTILISATION OF MEDIUM-TALL AND SHORT GRASSLAND COMMUNITIES BY RED HARTEBEEST.



CHAPTER 7

DIET SELECTION

INTRODUCTION

Quantitative and qualitative properties of grasses vary considerably during the seasonal cycle (Owaga 1980, Deshmukh 1986). Grasses have a short, active growing period, after which cell walls lignify as stems and leaves are formed, resulting in an increase of either partly or totally indigestible fibre (Weinmann 1959).

Buys (1987) indicated that the protein content of grasses in the non-growing season commonly declines below the 5% level, which Owen-Smith (1982) regards as the critical level necessary for the maintenance of cattle during the dry season. Consequently a large herbivore has to respond appropriately to these changes in order to meet its seasonal requirements.

In the present study no attempt was made to identify the selection criteria by which the choice of food items are made. The selection of food by mammals is a complex matter, involving flavour, taste, palatibility, colour and odour. It is often difficult to determine the controlling factor in situations where the detection system is so highly sophisticated (Harborne 1977).

A study of diet selection was possible only through the microscopic examination of plant fragments in the faeces. Putman (1984), in a review of the importance of faecal material in studies on herbivores, concluded that such material is readily available and collection causes no disturbance to the animals. The shyness of the red hartebeest herd under study precluded the use of other techniques for studying feeding selectivity and the collection of faecal material was considered the only viable option for studying their diet. A relatively small faecal sample (ca. 15) has been shown to give the same precision in estimating dietary composition when compared to 50 rumen samples (Anthony & Smith 1974).

The limitations of faecal analysis, the most important being the differential digestion of food items, have been discussed by Stewart (1967), as well as McInnes, Vavra & Krueger (1983).

Erasmus, Penzhorn & Fairall (1978) and Leslie & Starkey (1985) indicated that faecal nitrogen could be a reliable indicator of the nutritive quality of ingested food. The higher digestibility and transparent nature of the cellular structure of dicotyledenous material gives rise to the under-representation of the material in faecal samples (Zimmermann 1980, McInnes et al. 1983). Red hartebeest predominantly feed on grass, thereby minimizing the bias towards grass in the samples.

In this chapter an attempt was made to describe and interpret the feeding adaptations of red hartebeest to counter seasonal changes in nutrients.

METHODS

Ten fresh faecal samples were collected during the six observation periods. The samples were air dried, then oven dried to a constant mass at 50°C before chemical analyses were carried out.

Nutrient contents

The nitrogen content of the faeces was determined by means of the Kjeldahl method (A.O.A.C. 1975). The crude protein content was estimated by multiplying the nitrogen by a value of 6,25. The fibre contents were determined according to the methods described by Goering & Van Soest (1970). Three fibre fractions were analysed:

1. Neutral detergent fibre (NDF) which represents the total fibre contents.
2. Acid detergent fibre (ADF) which represents acid-soluble fibre.
3. Acid detergent lignin (ADL) which represents the indigestible lignin and cutin contents.

RESULTS AND DISCUSSION

Nutrient contents

The crude protein content of the faeces peaked during the wet humid period (Figure 16). During the winter period, the protein content declined, reaching a nadir in spring. With the onset of rains, the crude protein content increased rapidly. The crude protein content of the faecal material correlated positively with the dietary quality of grass ($r = 0.89$; $p<0.01$). This confirmed the suggestion by Erasmus et al. (1978) that faecal nitrogen is a reliable indicator of the ingested food material (Fig. 20). Hartebeest were found to graze almost exclusively throughout the seasonal cycle. The influence of ingesting dicotyledenous material was therefore minimal.

The % NDF and % ADF fibre fractions showed the same trend. These fractions reached their highest values during the winter months and declined to their lowest values during the summer months (Fig. 17 & 18).

The ADL content (Figure 19) of the faecal material is very difficult to interpret as one would expect ADL values to be highest during the most limiting period, which occurs just before the onset of the first rains. Grass quality, during this period, was suboptimal, especially in the tall Themeda grassland community which the red hartebeest favoured. The lower than expected ADL value could possibly be ascribed to the fact that some dicotyledenous material was included in their diet. The dicotyledons were found to be present in significant amounts only during the most limiting period of the year (Figure 21). It is thus suggested that the unexpecctedly high levels of dicotyledoneous material in the diet is an adaptive response to low rainfall periods. The higher nutrient intake level serve to alleviate the imposed constraints of lactation on the females.

The size of a ruminant mouth is likely to determine the degree of selectivity it can exercise over the plant material it includes in it's diet. (Owen-Smith, 1982; Janis & Ehrhardt, 1988). The relative width of the muzzle is relative to the degree of selectivity in the diet of ungulate species. The expectation is that grazers would have a relatively broader muzzle than browsers or mixed feeders, and that within grazers short-grass grazers would have relatively broader muzzles than tall grass grazers (Janis et al. 1988). Relating this to the present study, one could deduce that the relatively narrower muzzle width of red hartebeest allowed them to utilize the taller Themeda grassland in contrast to the relatively broader muzzle width of black wildebeest who specialized and outcompeted red hartebeest on the short Sporobolus grassland.

Surprisingly, Janis et al 1988 found that the tall grass specialists such as topi and hartebeest do not appear to have relatively narrower muzzles than do the short grass grazing wildebeest species (including black wildebeest). The hartebeest and topi do have narrower muzzles than the wildebeest but this difference appears to be related to the smaller body size.

Grazing ruminants, such as red hartebeest, tend to have a flatter incisor arcade as do similarly-sized browsers (Gordon & Illius 1988). The breadth of the incisor arcade is an important determinant of the rate of food intake for grazing ruminants (Illius & Gordon 1987). One could conclude that the oral morphology of red hartebeest is adapted to maximising the intake of forage during the limiting periods of the year. The narrower muzzles could aid red hartebeest in their selectivity for leaves in the medium-tall grasslands.

FIG.16. PROTEIN CONTENT OF RED HARTEBEEST FAECAL MATTER.

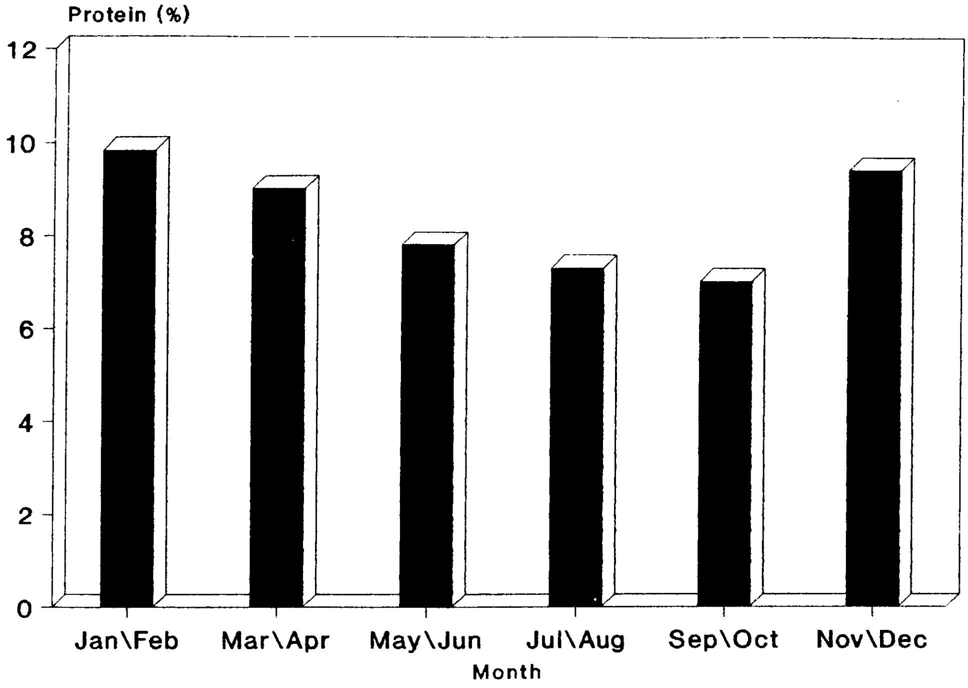


FIG.17. NDF CONTENT OF RED HARTEBEEST FAECAL MATTER.

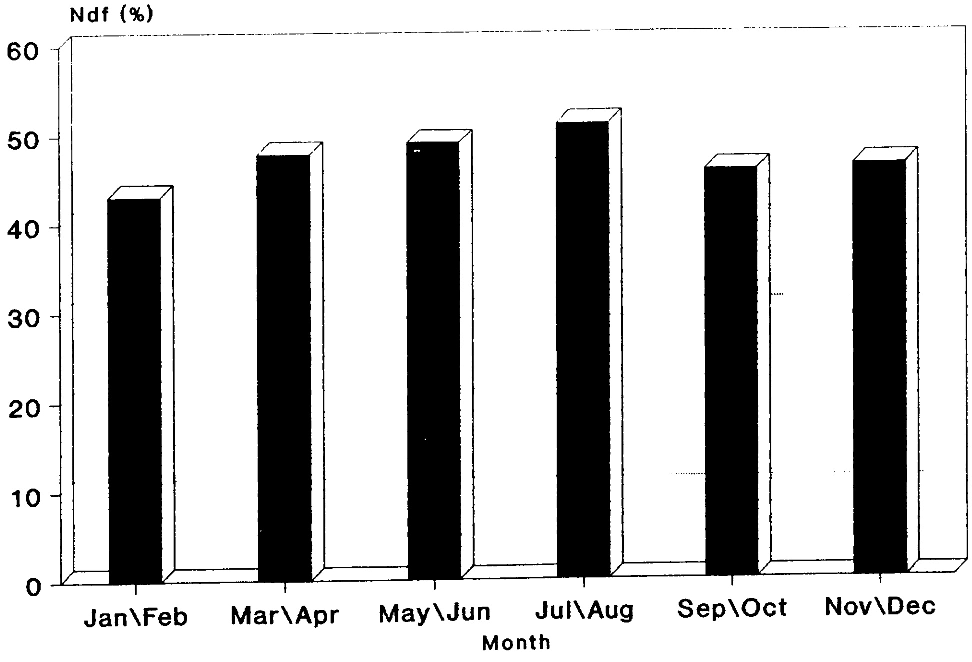


FIG.18. ADF CONTENT OF RED HARTEBEEST FAECAL MATTER.

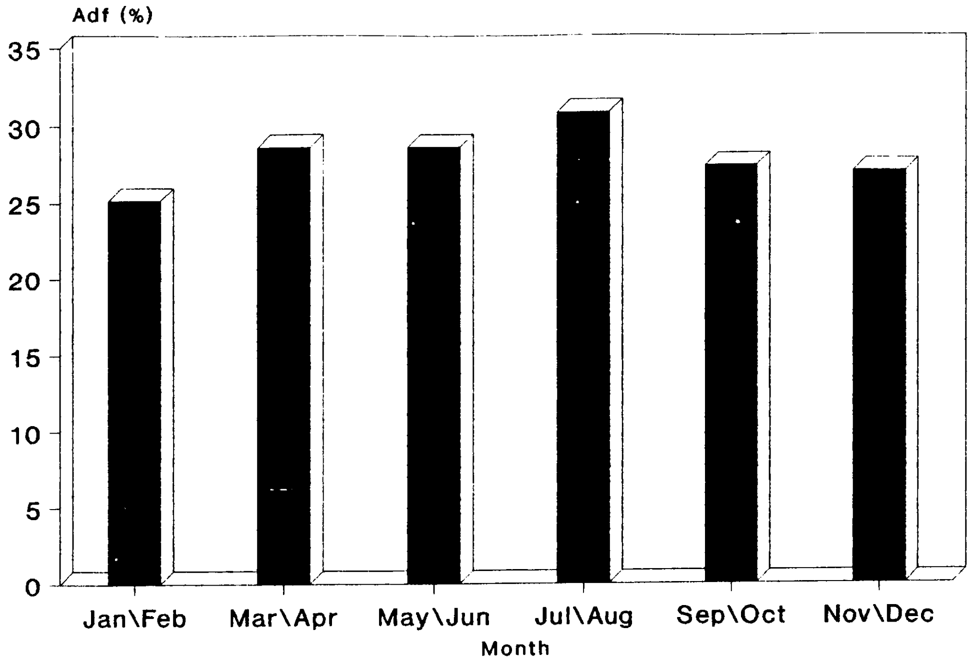


FIG.19. ADL CONTENT OF RED HARTEBEEST FAECAL MATTER.

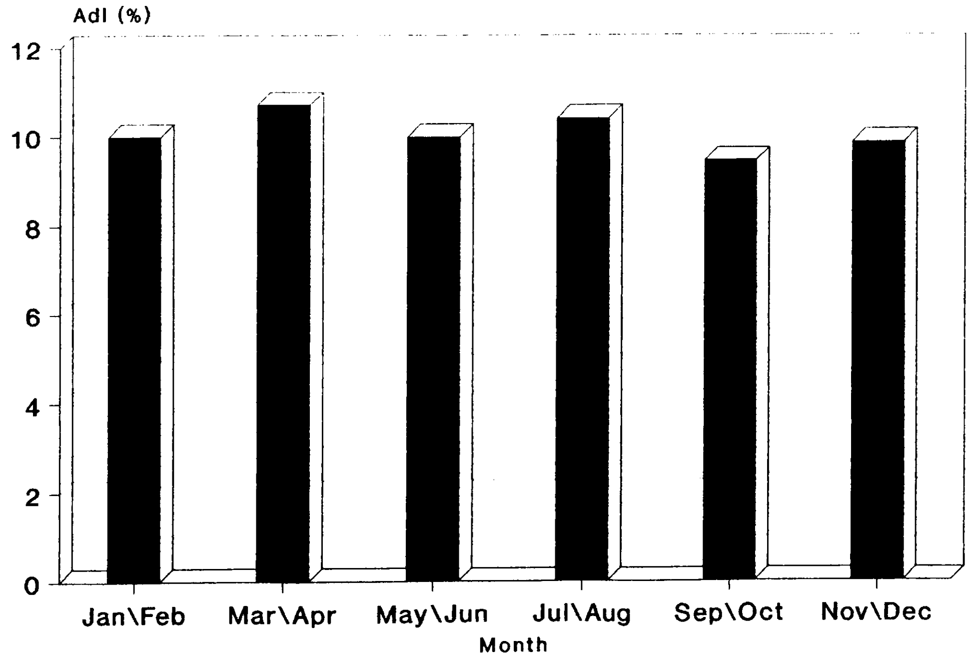
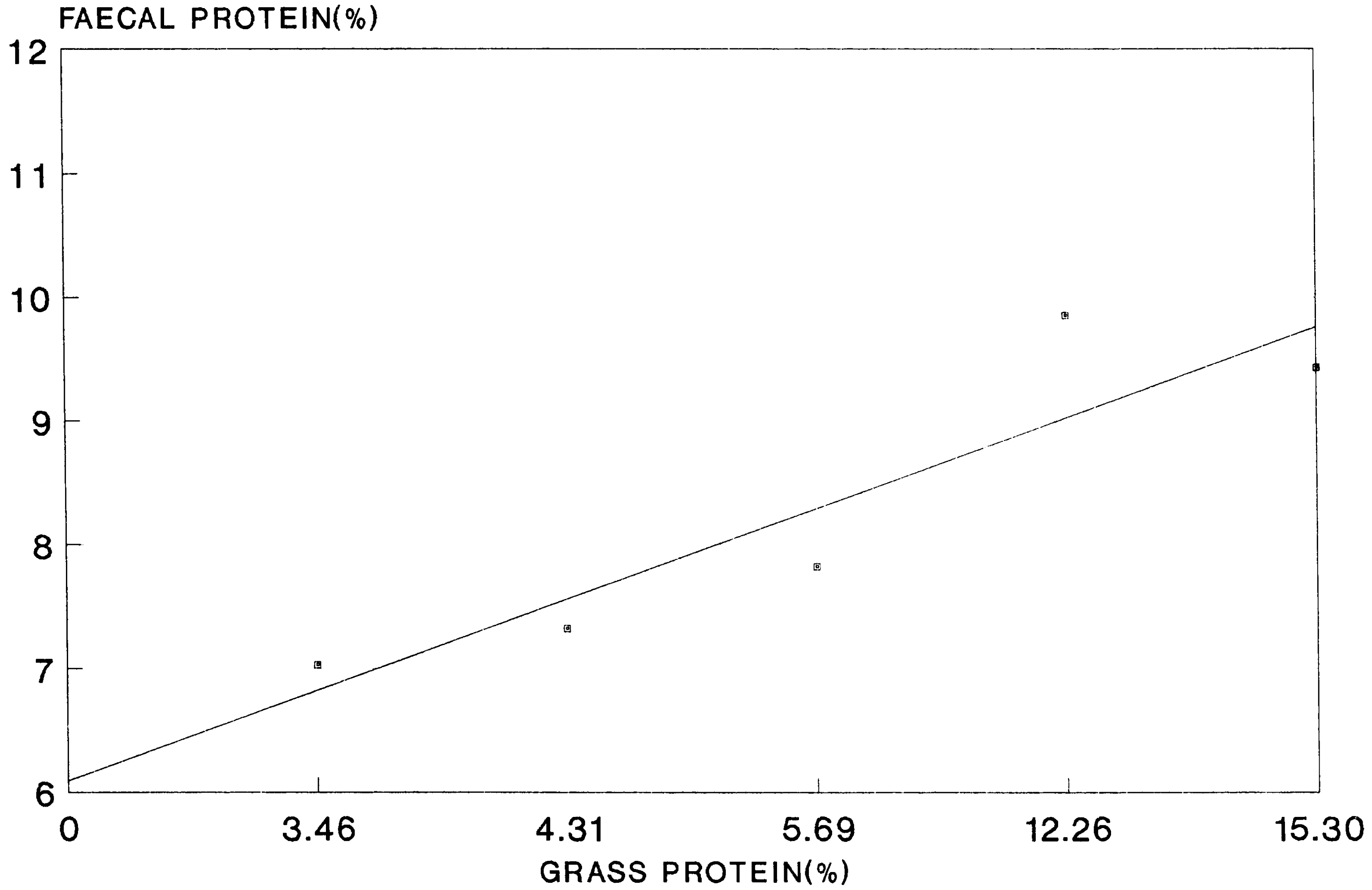
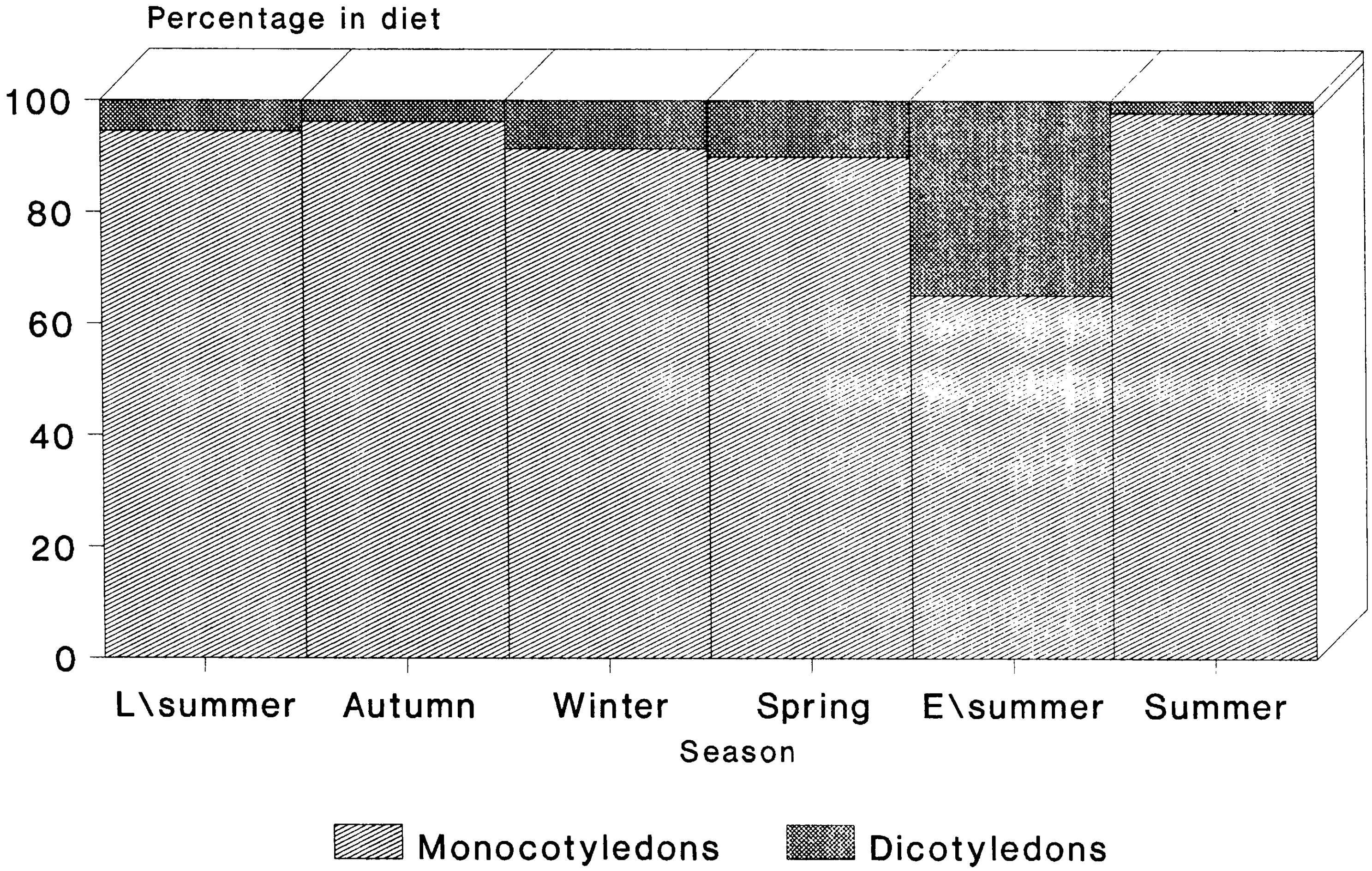


FIG.20. RELATIONSHIP BETWEEN GRASS PROTEIN AND FAECAL PROTEIN.



y = 6.412+0.228x
r = 0.945

FIG.21 . SEASONAL PERCENTAGE MONOCOTYLEDONS AND DICOTYLEDONS IN RED HARTEBEEST FAECAL MATTER.



CHAPTER 8

ACTIVITY PATTERNS

INTRODUCTION

In the preceding chapters, the magnitude of seasonal fluctuations in the food resource was illustrated as well as the subsequent utilization of space by the red hartebeest harem herd. Most animals have a limited amount of time in which to forage, because of the demands of other activities. Subsequently their fitness will be improved by increasing their energy intakes in their alotted foraging time (Schoener 1971).

The objective of this chapter was to assess the temporal responses of red hartebeest to fluctuations in quantitative and qualitative properties of the herb layer of the eastern alluvial floodplain. The impact of several physical variables on the activity patterns of the herd was additionally determined. The hypothesis that hartebeest, being roughage grazers, conserve energy by maximising food intake and minimising energy expenditure was developed for testing.

METHODS

Diurnal activity patterns

Due to several difficulties, no nocturnal activity could be recorded. Observations on the diurnal activity patterns commenced during the late summer period. As previously mentioned, the daily activities of the herd were monitored from the hides in the eastern alluvial floodplain. The use of the hides ensured that the harem herd was left undisturbed during the observations. If the herd happened to be disturbed due to human interference, observations were terminated for the remainder of the day. No focal animal studies were carried out.

The herd was located at dawn and observed until dusk. In the event of the herd being split or splitting up into district groups, observations were continued on the largest group. Group activity was recorded by scanning the harem herd at 5-min intervals during which all individuals were classified by the activity in which they were engaged.

Activity categories included feeding, walking, lying, standing, running and social interaction. Activities such as grooming, urinating and defaecating were grouped in a category "Other". Drinking could not be included into a category as the watering points were to some extent obscured from view from the hides. Related data included group size, sex and age composition. The data were recorded on computer coded tally sheets.

Physical factors

Weather data, recorded at 30-min intervals, included temperature, % cloudcover, windspeed, wind-direction and the presence or absence of rain. Temperature and % cloud cover were regarded as co-variates, thus contributing to explaining the variance of the activities, but not actually causing it.

Four categories for windspeed were recognized:

(i) 0 - no wind

(ii) 1 - slight wind

(iii) 2 - strong wind

(iv) 3 - very strong wind

Eight categories for wind-direction were recognized:

(i) 1 - North

(ii) 2 - North-east

(iii) 3 - East

(iv) 4 - South-east

(v) 5 - South

(vi) 6 - South-west

(vii) 7 - West

(viii) 8 - North-west.

Statistical methods

The data were analysed on the University of Pretoria computer using SAS handling procedures. An angular transformation (Rohlf & Sokal 1969) was used to normalize the percentage data.

Tukey's studentized (HSD) Range Test

This test was applied to the data set to determine:

i) the extent of seasonal differences in the activity categories

ii) which environmental variables exerted an influence on the activity categories within seasonal limits.

Analysis of Variance (ANOVA)

An Analysis of Variance was applied to the data set by means of SAS PROC GLM. The test was performed to assess the influence of the environmental variables on the different activity categories.

Pearson Correlation Coefficient (r)

The correlation coefficients were derived from the data set for estimating the contribution of temperature and % cloudcover on the diurnal activity patterns.

RESULTS

Diurnal activity patterns

The number of observations per season on the diurnal activity patterns of the herd is presented in Table 5. Seasonal activities expressed as percentages are presented in Table 6.

Table 5. Total number of observations on activites during the seasonal cycle.

Season	Late Summer	Autumn	Winter	Spring	Early Summer	Summer
Activity						
Feeding	1193	938	1804	534	577	852
Walking	1193	938	1804	534	577	852
Lying	1193	938	1804	534	577	852
Standing	1193	938	1804	534	577	852
Running	1193	938	1804	534	577	852
Social	1193	938	1804	534	577	852
Other	1193	938	1804	534	577	852

Table 6. Seasonal activities (%) during all seasons.

Season	Late Summer	Autumn	Winter	Spring	Early Summer	Summer
Activity						
Feeding	33,28	22,22	36,20	20,33	21,29	36,05
Walking	6,81	3,77	6,60	5,6	6,81	7,53
Lying	44,64	62,37	37,95	54,10	53,17	46,89
Standing	14,01	10,61	17,58	18,61	16,49	8,02
Running	0,25	0,44	0,12	0,14	0,13	0,12
Nursing	0,07	0,02	0,00	0,00	0,17	0,10
Social	0,51	0,14	0,33	0,10	0,22	0,28
Other	0,41	0,35	1,18	1,20	1,04	0,96

Feeding, walking, lying and standing accounted for more than 95% of all activities recorded annually.

Hartebeest exhibited a largely bimodal feeding activity pattern with pronounced peaks in the early morning and late afternoon (Fig. 22-24). The morning peak in feeding preceded a lengthy mid-morning to afternoon period of rest and rumination. Although feeding continued throughout this rest-rumination period, the degree of intensity was largely determined by the relevant season. Figs. 22-24 illustrate the seasonal differences in feeding and the extent of the feeding decline. During this decline in feeding, lying, followed by standing to a lesser extent, predominated in this period of rest.

Although a bimodal feeding pattern is evident throughout the seasonal cycle, several significant differences exist between the partitioning of hartebeest activities (Table 7). The values represent the difference between means, and between simultaneous upper and lower confidence limits.

Table 7. Comparison of significant differences between seasonal activities.

	Late Summer	Autumn	Winter	Spring	Early Summer	Summer
<u>Feeding</u>						
Late summer	0					
Autumn	-0,117*	0				
Winter	0,033*	0,150*	0			
Spring	-0,141*	ns	-0,174*	0		
Early Summer	-0,127*	ns	-0,160*	ns	0	
Summer	ns	0,136*	ns	0,159*	145*	0
<u>Walking</u>						
Late summer	0					
Autumn	-0,033*	0				
Winter	ns	0,028*	0			
Spring	ns	ns	ns	0		
Early Summer	ns	0,036*	ns	ns	0	
Summer	ns	0,037*	ns	ns	ns*	0
<u>Lying</u>						
Late summer	0					
Autumn	0,291*	0				
Winter	-0,053*	-0,345*	0			
Spring	0,187*	-0,104*	0,241*	0		
Early Summer	0,166*	-0,125*	0,219*	ns	0	
Summer	ns	-0,286*	0,059*	-0,182*	-0,160*	0
<u>Standing</u>						
Late summer	0					
Autumn	-0,036*	0				
Winter	-0,034*	0,071*	0			
Spring	0,048*	-0,085*	ns	0		
Early Summer	0,027*	-0,064*	ns	ns	0	
Summer	-0,065*	-0,286*	-0,099*	-0,113*	-0,093*	0
<u>Running</u>						
Late summer	0					
Autumn	ns	0				
Winter	ns	-0,003*	0			
Spring	ns	ns	ns	0		
Early Summer	ns	ns	ns	ns	0	
Summer	ns	ns	ns	ns	ns	0
<u>Nursing</u>						
Late summer	0					
Autumn	ns	0				
Winter	-0,001*	ns	0			
Spring	-0,001*	ns	ns	0		
Early Summer	0,001	0,001*	0,001*	0,001*	0	
Summer	ns	0,001*	0,001*	0,001*	-0,001*	0

	Late Summer	Autumn	Winter	Spring	Early Summer	Summer
Social interaction						
Late summer	0					
Autumn	-0,003*	0				
Winter	-0,001*	0,001*	0			
Spring	-0,004*	ns	-0,002*	0		
Early Summer	-0,002*	ns	ns	ns	0	
Summer	-0,002*	ns	ns	ns	ns	0
Other						
Late summer	0					
Autumn	ns	0				
Winter	-0,007*	0,008*	0			
Spring	-0,007*	0,008*	ns	0		
Early Summer	-0,006*	0,007*	ns	ns	0	
Summer	-0,005*	0,006*	ns	ns	ns	0

Comparisons significant at P<0,05 are indicated with *.

During the hot wet summer months, red hartebeest maintained high levels of feeding. These feeding levels were significantly higher than the levels during the intermediate season (Autumn) and the dry warm season (Spring and Early Summer). During the latter three seasons, feeding declined sharply to levels of 20-22%. In contrast to the dry, warm season red hartebeest spent significantly more time feeding (36%) during the cold, dry months. No significant difference in time spent feeding existed between early summer and winter. Hartebeest spent significantly less time feeding during late summer, compared to winter.

The occurrence of lying was significantly higher during autumn than all other seasons sampled. In contrast, significantly less time was spent lying in winter than all other seasons. The incidence of lying was significantly higher during the warm dry periods than the hot dry periods.

Hartebeest spent significantly less time walking during autumn than all other seasons, except spring. The occurrence of running was significantly higher during autumn, compared to winter. The frequency occurrence of running was low during all seasons.

The amount of time devoted to nursing was found to be significantly higher during early summer than all other seasons. Nursing declined gradually from early summer up to autumn and winter, when a significant depression occurred.

During late summer, social interactions among herd members increased to significantly high levels, while other seasons experienced significant depressions in this activity category.

Physical factors

The effect of physical factors influencing diurnal activity patterns is presented in Table 8. Comparisons significant at the 5% level (p<0,05) are indicated by *.

Table 8. Results of ANOVA for the comparison of activities influenced by factors and co-factors.

	Factors			Co-factors		
Activity	Windspeed	Wind-direction	Rain	Time	Temperature	Cloud cover %
Late Summer						
Feeding	0,3825	0,0001*	0,8775	0,0001*	0,0001*	0,4803
Walking	0,3109	0,0001*	0,6784	0,0001*	0,0001*	0,5206
Lying	0,0001*	0,0001*	0,0001*	0,0001*	0,7272	0,2292
Standing	0,0001*	0,0783	0,0001*	0,0001*	0,0001*	0,0032*
Running	0,9511	0,9937	0,7986	0,0632	0,0085	0,5591
Nursing	0,3755	0,4653	0,5889	0,1064	0,3215	0,7272
Social	0,0013*	0,0098	0,4642	0,0004*	0,1873	0,0001*
Other	0,5362	0,7453	0,4919	0,0908	0,4484	0,9712

		Factors			Co-factors	
Activity	Windspeed	Wind-direction	Rain	Time	Temperature	Cloud cover %
Autumn						
Feeding	0,0140*	0,0001*	0,0001	*0,0001*	0,5373	0,7026
Walking	0,2606	0,0204*	0,74340	0,0001*	0,0443*	0,7016
Lying	0,2979*	0,0001*	0,0160*	0,0001*	0,0835	0,0692
Standing	0,8468	0,0001*	0,7982	0,0001*	0,0001*	0,9468
Running	0,4410	0,9208	0,9794	0,0240*	0,8944	0,1294
Nursing	0,8823	0,9710	0,4851	0,0008	0,7158	0,0106*
Social	0,3825*	0,2670	0,7441	0,0004*	0,7653	0,8496
Other	0,0137	0,1798	0,5165	0,4015	0,0001*	0,0015
Winter						
Feeding	0,0036*	0,0178*	-	0,0001*	0,3858	0,0848
Walking	0,4795	0,1313*	-	0,0001*	0,1834*	0,2112
Lying	0,0001*	0,0001*	-	0,0001*	0.0332*	0,0047
Standing	0,0426*	0,0001*	-	0,0001*	0,0001*	0,8197
Running	0,6015	0,0001*	-	0,6778	0,5772	0,4306
Nursing	0,7276	0,9990	-	0,4777	0,4504	0,8474
Social	0,6601*	0,0571	-	0,3462	0,1208	0,5123
Other	0,0413*	0,0058	-	0,0001*	0,2474*	0,9416
Spring						
Feeding	0,0001*	0,0177*	0,7499	0,0001*	0,4801	0,7532
Walking	0,2914	0,0002*	0,7902	0,0001*	0,0008*	0,9818
Lying	0,0001*	0,0001*	0,0170	0,0001*	0.0002*	0,0034*
Standing	0,0001*	0,0001*	0,0490	0,0001*	0,0020*	0,9800
Running	0,6448	0,4185*	0,9475	0,4350	0,1048	0,9800
Nursing	0,6150	0,1869	0,9820	0,7021	0,9648	0,4344
Social	0,0280*	0,4913	0,9114	0,3292	0,0857	0,4496
Other	0,2424*	0,0651	0,6554	0,0007*	0,0886*	0,4969
Early Summer						
Feeding	0,0675*	0,0001*	0,4523	0,0001*	0,0585	0,0103*
Walking	0,5047	0,9252*	0,0078	0,0001*	0,0015*	0,0063*
Lying	0,8044*	0,0001*	0,6878	0,0001*	0.7537*	0,0256*
Standing	0,0273*	0,0001*	0,9035	0,0001*	0,5145*	0,3739
Running	0,5267	0,2128*	0,9084	0,0309*	0,1584	0,0482*
Nursing	0,5086	0,9507	0,6566	0,0673	0,9856	0,0626
Social	0,8282*	0,2142	0,9105	0,4228	0,8819	0,4158
Other	0,7009*	0,4175	0,5705	0,2336	0,0290*	0,0023*
Summer						
Feeding	0,0786*	0,0001*	0,1823	0,0001*	0,0001*	0,5394*
Walking	0,0357	0,1503*	0,2772	0,0001*	0,0001*	0,1368*
Lying	0,0001*	0,0001*	0,1562	0,0001*	0.0001*	0,5326*
Standing	0,1313*	0,0008*	0,6946	0,0001*	0,0458*	0,3528
Running	0,7367	0,0984*	0,4467	0,0001*	0,0046*	0,7798*
Nursing	0,6223	0,8369	0,9436	0,0129*	0,9183	0,6826
Social	0,3021*	0,4089	0,7391	0,1842	0,9955	0,5794
Other	0,9018*	0,8397	0,9927	0,0995	0,1592	0,1079

Time as a variable was an important force in determining the four major activities of red hartebeest, irrespective of the seasonal variation in photoperiod. Windspeed and wind-direction elicited significant responses from red hartebeest, mainly in the four major seasonal activities. Windspeed, wind-direction, temperature and % cloud cover, as factors and co-factors, respectively, might act in combination to determine the activity regimes.

The influence of temperature on the seasonal diurnal activity pattern is presented in Table 9. Percentage cloudcover did not elicit any direct or obvious response from red hartebeest and is thus omitted from the discussion.

Table 9 The influence of temperature on the daily activity patterns of red hartebeest as determined by the Pearson correlation coefficient(r). Significant correlations ($p<0.05$) are indicated by *.

Season	Late Summer	Autumn	Winter	Spring	Early Summer	Summer
Activity						
Feeding	-0,410*	-0,438*	-0,280*	-0,443*	-0,502*	-0,435*
Walking	0,061	-0,142*	-0,075	-0,295*	-0,030	-0,127
Lying	0,370*	0,558*	0,275*	0,499*	0,486*	0,441*
Standing	-0,050	-0,432*	-0,046	-0,132	-0,246*	-0,041
Running	0,037	-0,068	0,021	-0,064	-0,046	-0,022
Nursing	-0,072	0,056	0,000	-0,000	-0,091	-0,031
Social	-0,289*	-0,118	0,010	-0,089	-0,083	-0,081
Other	-0,113*	-0,186	-0,047	-0,089	-0,129	-0,225*

Although the relationship between temperature and the seasonal activities is not high, it is indicative that temperature contributed significantly to explaining the variance of some of the seasonal activities. An inverse relationship between temperature and seasonal % feeding is evident from Table 9. In contrast, a positive correlation was illustrated between temperature and % lying.

DISCUSSION

Daily activity patterns

Consistent with all seasons, time of day (photoperiod) is implicated as being the proximate cause which determined peaks of feeding activity, at dawn and dusk. Peaks in feeding coincided with sunrise and sunset times on the SALNR (Fig 25). Alternatively, temperature, inversely correlated with feeding, contributed largely to the depressions in the diurnal feeding pattern. These findings agree with those of Berry, Siegfried & Crowe (1982) in a study on seasonal activity patterns of blue wildebeest at Etosha National Park, Namibia.

During all seasons, the members of the harem herd were found to be highly synchronous in the respective activity categories. The synchrony within herds is probably a function of social behaviour, causing the herd to be cohesive in its temporal activities.

During the hot, wet summer months, an abundance of food items is available to red hartebeest. The high qualitative and quantitative properties of grass are reflected in the length of time spent feeding, as well as the intensity of the feeding peaks. The nutrient components of grass serve to facilitate the digestive process, which in turn ensures a high turnover rate in rumen contents. The high occurrence of nursing induced high demands on the lactating females to maintain a positive energy balance. The females reacted to these demands by prolonging the foraging periods. Murray (1991) concluded that incremental heat production in locomotion constitutes a major constraint on the optimum level of diet selection and maximum energy retention. The extensive daily movement patterns (Fig. 26 & 28) during the hot, wet summer period suggest that hartebeest feed selectively despite the constraints of locomotion.

Temperature, inversely correlated with % feeding (r = -0,410 for late summer; r = 0,435 for summer) and positively correlated with lying (r = +0,371; r = +0,0441), contributed significantly to the mid-afternoon depression in the % feeding. The weekly correlations could probably be ascribed to the pelage properties of red hartebeest. Hofmeyr (1985) indicated that the thermal properties of the pelage, including thickness and a low absorbance rate, provide significant protection against solar gain. These qualities indicated their adaptability to hot, arid climates. The frequency occurrence of temperatures during the entire observation period (Fig. 29) is indicative of the low exposure of red hartebeest in the western Transvaal Highveld to high extremes of temperature. The significantly high social interactions could be ascribed to rutting, which was most prevalent during the late summer period.

Apart from a little rainfall in May, no rain fell during winter. Intuitively one might expect red hartebeest to exhibit depressed levels of feeding during the dry, cold winter period, due to digestive constraints incurred by the low nutrient content of grass. Moreover, Du Plessis (1968) recorded a marked reduction in activity of blesbok in winter compared to summer, indicative of energy conservation during periods of stress. In contrast the increased feeding levels and daily movement patterns (Figs. 26 & 28) by red hartebeest in the hot, wet season seemed to be indicative of selective feeding. The short periods of lying suggest a higher rate of food passage resulting from the ingestion of more digestible matter.

Selective feeding, concomitant with high energy expenditure, could be interpreted by both social and physical factors. The energetic cost of nursing is minimised when calves have been weaned. The negligible contribution of mild temperatures to explain the variance in the activities, were reflected in the weakly correlated relationship with feeding (r = 0,28) and lying (r = 0,275). The mild temperatures during the winter period, facilitated the prolonged foraging periods, concomitant with the extensive daily movement patterns (Fig. 27).

No rainfall was recorded for spring, indicative of below average rainfall. The significantly depressed levels of feeding and the relatively shorter daily distances moved (Fig. 27), suggest that red hartebeest increased food intake and reduced energy expenditure. Subsequently, the ingestion of low quality grass led to rumenfill being attained in the shortest possible period. One could therefore deduce from these results that the costs of locomotion have become prohibitively high, as opposed to winter and particularly summer. Although no calves were born during this period of temporal observations, spring heralds the onset of parturition, with the concomitant increased burden of nursing on the females, when the intermediate to warm temperatures, compared to winter, correlated moderately higher with feeding (r = 0,443) and lying (r = 0,499).

Only 11,4% of the total rainfall for the early summer period was recorded during the period of observation on the herd. The highest environmental constraints were thus imposed on the herd during this period. The low quantitative and qualitative properties of grass were reflected in both the short periods devoted to feeding and long periods of lying. Hartebeest thereby conserve energy, similar to behaviour in spring, but more pronounced. The energy requirements of females reached maximum levels due to the high demands of nursing. The relationship between feeding and ambient temperature was r = -0,502, indicating the most significant correlation for all seasons.

In contrast to other seasons, the interpretation of the results obtained during autumn, presented several anomalies. During 1985, less rain was recorded for the period March/April than the mean rainfall for this period over 25 years. However, February received an above average rainfall compared to the 25 year mean. The effect of the rainfall in February was manifested in the high biomass values of the grassland communities. Climatically autumn compared favourably with the hot, wet summer months. The moderate temperatures and relatively low demand from nursing suggested that hartebeest would feed selectively. Despite the climatic similarities with the summer months, hartebeest maximised food intake and reduced energy consumption. The magnitude of the feeding depression and the corresponding peak in lying, similar to early summer, corroborate the assumption of non-selective feeding.

As previously illustrated, the eastern alluvial floodplain consists of a mosaic of tall and short grass patches. Due to the above average rainfall, the increase in the biomass of the short S. ioclados grassland community might have enabled hartebeest to sustain themselves for longer periods on the highly nutritious short grasses. During average rainfall periods, the denudation process of short grasses is accelerated, resulting in hartebeest moving to the less nutritious tall grassland areas.

To summarize, hartebeest adjusted their energy budgets to seasonal fluctuations by:

i) increasing the foraging effort during the hot wet summer periods and the cold dry winter periods.

ii) decreasing the foraging effort during autumn and the early summer period preceding the onset of the rainy season.

The foraging adaptations were aided by the availablity of free draining water and the pelage properties of the red hartebeest (Finch 1972). The flexibility in adapting feeding behaviour under varying stressful environmental conditions, is indicative of the adaptability of red hartebeest on the western Transvaal Highveld.

The hypothesis that red hartebeest are bulk feeders is supported during periods of stress, but rejected during optimal environmental conditions, when selective feeding is more appropriate.

FIG.22. DIURNAL FEEDING ACTIVITY OF RED HARTEBEEST DURING LATE SUMMER AND AUTUMN.

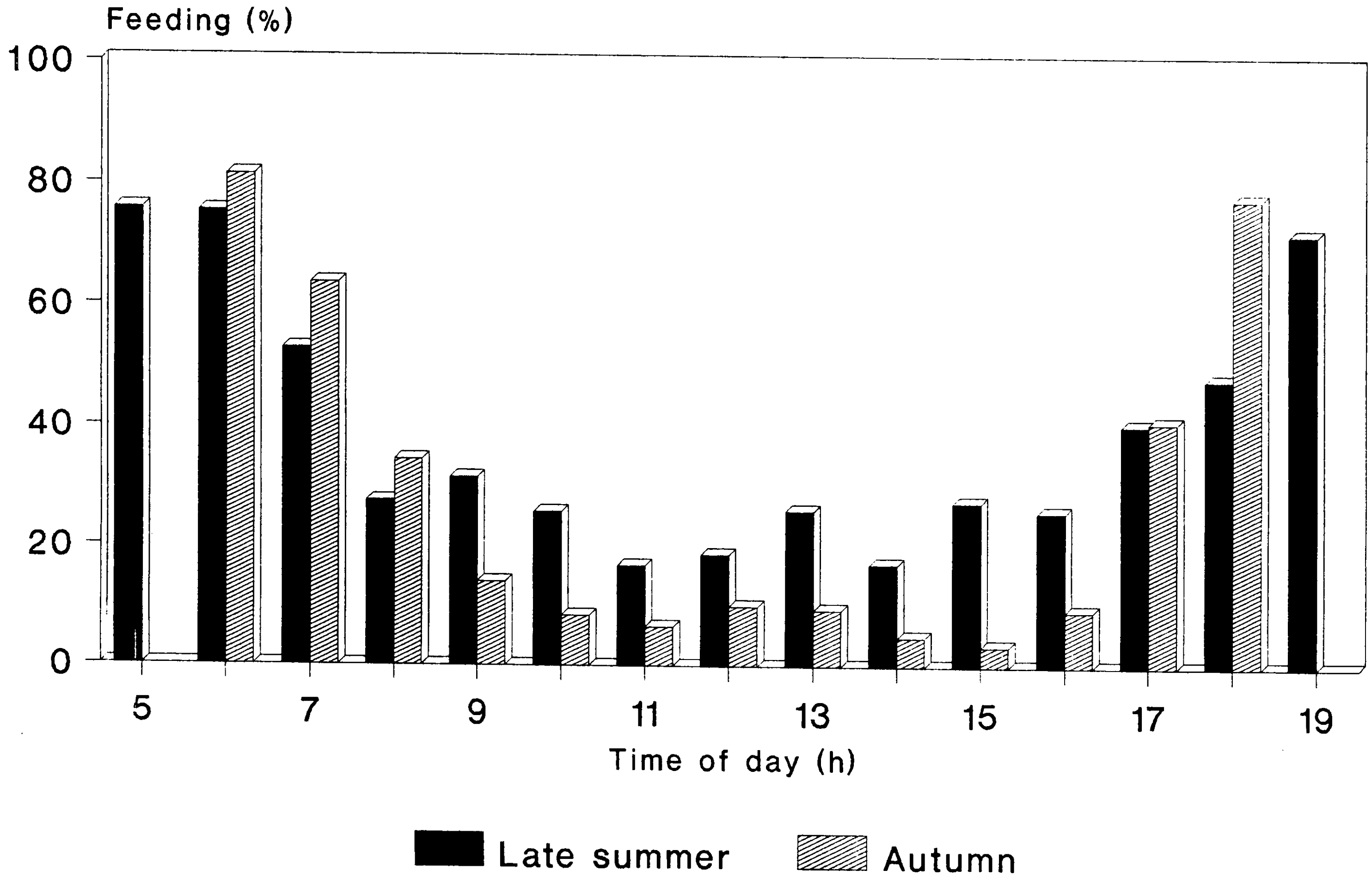


FIG.23. DIURNAL FEEDING ACTIVITY OF RED HARTEBEEST DURING WINTER AND SPRING.

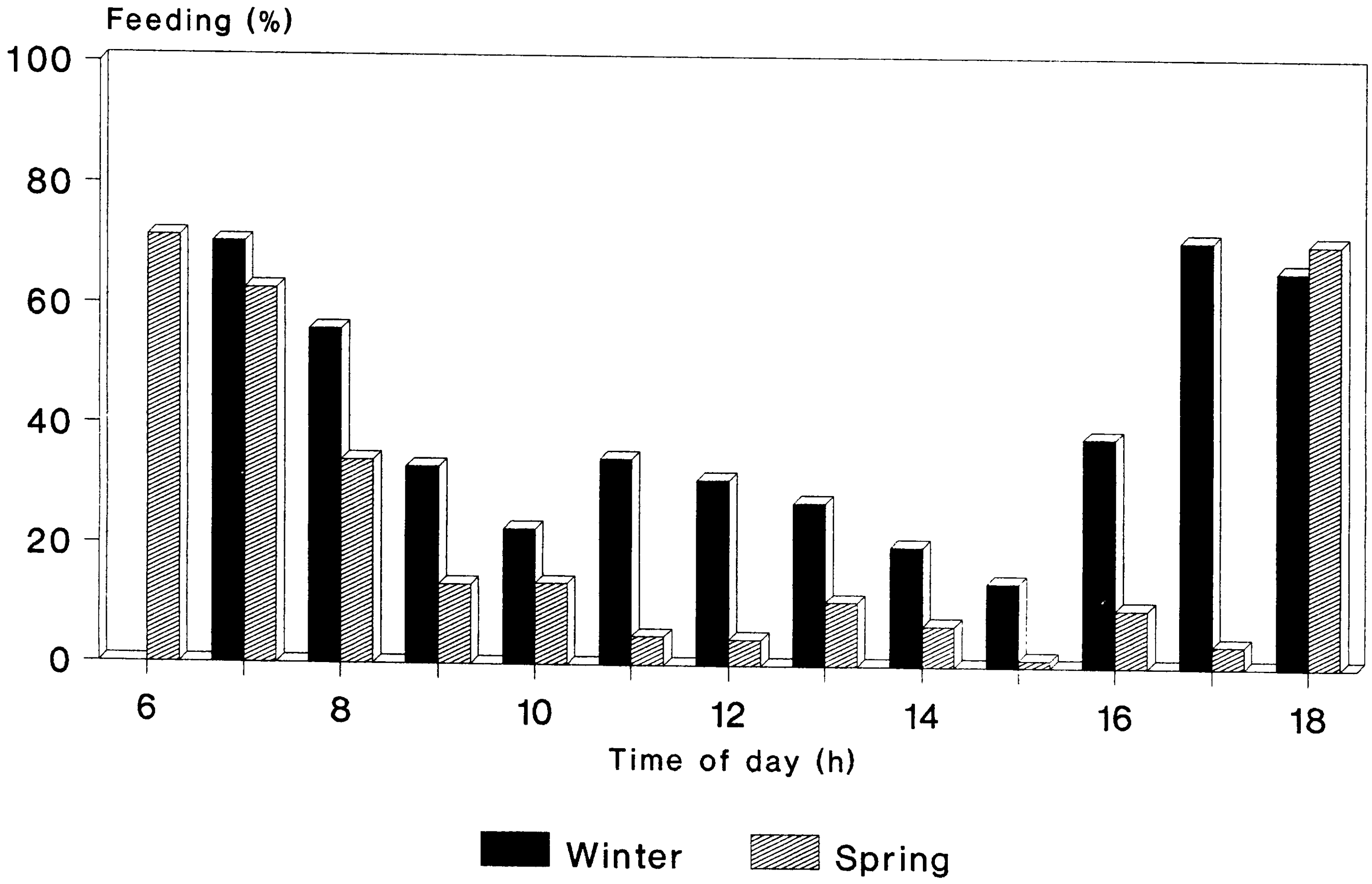


FIG.24. DIURNAL FEEDING ACTIVITY OF RED HARTEBEEST DURING EARLY SUMMER AND SUMMER

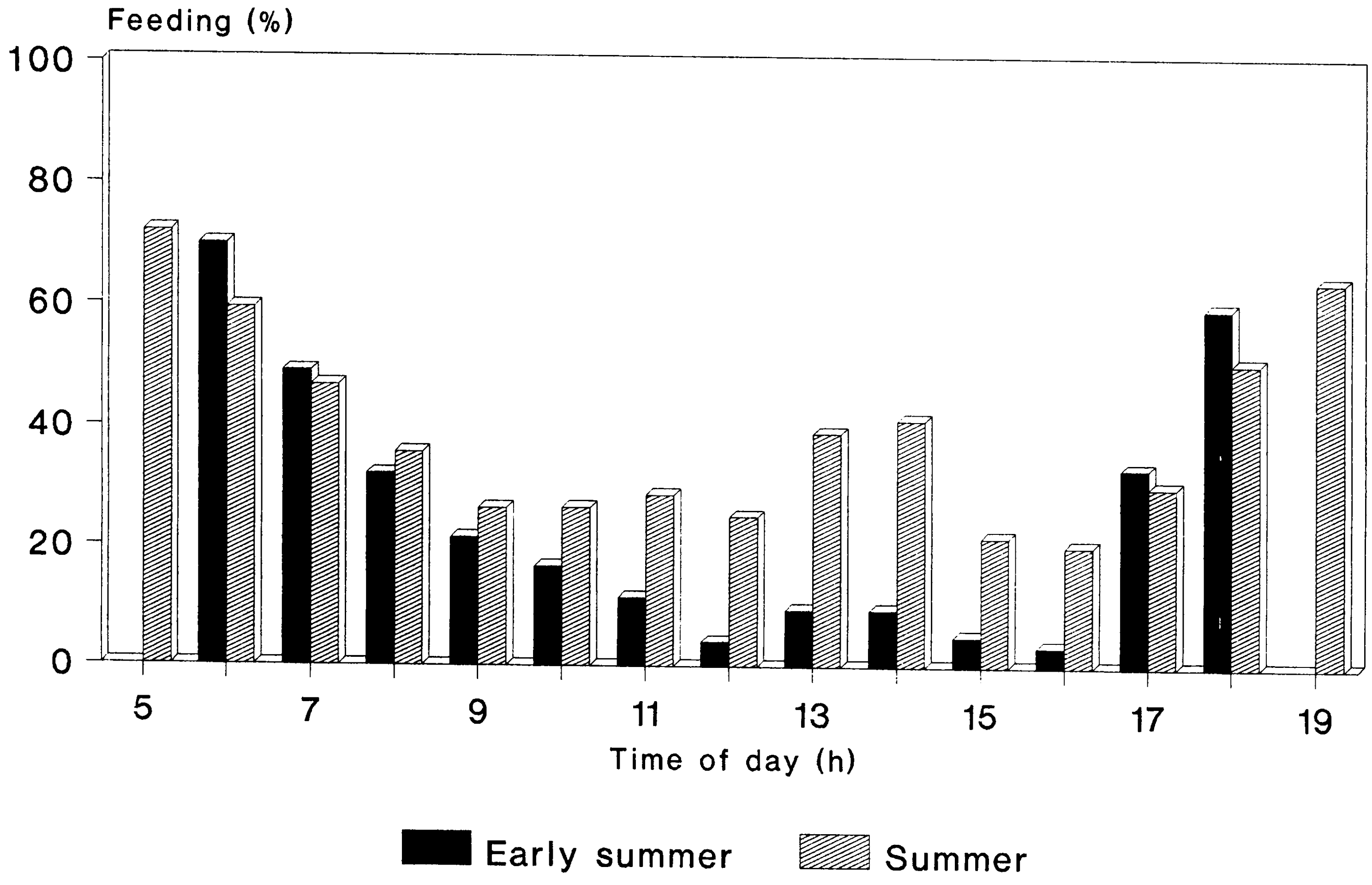


FIG.25. SUNRISE AND SUNSET TIMES ON THE SALNR.

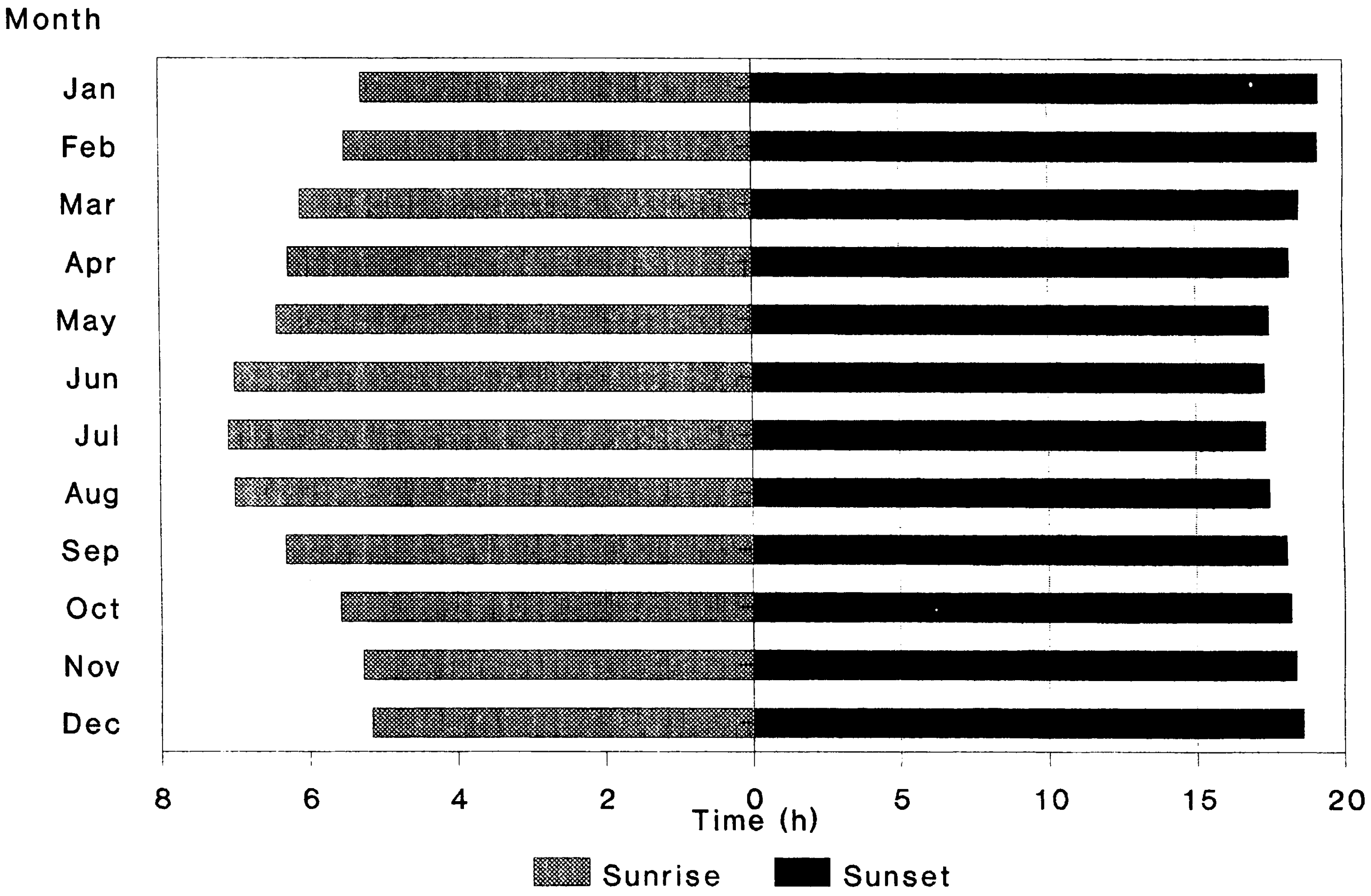


FIG.26. MEAN DISTANCE MOVED PER TIME INTERVAL DURING LATE SUMMER AND AUTUMN.

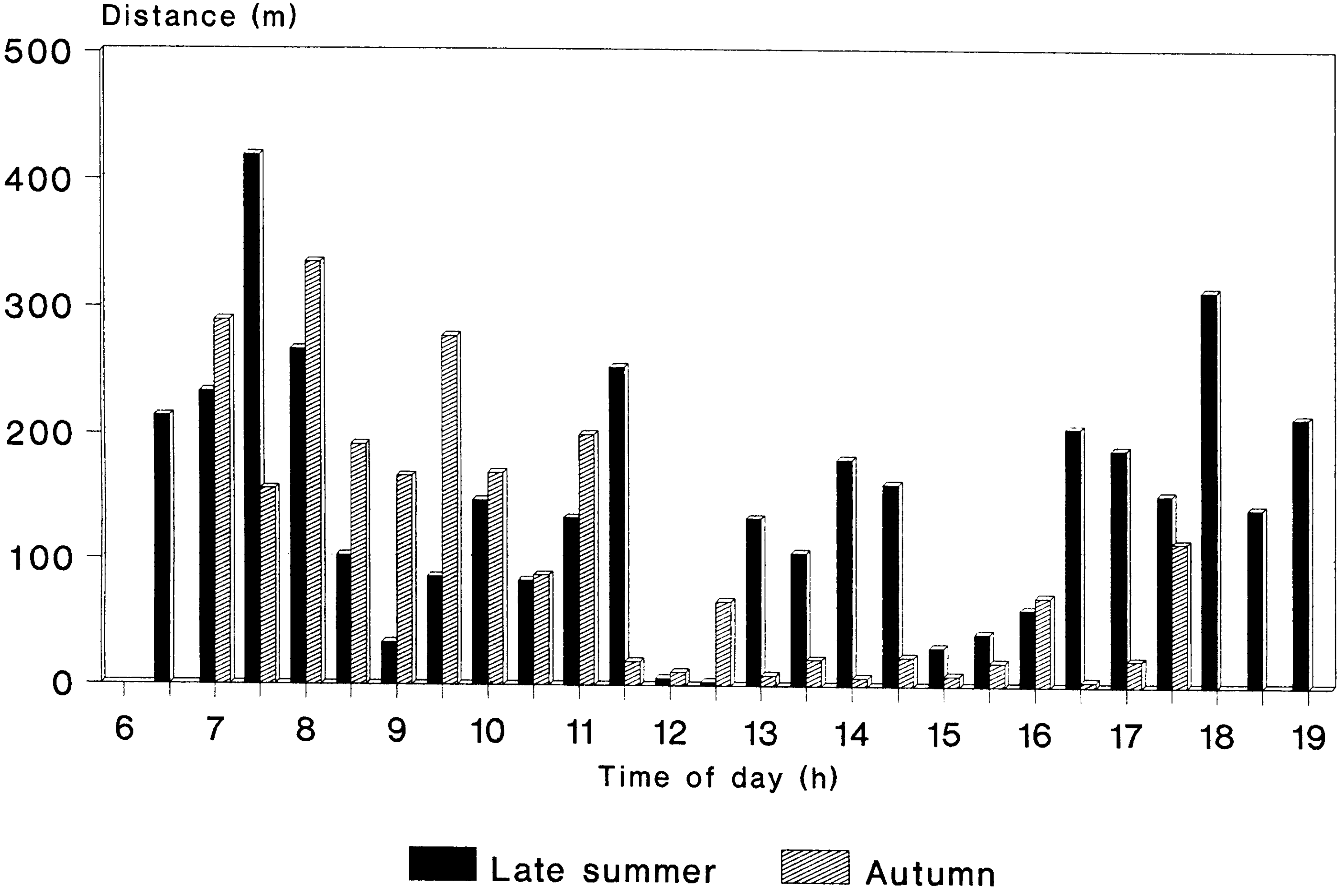


FIG.27. MEAN DISTANCE MOVED PER TIME INTERVAL DURING WINTER AND SPRING.

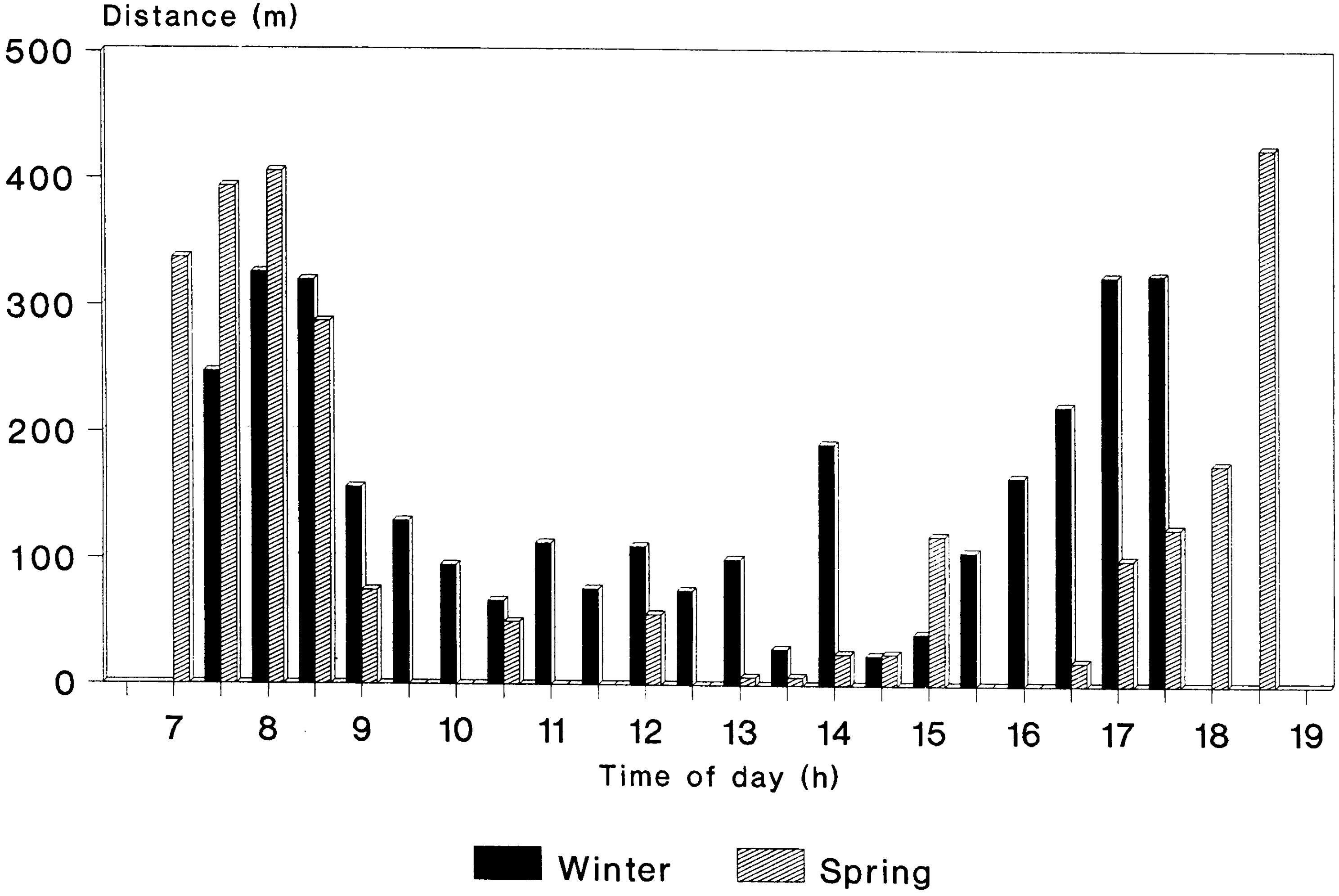


FIG.28. MEAN DISTANCE MOVED PER TIME INTERVAL DURING EARLY SUMMER AND SUMMER.

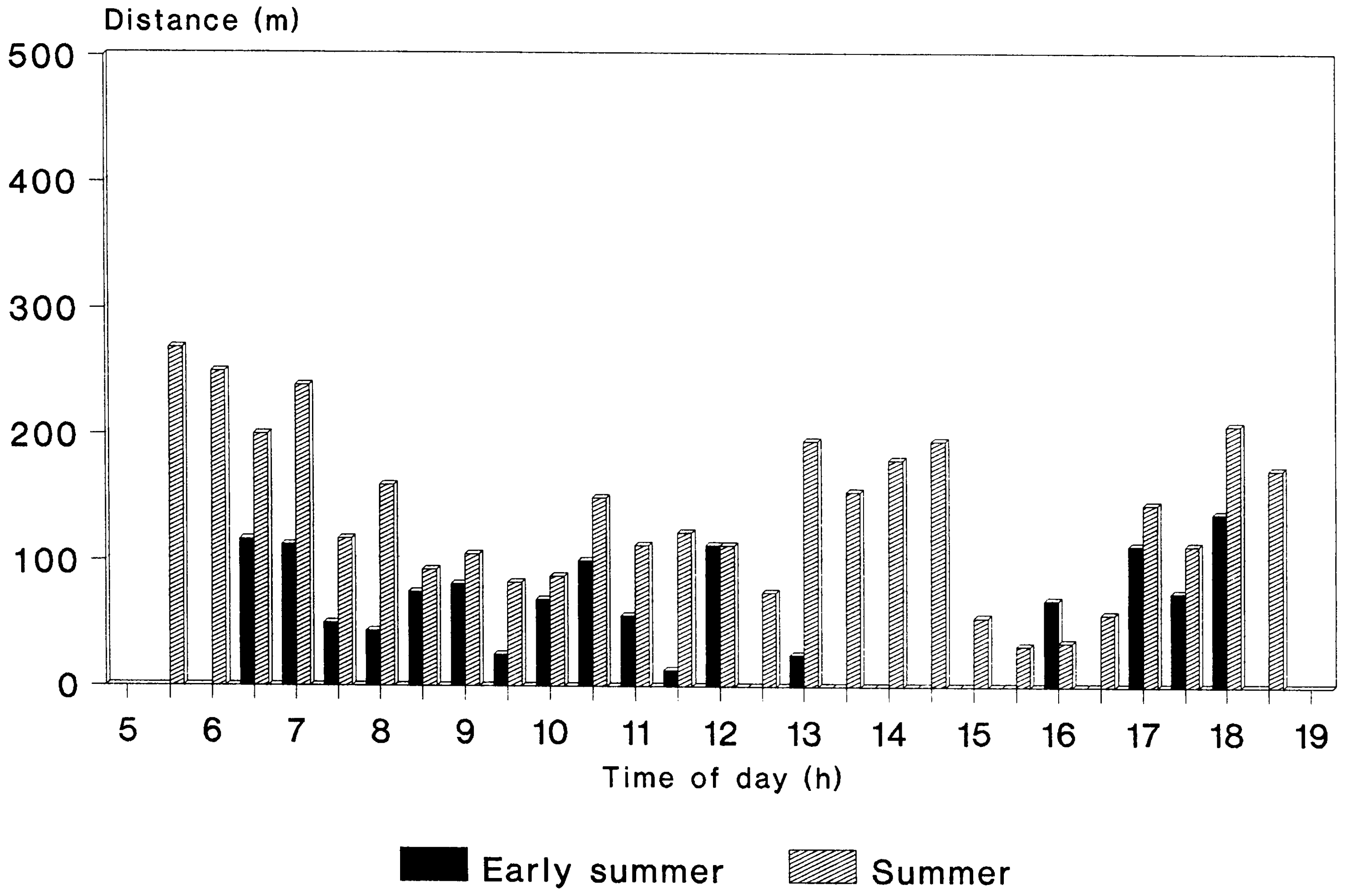
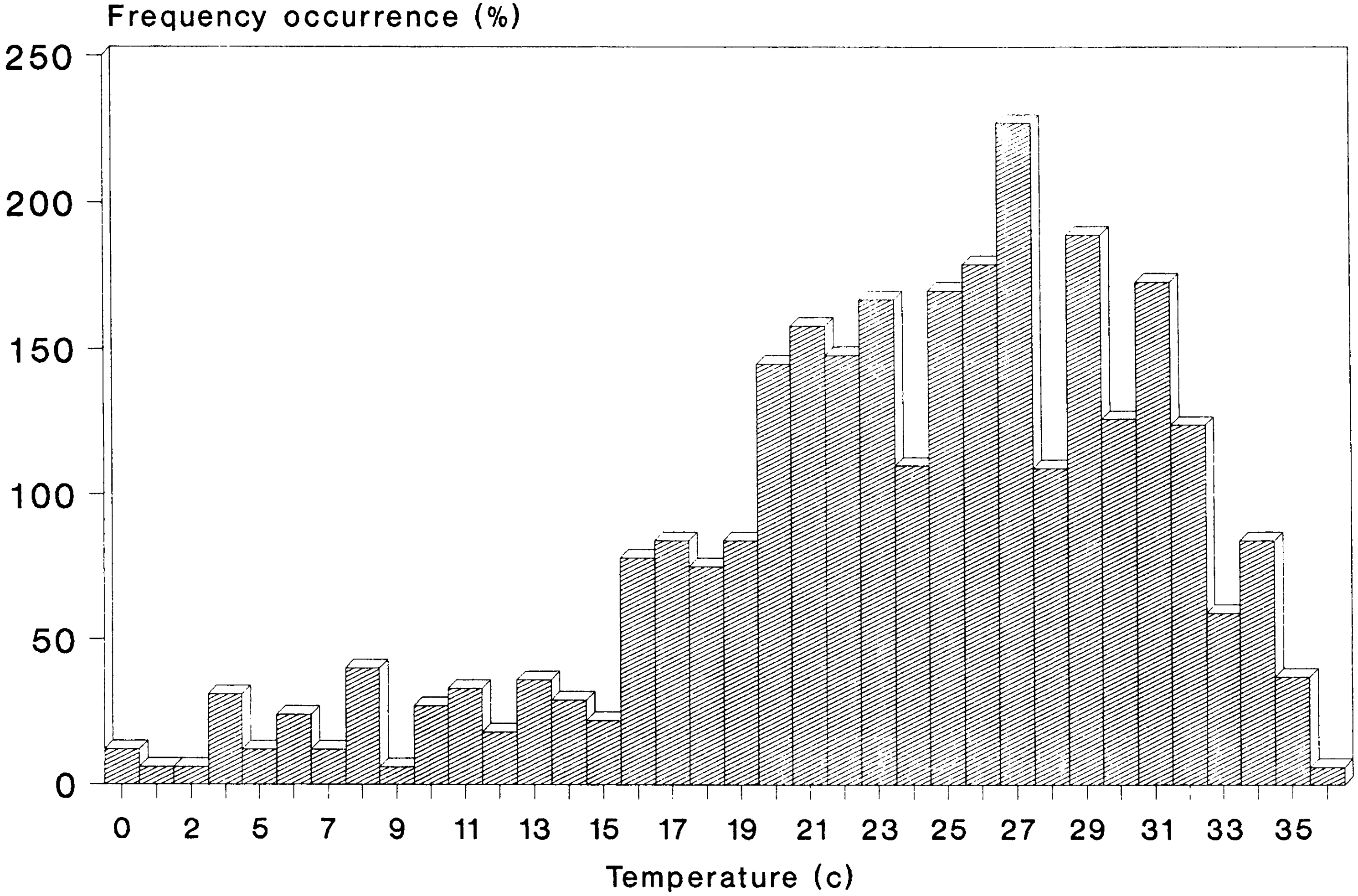


FIG.29. FREQUENCY OCCURRENCE OF AMBIENT TEMPERATURES MEASURED DURING OBSERVATIONS ON RED HARTEBEEST.



CHAPTER 9

CONCLUSIONS

The study indicated that several behavioural and morphological adaptations enable red hartebeest to optimally utilize the plant communities on the S.A. Lombard Nature Reserve. This was achieved through several mechanisms:

(i) The high calving percentage and high survival rate amongst neonates could partly be attributed to the fact that red hartebeest react to daylength as the environmental cue for the initiation of breeding. This ensures that parturition and optimal environmental conditions coincide, thus enhancing the survival of the young after birth.

(ii) Hartebeeest, being highly mobile, responded to biomass fluctuations in the herb layer by adopting a pasture rotation pattern, which provided an adequate food intake for the harem herd over all seasons.

(iii) The seasonal fluctuation in the tendency and degree of fusion-fission within the harem herd alleviated the effects of competition amongst individuals. This pattern ensured that the seasonal requirements of the harem herd could be met.

(iv) The flexibility of the feeding behaviour, by adopting to both energy expenditure and conservation in relation to season, is facilitated mainly by the morphological features of the pelage and dentition. The relatively thick pelage and the low absorbance rate provide adequate protection against solar gain. These qualities exclude the need for seeking out the sparse shade in the eastern alluvial floodplain, which is the most preferred habitat.

(v) The ability of red hartebeest, although exclusively grazers, to select dicotyledons during the most limiting period, alleviated nutritional stress on especially the lactating females, thus enhancing and promoting the survival of the neonates.

MANAGEMENT RECOMMENDATIONS

The skew sex ratio of 1 harem bull to 30 adult females is the result of culling single territorial bulls prior to the onset of the observations. No territorial bulls were observed for the remainder of the study. The fact that the remaining 15 bachelor bulls could not displace the harem herd bull, is considered the proximate factor stimulating the formation of a single large harem herd.

The results on the spatial utilization of plant communities on the SALNR indicated a large preference for the climax communities of the eastern alluvial floodplain. The resultant high grazing pressure on especially the short grassland has led to some degree of veld degradation, indicated by the presence of unpalatable Increaser grass species. The large number of red hartebeest in the harem herd exascerbated the degradation.

The management of the red hartebeest population should therefore focus on relieving the high grazing pressure by stimulating the formation of smaller harem herds, which could allow a more even distribution of red hartebeest. This could be achieved by ceasing the culling of territorial bulls. This would facilitate the displacement of the harem herd bull and the subsequent formation of smaller harem herds.

SUMMARY

A single breeding herd of red hartebeest occurred at the time of observation on the S.A. Lombard Nature Reserve. The spatial and temporal utilization of resources were intensively studied for the duration of one year, which ensured that seasonal variability was accounted for.

A summer rainfall pattern, with rains from October to March, was prevalent at the Reserve. A coefficient of variation of 36% in the total amount of rainfall indicated an erratic rainfall pattern.

Red hartebeest exhibited a highly synchronous seasonal breeding pattern, with the bulk of the neonates born during the period September/October. The absence of large predators and the optimum resource availability led to a high survival rate of the calves.

The plant survey effectively divided the reserve into a dry, western Cymbopogon-Themeda veld and the eastern alluvial floodplain. Due to the higher complement of Decreaser grasses, representing a vegetational climax state, the eastern alluvial floodplain was highly suitable to red hartebeest. Due to the prominence of several Increaser grass species, the western dry Cymbopogon-Themeda veld was found to be less suitable for sustained optimal use by red hartebeest.

The utilization of plant communities by the harem herd was not random. Hartebeest selected for short grasslands during the hot, wet summer months and for medium - tall grasslands during the cold, dry winter months until the onset of the first rains.

Selection for the short grasslands coincided with a high degree of fusion amongst the herd members. In contrast, declining food resources during the winter period stimulated a pattern of fission amongst the herd members.

Faecal nitrogen was found to be a reliable indicator of the quality of ingested food material. Hartebeest grazed almost exclusively during the seasonal cycle. Dicotyledons were ingested in significant amounts only during the most limiting period of the year. The inclusion of dicotyledons promoted lower levels of indigestible lignin (ADL) in the food. The dental morphology enabled and facilitated the flexible foraging behaviour of red hartebeest.

During all seasons, members of the breeding herd were highly synchronous in the respective activity categories. Hartebeest adjusted their energy budgets to environmental factors by:

(i) increasing the foraging effort during the hot, wet summer periods and the cold dry winter periods.

(ii) decreasing the foraging effort during autumn and the early summer period preceding the onset of the rainy season.

Time of day was implicated as being the proximate cause determining peaks of feeding activity. Alternatively, temperature as a co-factor contributed largely to the depressions in the feeding pattern.

The temporal and spatial adaptations to the fluctuating environmental conditions on the S.A. Lombard Nature Reserve ensured that optimal use of available resources was achieved by the red hartebeest breeding herd.

OPSOMMING

'n Enkele teeltrop rooihartbeeste, bestaande uit een volwasse harembul, verskeie volwasse koeie, onvolwassenes en kalwers het tydens die studie tydperk op die S.A. Lombard Natuur-reservaat voorgekom. Die ruimtelike en tydsbenutting van hulpbronne deur die trop is intensief vir 'n tydsduur van een jaar bestudeer.

Die reënseisoen het van Oktober tot Maart gestrek, wat 'n duidelike somer-reënval patroon weerspieel. 'n Variasie van 36% in die totale reënvalsyfer vir die SALNR weerspieël die wisselvalligheid van reën in hierdie gebied.

Die hoogs gesinchroniseerde kalftydperk onder rooiharbeeste het aanleiding daartoe gegee dat die meerderheid kalwers gedurende die periode September/ Oktober, met 'n duidelike piek in Oktober, gebore word. Die hoë oorlewingssyfer onder die kalwers kan toegeskryf word aan beide die afwesigheid van groot roofdiere asook die feit dat optimale veldtoestande saamval met die geboortes.

Die Braun-Blanquet veldopname het die reservaat floristies verdeel in 'n westelike droë Cymbopogon-Themeda deel en 'n oostelike alluviale vloedvlakte. Die groter komplement van Afnemer grasse in die vloedvlakte het bygedra tot die geskiktheid van die area vir benutting deur die harem trop. Vanweë die hoër komplement van Toenemer grasse is die westelike droë gebied nie benut nie.

Die benutting van plantgemeenskappe deur die haremtrop was nie ewekantsig nie. Voorkeur is verleen aan die kortgrasveld gemeenskappe tydens die warm, nat somermaande. Die medium-lang tot langgrasvelde is gedurende die koue, droë winter maande tot en met die aanvang van die reënseisoen benut.

Die stikstofinhoud van mis was 'n goeie aanwyser van die kwaliteit van die grasse wat die haremtrop benut het. Monokotiele is byna uitsluitlik deur die trop benut, met die uitsondering van die periode voor die aanvang van die reënseisoen toe dikotiele materiaal in betekenisvolle hoeveelhede ingeneem is. Die inname van dikotiele gedurende dié beperkende periode het aanleiding gegee tot 'n verlaagde inname van onverteerbare lignien. Die morfologiese kenmerke van die mondele van rooihartbeeste verklaar en vergemaklik die buigsaamheid van hulle seisonale voedingsgedrag.

Die seisoenale aktiwiteitspatrone van rooihartbeeste is deur 'n hoë mate van sinkronisasie gekenmerk. Die haremtrop het hulle seisonale voedingsaktiwiteite as volg aangepas:

(i) 'n Verlaging in die tyd spandeer aan voeding gedurende die warm, nat asook koue, droë periodes.

(ii) Afname in tyd spandeer aan voeding gedurende herfs en die periode wat die reënseisoen voorafgaan.

Tydsperiodes binne 'n dag, oor alle seisoene, was die onmiddelike oorsaak wat aanleiding gegee het tot die pieke in voedingsakatiwiteit. Temperatuur, as 'n ko-faktor het betekenisvol bygedra tot verlaagde voedingsaktiwiteite.

Die morfologiese, en gedragsaanpasings van rooihartbeeste het aanleiding gegee tot die optimale benutting van die S.A. Lombaard Natuurreservaat.

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APPENDIX 1: Rainfall data for S.A. Lombard, representing 25 years

Month	Years	Mean	Standard Deviation	Minimum Value -	Maximum Value	Std Error of mean	Variance	C.V. * %
JAN	25	98,368	83,876	13,000	374,000	16,775	7035,282	85,268
FEB	25	106,308	66,497	11,500	294,000	13,299	4421,967	62,552
MAR	25	67,352	47,597	2,300	160,000	9,519	2265,538	70,670
APR	25	40,780	30,077	3,500	112,500	6,015	904,653	73,755
MAY	25	21,344	26,003	0,000	98,700	5,200	676,186	121,831
JUNE	25	3,788	4,691	0,000	15,200	0,938	22,006	123,843
JULY	25	3,432	5,750	0,000	23,000	1,150	33,068	167,555
AUG	24	7,887	13,336	0,000	59,800	2,722	177,854	169,080
SEPT	24	13,995	21,949	0,000	77,400	4,480	481,783	156,829
OCT	25	38,264	40,928	2,000	166,000	8,185	1675,165	106,964
NOV	25	56,272	39,535	1,500	185,000	7,907	1563,082	70,258
DEC	25	53,760	35,106	7,900	142,500	7,021	1232,486	65,303
TOTAL:	25	510,676	183,864	248,700	965,300	36,772	33805,986	36,004

* Coefficient of variation (%)

APPENDIX 2: Rainfall data for Hertzogville, representing 25 years

Month	Years	Mean	Standard Deviation	Minimum Value -	Maximum Value	Std Error of mean	Variance	C.V. * %
JAN	25	88,340	70,853	10,500	272,500	14,170	5020,214	80,205
FEB	25	85,560	64,573	6,500	279,500	12,914	4169,783	75,472
MAR	25	78,284	62,485	0,000	238,000	12,497	3904,388	79,818
APR	25	47,536	46,660	0,000	177,000	9,332	2177,197	98,158
MAY	25	21,320	28,691	0,000	101,500	5,738	823,190	134,575
JUNE	25	5,176	7,153	0,000	25,000	1,430	51,169	138,201
JULY	25	5,032	8,241	0,000	24,000	1,648	67,917	163,776
AUG	25	8,848	14,829	0,000	54,600	2,965	219,907	167,600
SEPT	25	23,488	38,218	0,000	119,500	7,643	1460,661	162,715
OCT	25	47,588	47,357	0,000	200,300	9,471	2242,713	99,515
NOV	25	57,092	32,656	10,000	161,000	6,531	1066,469	57,200
DEC	24	60,975	38,569	0,000	126,700	7,872	1487,570	63,254
TOTAL:	25	526,800	177,651	273,400	1082,800	35,530	13170,000	33,723

* Coefficient of variation (%)

APPENDIX 3: Rainfall data for Christiana, representing 25 years

Month	Years	Mean	Standard Deviation	Minimum Value -	Maximum Value	Std Error of mean	Variance	C.V. * %
JAN	25	87,080	69,244	6,000	286,400	13,848	4794,790	79,518
FEB	25	84,884	72,784	15,000	358,300	14,556	5297,653	85,746
MAR	25	70,780	56,855	0,000	202,400	11,371	3232,588	80,328
APR	25	36,664	35,313	0,000	128,000	7,062	1247,039	96,316
MAY	25	15,044	19,104	0,000	67,000	3,820	364,974	126,989
JUNE	25	4,176	7,736	0,000	30,500	1,547	59,859	185,270
JULY	25	4,940	7,701	0,000	22,000	1,540	59,319	155,909
AUG	25	7,088	13,267	0,000	41,500	2,653	176,018	187,178
SEPT	24	18,804	30,881	0,000	85,000	6,303	953,638	164,224
OCT	25	36,348	33,954	0,000	126,500	6,790	1152,911	93,415
NOV	25	54,572	38,150	3,500	139,000	7,630	1455,443	69,908
DEC	23	55,226	39,708	0,000	154,000	8,279	1576,782	71,902
TOTAL:	25	470,436	186,452	240,300	1016,300	37,290	34764,562	39,634

* Coefficient of variation (%)

APPENDIX 4: Rainfall data for Bloemhof, representing 25 years

Month	**Years**	**Mean**	**Standard Deviation**	**Minimum Value -**	**Maximum Value**	**Std Error of mean**	**Variance**	**C.V. * %**
JAN	25	96,844	95,159	17,000	472,500	19,031	9055,367	98,261
FEB	25	89,060	53,092	0,000	208,500	10,618	2818,769	59,614
MAR	25	70,824	57,743	0,000	233,000	11,548	3334,316	81,531
APR	25	40,348	28,716	0,000	105,900	5,743	824,640	71,172
MAY	25	18,128	25,965	0,000	106,500	5,193	674,188	143,232
JUNE	25	2,764	5,117	0,000	16,000	1,023	26,188	185,146
JULY	25	3,824	7,287	0,000	27,500	1,457	53,107	190,573
AUG	25	7,732	14,367	0,000	65,000	2,873	206,433	185,822
SEPT	24	18,325	30,460	0,000	112,500	6,217	927,840	166,224
OCT	25	40,484	33,646	0,000	118,500	6,729	1132,063	83,110
NOV	24	55,991	40,272	9,900	195,500	8,220	1621,860	71,926
DEC	25	57,884	35,918	0,000	120,000	7,183	1290,112	62,052
TOTAL:	25	499,236	154,304	288,100	968,700	30,860	23809,827	30,908

* Coefficient of variation (%)

APPENDIX 5: Rainfall data for Schweizer-Reineke, representing 25 years

Month	**Years**	**Mean**	**Standard Deviation**	**Minimum Value -**	**Maximum Value**	**Std Error of mean**	**Variance**	**C.V. * %**
JAN	25	97,916	68,839	22,000	269,100	13,767	4738,817	70,304
FEB	25	80,156	53,037	0,000	265,000	10,607	2812,999	66,168
MAR	25	79,280	54,221	12,000	161,700	10,844	2939,921	68,392
APR	25	40,932	29,165	3,000	118,000	5,833	850,617	71,253
MAY	25	17,992	29,513	0,000	123,300	5,902	871,057	164,038
JUNE	24	5,279	6,780	0,000	23,000	1,383	45,970	128,432
JULY	25	3,920	8,103	0,000	32,000	1,620	65,663	206,717
AUG	25	7,272	15,694	0,000	71,000	3,138	246,302	215,815
SEPT	25	16,264	23,543	0,000	97,500	4,708	554,301	144,759
OCT	25	46,924	46,348	0,000	173,600	9,269	2148,190	98,774
NOV	25	60,572	52,354	6,000	211,400	10,470	2740,983	86,433
DEC	25	60,268	40,350	3,000	186,100	8,070	1628,128	66,951
TOTAL:	25	516,564	153,760	243,000	905,800	30,752	23642,380	29,766

* Coefficient of variation (%)

APPENDIX 6: Rainfall data for Wolmaransstad, representing 25 years

Month	Years	Mean	Standard Deviation	Minimum Value -	Maximum Value	Std Error of mean	Variance	C.V. * %
JAN	22	107,463	77,028	13,500	294,200	16,422	5933,419	71,679
FEB	22	89,322	47,407	14,500	185,000	10,107	2247,426	53,074
MAR	22	79,095	66,653	0,000	295,000	14,210	4442,646	84,269
APR	22	49,513	36,646	0,000	108,000	7,812	1342,937	74,012
MAY	22	14,068	22,709	0,000	81,500	4,841	515,721	161,425
JUNE	22	4,068	7,010	0,000	28,000	1,494	49,149	172,330
JULY	22	3,272	5,337	0,000	18,500	1,138	28,493	163,103
AUG	22	10,827	21,034	0,000	96,500	4,484	442,432	194,269
SEPT	22	19,222	31,500	0,000	134,500	6,715	992,252	163,869
OCT	22	47,681	35,250	4,000	127,000	7,515	1242,593	73,928
NOV	22	70,263	40,800	22,000	169,000	8,698	1664,641	58,067
DEC	22	70,181	47,615	13,100	214,500	10,151	2267,261	67,846
TOTAL:	22	564,981	159,430	266,800	857,200	33,990	25418,107	28,219

* Coefficient of variation (%)

APPENDIX 7: Categorized grasses on the SALNR

Species	Decreasers	Increasers	Increasers	Increasers
		IIa	IIb	IIc
Echinochloa holubii			*	
Panicum maximum		*		
Cynodon dactylon				*
Chloris virgata				*
Aristida congesta				*
Aristida barbicollis				*
Eragrostis curvula				*
Eragrostis rigidior				*
Eragrostis obtusa				*
Aristida curvata				*
Themeda triandra		*		
Eragrostis superba				*
Panicum laevifolium			*	
Digitaria argyrogrypta				*
Heteropogon contortus	*			
Fingeruthia africana			*	
Enneapogon scoparius				*
Eragrostis curvula				*
Cymbopogon plurinoides				*
Sporobolus fimbriatus			*	
Sporobolus ioclados				*
Digitaria eriantha		*		
Setaria flabellata		*		
Eragrostis lehmanniana				*
Eragrostis gummiflua				*
Pogonarthria squarrosa				*
Eragrostis cilianensis				*
Elyonurus muticus				*
Brachiaria eruciformis				*
Aristida diffusa				*
Aristida meridionalis				*
Trichoneura grandiglumis				*
Aristida vestita				*
Aristida uniplumis				
Aristida scabrivalvis				*
Eragrostis bicolor				*
Eragrostis pallens				*
Eragrostis denudata				*
Eragrostis rotifer				*
Eragrostis homomalla				*
Panicum coloratum				*

APPENDIX 8: **Bonferroni simultaneous confidence intervals for the use of community types by red hartebeest in the eastern alluvial floodplain during the period January/February (Late Summer)**

COMMUNITY TYPE	TOTAL AREA (ha)	EXPRO	EXPUSE	OBSUSE	OBSPRO	BSCI
Echinochloa holubii Panicum maximum grassland	25,0	0,016	359	467	0,0208	0,0182 $\leq$ p $\leq$ 0,0234
Sporobolus ioclados grassland	156,2	0,102	2 288	6 325	0,2819	0,2737 $\leq$ p $\leq$ 0,2901
Themeda triandra grassland	1 062,5	0,694	15 572	12 833	0,5719	0,5629 $\leq$ p $\leq$ 0,5809
Themeda triandra (variant) grassland	68,7	0,044	987	2 658	0,1185	0,1126 $\leq$ p $\leq$ 0,1244
Dry pan	43,7	0,028	628	-	-	0 $\leq$ p $\leq$ 0
Rhus lancea woodland	25,0	0,0163	365	-	-	0 $\leq$ p $\leq$ 0
Diospyros lycioides/ Ziziphus mucronata woodland	112,5	0,073	1 638	-	-	0 $\leq$ p $\leq$ 0
Tarchonanthus camphoratus woodland	37,5	0,0264	538	156	0,0070	-0,0008 $\leq$ p $\leq$ 0,0085
	1 531 ha			22 439		

* indicates the difference at the 0.05 level of significance

APPENDIX 9: **Bonferroni simultaneous confidence intervals for the use of community types by red hartebeest in the eastern alluvial floodplain during the period March/April (Autumn)**

COMMUNITY TYPE	TOTAL AREA (ha)	EXPRO	EXPUSE	OBSUSE	OBSPRO	BSCI
Echinochloa holubii Panicum maximum grassland	25,0	0,016	309	533	0,0275	0,0243 $\leq$ p $\leq$ 0,0307
Sporobolus ioclados grassland	156,2	0,102	1 974	2 499	0,1291	0,1225 $\leq$ p $\leq$ 0,1357
Themeda triandra grassland	1 062,5	0,694	13 437	15 475	0,7992	0,7913 $\leq$ p $\leq$ 0,8071
Themeda triandra (variant) grassland	68,7	0,044	851	606	0,0313	0,0279 $\leq$ p $\leq$ 0,0347
Dry pan	43,7	0,028	542	52	0,0027	0,0017 $\leq$ p $\leq$ 0,0037
Rhus lancea woodland	25,0	0,0163	315	-	-	0 $\leq$ p $\leq$ 0
Diospyros lycioides/ Ziziphus mucronata woodland	112,5	0,073	1 413	-	-	0 $\leq$ p $\leq$ 0
Tarchonanthus camphoratus woodland	37,5	0,024	464	197	0,0102	0,0082 $\leq$ p $\leq$ 0,0122
	1 531 ha			19 362		* indicates the difference at the 0.05 level of significance

APPENDIX 10: Bonferroni simultaneous confidence intervals for the use of community types by red hartebeest in the eastern alluvial floodplain during the period May - August (Winter)

COMMUNITY TYPE	TOTAL AREA (ha)	EXPRO	EXPUSE	OBSUSE	OBSPRO	BSCI
Echinochloa holubii *Panicum maximum* grassland	25,0	0,016	421	461	0,0175	$0{,}0153 \leq p \leq 0{,}0197$
Sporobolus ioclados grassland	156,2	0,102	2 684	665	0,0253	$0{,}0227 \leq p \leq 0{,}0279$
Themeda triandra grassland	1 062,5	0,694	18 266	24 980	0,9491	$0{,}9454 \leq p \leq 0{,}9528$
Themeda triandra (variant) grassland	68,7	0,044	1 158	121	0,0046	$0{,}0035 \leq p \leq 0{,}0057$
Dry pan	43,7	0,028	736	-	-	$0 \leq p \leq 0$
Rhus lancea woodland	25,0	0,0163	429	-	-	$0 \leq p \leq 0$
Diospyros lycioides/ *Ziziphus mucronata* woodland	112,5	0,073	1 921	-	-	$0 \leq p \leq 0$
Tarchonanthus camphoratus woodland	37,5	0,024	631	93	0,0035	$0{,}0025 \leq p \leq 0{,}0045$
	1 531 ha			26 320		

* indicates the difference at the 0.05 level of significance

APPENDIX 11: **Bonferroni simultaneous confidence intervals for the use of community types by red hartebeest in the eastern alluvial floodplain during the period September (Spring)**

COMMUNITY TYPE	**TOTAL AREA (ha)**	**EXPRO**	**EXPUSE**	**OBSUSE**	**OBSPRO**	**BSCI**
Echinochloa holubii *Panicum maximum* grassland	25,0	0,016	100	42	0,0067	$0,0039 \leq p \leq 0,0095$
Sporobolus ioclados grassland	156,2	0,102	638	80	0,0128	$0,0089 \leq p \leq 0,0167$
Themeda triandra grassland	1 062,5	0,694	4 347	6 127	0,9781	$0,9731 \leq p \leq 0,9831$
Themeda triandra (variant) grassland	68,7	0,044	275	-	-	$0 \leq p \leq 0$
Dry pan	43,7	0,028	175	-	-	$0 \leq p \leq 0$
Rhus lancea woodland	25,0	0,0163	102	-	-	$0 \leq p \leq 0$
Diospyros lycioides/ *Ziziphus mucronata* woodland	112,5	0,073	457	11	0,0018	$0,0003 \leq p \leq 0,0033$
Tarchonanthus camphoratus woodland	37,5	0,024	150	4	0,0006	$-0,0002 \leq p \leq 0,0014$
	1 531 ha			6 264		

* indicates the difference at the 0.05 level of significance

APPENDIX 12: **Bonferroni simultaneous confidence intervals for the use of community types by red hartebeest in the eastern alluvial floodplain during the period October (Early summer)**

COMMUNITY TYPE	TOTAL AREA (ha)	EXPRO	EXPUSE	OBSUSE	OBSPRO	BSCI
Echinochloa holubii Panicum maximum grassland	25,0	0,016	99	90	0,0144	0,0103 $\leq$ p $\leq$ 0,0185
Sporobolus ioclados grassland	156,2	0,102	636	79	0,0127	0,0088 $\leq$ p $\leq$ 0,0166
Themeda triandra grassland	1 062,5	0,694	4 331	6 025	0,9652	0,9589 $\leq$ p $\leq$ 0,9715
Themeda triandra (variant) grassland	68,7	0,044	274	48	0,0077	0,0047 $\leq$ p $\leq$ 0,0107
Dry pan	43,7	0,028	175	-	-	0 $\leq$ p $\leq$ 0
Rhus lancea woodland	25,0	0,0163	102	-	-	0 $\leq$ p $\leq$ 0
Diospyros lycioides/ *Ziziphus mucronata* woodland	112,5	0,073	457	-	-	0 $\leq$ p $\leq$ 0
Tarchonanthus camphoratus woodland	37,5	0,024	150	-	-	0 $\leq$ p $\leq$ 0
	1 531 ha			6 242		

* indicates the difference at the 0.05 level of significance

APPENDIX 13: **Bonferroni simultaneous confidence intervals for the use of community types by red hartebeest in the eastern alluvial floodplain during the period December (Summer)**

COMMUNITY TYPE	TOTAL AREA (ha)	EXPRO	EXPUSE	OBSUSE	OBSPRO	BSCI
Echinochloa holubii *Panicum maximum* grassland	25,0	0,016	249	3914	0,2516	$0,2421 \leq p \leq 0,2611$
Sporobolus ioclados grassland	156,2	0,102	1587	3453	0,2219	$0,2129 \leq p \leq 0,2309$
Themeda triandra grassland	1 062,5	0,694	10795	7709	0,4955	$0,4845 \leq p \leq 0,506$
Themeda triandra (variant) grassland	68,7	0,044	684	216	0,0138	$0,0108 \leq p \leq 0,0168$
Dry pan	43,7	0,028	436	-	0	$0 \leq p \leq 0$
Rhus lancea woodland	25,0	0,0163	254	-	0	$0 \leq p \leq 0$
Diospyros lycioides/ *Ziziphus mucronata* woodland	112,5	0,073	1136	-	0	$0 \leq p \leq 0$
Tarchonanthus camphoratus woodland	37,5	0,024	373	263	0,0169	$0,0021 \leq p \leq 0,0409$
	1 531 ha					

* indicates the difference at the 0.05 level of significance