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Ecological separation of the black and blue wildebeest on Ezemvelo Nature Reserve in the highveld grasslands of South Africa

by

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Submitted in partial fulfilment of the requirements for the degree

MAGISTER SCIENTIAE (WILDLIFE MANAGEMENT)

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I declare that the dissertation, which I hereby submit for the degree Master of Science (Wildlife Management) at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

SIGNATURE: ..…………………………….
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ABSTRACT

The present study was conducted on Ezemvelo Nature Reserve in the highveld grasslands of South Africa. The evidence for ecological separation between the black and blue wildebeest was investigated in an area with suboptimal habitat for both types of wildebeest. Habitat selection and separation of the black and blue wildebeest population were investigated at three main scales. A combination of logistic regression analysis, discriminant analysis and hypothesis testing techniques were used to determine whether habitat separation occurred between the black and blue wildebeest at the various scales. Seasonal, social group and weather influences on the habitat selection of both types of wildebeest were also investigated. Black and blue wildebeest showed resource partitioning in terms of habitat at the macro and mesoscales but not at the microscale. The preference for open areas by the black wildebeest and its more specialised territoriality were found to be the main driving factors contributing to the habitat separation of the two types of wildebeest. The population of black wildebeest was found to be decreasing while the blue wildebeest population was found to be increasing in the study area during the study period. Spatial overlap between the black and blue wildebeest was found to be low. Little evidence of interference interspecific competition between the black and blue wildebeest was found. It was, however, concluded that exploitative competition between the two types of wildebeest would be found in areas with low habitat heterogeneity. Ecological separation between the black and blue wildebeest was found to be incomplete. However, the coexistence of the black and blue wildebeest was deemed possible provided habitat heterogeneity in terms of the factors found to be important for habitat separation was high and population sizes were strictly monitored and actively controlled. Finally, a number of additional management recommendations for the black and blue wildebeest at Ezemvelo Nature Reserve and for other reserves confining both types of wildebeest together based on the results of this study were made.

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CHAPTER 1: INTRODUCTION

The term ecological separation has been defined as the partitioning of a natural resource such as food, among two or more species, so that each species has access to a different part of the resource (Chapman and Reiss 1995). Species in a community where ecological separation has occurred will utilise all the available habitats optimally. Resource partitioning is defined as the differential use by organisms of resources such as food and space (Schoener 1974a). Therefore resource partitioning is the mechanism by which ecological separation is achieved. Ecological separation explains how species can coexist even though they may have extensive overlap in their ecological requirements (May 1973). Competition has been considered to be the major selective force causing differential use of resources. Therefore competition is usually cited as being limited by ecological separation (Von Holdt 1999). However, resource partitioning may also occur through processes such as predation and different responses of species to environmental gradients (Schoener 1986).

African herbivores have evolved as an integrated community, whereby the available habitats are fully utilised. Therefore, species, which occur naturally in the same geographical area, are ecologically separated (Riney 1982). However, the introduction of wildlife into areas where they have not naturally occurred in the past may upset this balance.

A study of the ecological separation between two species involves the quantification of spatial distributions, habitat selection, temporal activity patterns and feeding habits pertinent to the niche relationships of the two species (Pianka 1973; Anthony and Smith 1977). Additional studies of the potential competition among the species of an area may provide further insight into the ecological separation of the species under consideration (Scogings *et al.* 1990).

For the last four decades, research on African ungulates has described ecological separation by habitat choice (e.g.: Lamprey 1963; Hirst 1975, Engelbrecht 1986; Scogings *et al*. 1990; Wentzel 1990; Weaver 1995; Dekker 1996; Von Holdt 1999), by feeding ecology (De Wet 1988; Wentzel 1990; Von Holdt 1999) and by social behaviour (Keast 1965). Most of these and similar studies on ecological separation have concentrated on wildlife which have naturally evolved together and which tend to have obvious differences in terms of physiology, morphology, behaviour and ecological requirements.

Presently, with the large-scale increase in the number of wildlife ranches being developed throughout South Africa, landowners are keeping a wide range of species on their properties (Bothma 2002a). This is primarily being done to cater for local and overseas hunters and ecotourists. Therefore, more and more properties are confining ecologically similar wildlife within the same area. As a general rule in wildlife management, ecologically similar taxa should not be confined in small areas together. Wildlife that have the potential to hybridise will produce hybrids when the area of confinement is too small and the minimum herd size is not maintained (Du Toit *et al*. 2002).

The black wildebeest *Connochaetes gnou* and the blue wildebeest *Connochaetes taurinus* subsp*. taurinus* are two such ecologically similar types of wildlife that are currently being confined on the same properties in southern Africa. These two types of wildebeest separated from a common ancestor just over 1 million years ago (Brink *et al*. 1999). They therefore still have many morphological, physiological and behavioural characteristics in common. In addition they are able to hybridise, as reproductive isolation has not yet evolved (Fabricius *et al.* 1988), and the resulting offspring are fertile. Such hybridisation can have serious implications for the conservation of the two types of wildebeest and warrants urgent attention.

Many vital questions about the hybridisation process between the black and blue wildebeest remain unanswered. Factors that lead to hybridisation are still poorly understood and the ecological and behavioural differences between the two types of wildebeest still require in-depth investigation (Anon 2003a). Further research is also required to quantifiably define the ecological niche of the two types of wildebeest found in South Africa (Vrahimis 2003a). Such a study would be important in understanding whether there is any ecological separation between them. This information would also enable researchers to pinpoint possible ecological factors that can lead to hybridisation in areas where the two types occur together (Vrahimis 2003b).

Ecological separation, if it occurs between the two types of wildebeest, would be a mechanism that could limit interspecific competition and also aid in minimising hybridisation. If, however, the ecological requirements of both types of wildebeest do not differ in terms of spatial distribution, habitat, diet and behaviour, they would be considered to be too closely related ecologically to be kept in the same area without harming each other or the habitat, and the possibility of hybridisation would be high.

Under natural conditions, different habitat preferences are probably the main mechanisms that are ecologically separating the black and blue wildebeest (Codron and Brink In press). Factors that reduce the extent of contact between these two types of wildebeest, such as large areas with enough habitat heterogeneity to provide suitable, but separate, habitats for both types of wildebeest, or with distinctive geographic barriers, may assist in reducing, but not necessarily eliminating, the hybridisation risk (Vrahimis 2003a). Although areas may look structurally and compositionally homogeneous, the two types of wildebeest may prefer them differentially. Subtle differences in specific vegetation parameters such as grass height, plant biomass, veld condition, species composition and grass canopy cover may be responsible for such differential choice. However, this may not occur when they are both confined to an area where habitat diversity is low.

Both the extant types of wildebeest in South Africa have similar mating and calving seasons as well as a fairly similar social organisation. It has been suggested that the width of the mouth determines the level of selection for high-quality food items (Owen-Smith 1982) and therefore different ungulate species may be more proficient when feeding in grass swards of different growth stages (Murray and Brown 1993). Morphological observations do not support a trophic difference between the two types of wildebeest as there is no statistical difference in the width of the premaxillae (Brink *et al*. 1999). Measurements of the premaxillae show a mean width of 72.3 mm in the blue wildebeest and one of 74.9 mm in the black wildebeest (Roberts 1951). This suggests that grasses will be cropped at the same height and in essentially a similar way by the black and the blue wildebeest. Both are also specialised grazers of short grasses. It is, therefore, unlikely that there will be any separation in terms of their feeding height.

Fossil evidence suggests that the morphological traits that are associated with the distinct territorial social behaviour of black wildebeest were the first to change, indicating that a shift in breeding behaviour (especially territoriality) accompanied the appearance of the first ancestral black wildebeest (Brink *et al*. 1999.). A shift to a more territorial behaviour is linked to the evolution of treeless grasslands in the central interior of southern Africa over a million years ago. According to Brink (*op.*

cit.) some of the black wildebeest's characteristic features, such as its large eye sockets, reduced nasal area and forward pointing horns, reflect its more territorial behaviour in comparison with the blue wildebeest. Such territorial behaviour is often observed in captivity by zookeepers, some of whom have, in the past, been attacked and killed by black wildebeest individuals. The evolution of larger eye sockets, reduced nasal area and forward pointing horns in the black wildebeest are all probably a response to the need to visually patrol and defend breeding territories in a treeless habitat without visual obstruction. In support of this view, it has been observed that dominant black wildebeest bulls that are kept in captivity in bushy areas tend to remove bush and tree branches with their horns, and break down tree canopies in an attempt to clear the area for better visibility (African Wildlife 2003). It can therefore, be expected that territorial behavioural differences between the black and blue wildebeest could be important as ecologically separating mechanisms where the two types are forced to co-inhabit an area with low habitat diversity.

Ezemvelo Nature Reserve in South Africa is a property where both types of wildebeest have been confined together. Its location on the inland plateau of South Africa, its diversity of habitats and its relatively large size (8 468 ha), provided an opportunity to investigate the ecological separation of the black and blue wildebeest where they have been confined together. According to Du Plessis (1969) blue wildebeest did not naturally occur on sourveld and Mentis and Duke (1976) found that it was ill adapted to such conditions. Von Richter (1971b) has also indicated that sour grassveld is not suitable habitat for black wildebeest. Therefore the mainly sourveld nature of Ezemvelo Nature Reserve forms a sub-optimal habitat for both types of wildebeest.

The objective of the present study was therefore to investigate the evidence for ecological separation of the two types of wildebeest at Ezemvelo Nature Reserve. To determine the possible ecological separation, the habitat preferences, resource utilization and potential interspecific competition between the two types of wildebeest, was investigated as recommended by Scogings *et al.* (1990). This information will be used to provide recommendations on the management of the two types of wildebeest in areas where they are confined together.

In view of the historical blue and black wildebeest distribution, their occasionally overlapping populations and their morphological, physiological and ecological similarities, it was expected that interspecific competition would occur between the two types of wildebeest in areas where they may be confined together. If so, it would act as a limiting factor to the black wildebeest mainly because of its smaller size as compared to the blue wildebeest. The aggressiveness and higher degree of territoriality of the black wildebeest bulls in comparison with the blue wildebeest bulls may, however, play some role in rivalling the overall dominance of the blue wildebeest under certain circumstances. On the other hand, the black wildebeest is less adaptable in terms of habitat use and area selectivity than the blue wildebeest. This characteristic makes the black wildebeest more prone to displacement by the more versatile blue wildebeest, due to exploitative interspecific competition. It was therefore expected that the black and the blue wildebeest were too similar ecologically to be kept together on Ezemvelo Nature Reserve, without harming each other or the habitat.

To arrive at the objective of investigating the evidence for ecological separation between the black and blue wildebeest, and to develop a relevant management proposal for the two types of wildebeest where they are confined together, the following key questions were addressed in the present study:

1. Is there any evidence of ecological separation between the two types of wildebeest in terms of habitat preferences, spatial distribution, temporal activity budgets and diet?
2. Does interspecific competition occur between the two types of wildebeest in terms of behaviour and resource use?
3. What are the population dynamics of the two types of wildebeest?
4. What is the impact of the black and the blue wildebeest on their habitat?
5. If the two types of wildebeest are to be kept on the same property, what management actions should be implemented to avoid interspecific competition if such interspecific competition is found to occur?
6. What management actions should be implemented to avoid damage to the habitat by the black and blue wildebeest if such damage is found to occur?

CHAPTER 2: THE STUDY AREA

INTRODUCTION

This study was conducted at Ezemvelo Nature Reserve in South Africa (Figure 2.1). The name eZemvelo means "back to nature" in the Zulu language. Currently Ezemvelo Nature Reserve is one of the largest privately owned grassland reserves in South Africa. It is an extremely important reserve from an ecological point of view as the grassland biome is a meagrely conserved biome due to the preponderance of agricultural activities and urbanisation in the areas that were previously open grasslands. Only approximately 1% of this biome is formally conserved in South Africa and many rare and endangered species can be found in the grasslands as it has an extremely high biodiversity (Low and Rebelo 1996).

Black and blue wildebeest have a long history of co-occurrence on certain areas of Ezemvelo Nature Reserve. In other sections of the reserve their co-occurrence is relatively recent. The entire reserve formed the study area for the present study.

Ezemvelo Nature Reserve supports ecotourism in the form of overnight accommodation, hiking trails, wildlife viewing and birding. It conserves a healthy population of oribi *Ourebia ourebi*, South Africa's rarest antelope, and provides habitat for a high diversity of grassland bird species.

LOCALITY

Ezemvelo Nature Reserve is situated 24 km northeast of Bronkhorstspruit on both sides of the border of the Gauteng and Mpumalanga provinces in South Africa. It lies between latitudes 25º 38' and 25º 45' South and longitudes 28º 55' and 29º 03' East on the topographical map sheets 2528DB and 2529CA (Government Printer 1996 and 1998). Figure 2.1 shows the position of the study area in South Africa within the grassland biome. The reserve falls within the mesic highveld grassland bioregion (Mucina *et al.* 2005) on the inland plateau of South Africa. The reserve is approximately 8 468 ha (84.68 km^2) in size, with approximately 45 km of boundary fencing. It is bounded on its southern side by Renosterpoort Private Nature Reserve and is surrounded on all its other boundaries by private farmland where both cattle production and crop agriculture are dominant practices.

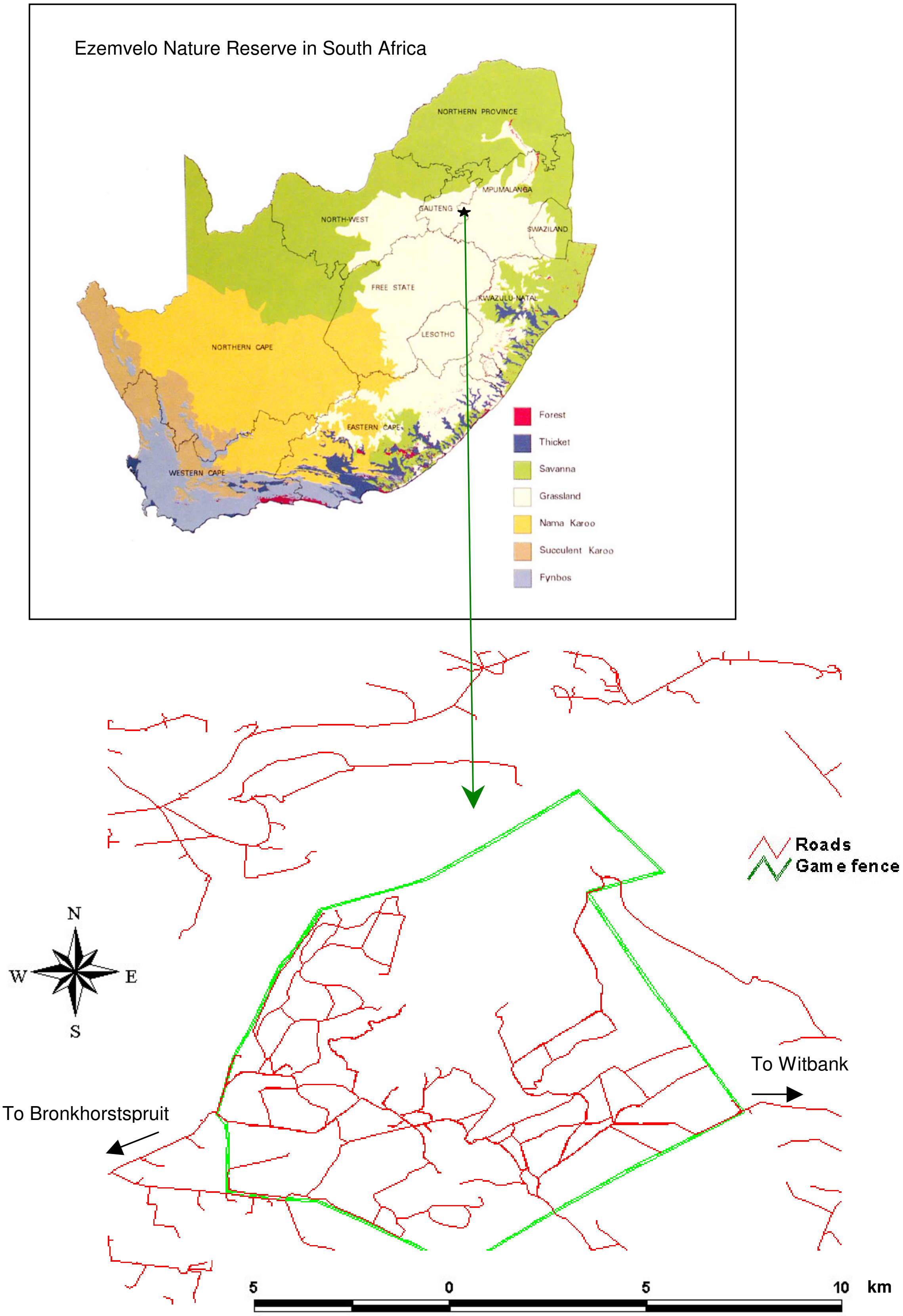


Figure 2.1: The location and boundaries of Ezemvelo Nature Reserve in the Grassland Biome of South Africa, indicating its position (star) on the border between the Gauteng and Mpumalanga provinces (Adapted from the map of Low and Rebelo 1996).

PHYSIOGRAPHY

Topography

Ezemvelo Nature Reserve ranges in altitude from 1 240 m above sea level at its lowest point to approximately 1 500 m above sea level at its highest point (Figure 2.2.). The landscape is dominated by open, grassy plains, which are broken by wooded, rocky ridges. The grassy plains occur on undulating hilly terrain. The east to west profile of the reserve consists of undulating hills in the east sloping gradually down to the Wilge River which bisects the reserve and then open plains gradually rising to the west. In the southeastern section of the reserve the topography is very broken, consisting of rocky cliffs where the Wilge River has cut through the landscape. The topography toward the north, slopes downward into a wide valley which stretches across the reserve from east to west and which is bound on the northern side by a steep ridge rising to a northern plateau. This open plateau is bounded by steep slopes in the north. The Grootspruit forms the northern boundary of the reserve in the west and drains eastwards into the Wilge River that continues in a north-easterly direction to form the northern boundary of the reserve in the east.

The Wilge River forms the northern boundary of the reserve in the northeastern section (Figure 2.2). The range in slope is from 0 to 30° and the slope shape is mostly convex (Land Type Survey Staff 1987).

Drainage

The perennial Wilge River divides the reserve almost in half and is fed by numerous streams that originate from higher-lying wetlands or sponge areas (Figure 2.2). The Wilge River flows northwards and eventually joins the Olifants River to the sea. The Grootspruit joins the Wilge River in the north and forms the northern boundary of the reserve in the west. The Sterkfonteinspruit occurs in the south of the reserve and joins the Wilge River in the middle of the reserve. Both of these smaller streams, along with another one, which flows to the eastern boundary of the reserve, contain water year round. Two large dams that are fed by perennial streams occur on the reserve, one on the western side and one on the eastern side. One small dam, also fed by a small stream, occurs in the northwestern part of the reserve. A few depressions fed only by rainfall also occur on the reserve.

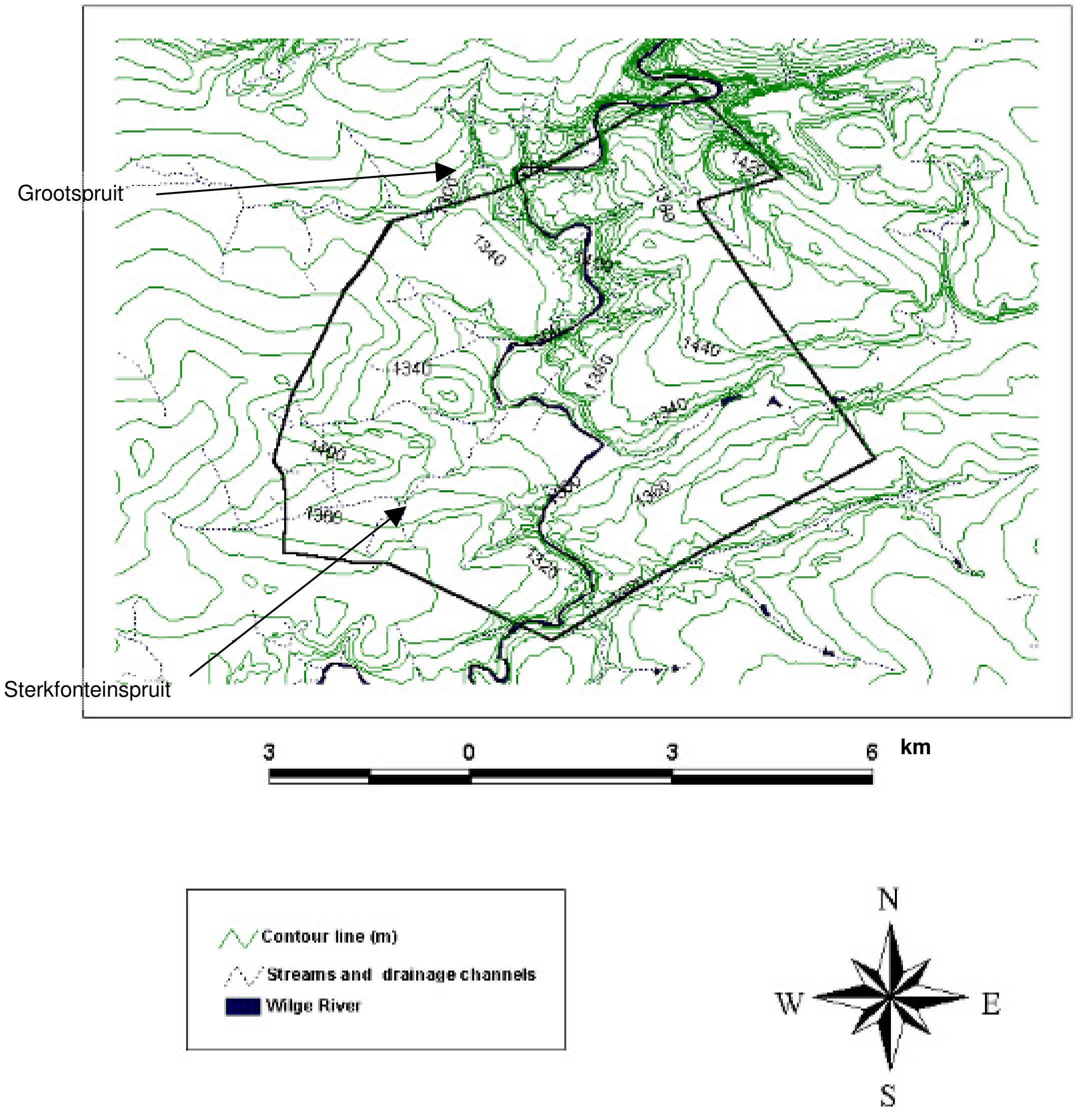


Figure 2.2: The topography and drainage at Ezemvelo Nature Reserve, South Africa. Adapted from the topographical mapsheets 2528DB and 2529CA (Government Printer 1996 and 1998).

There are no maintained artificial watering holes on the reserve as the available natural water sources have proved sufficient for the wildlife during normal rainfall years.

GEOLOGY AND SOILS

The reserve lies on the Wilge River Formation of the Waterberg Group and on the Ecca and Dwyka Formations of the Karoo Group that were formed during the Mokolian and Palaeozoic Eras respectively (1:250 000 geological series map sheet 2528 Pretoria (Geological survey staff 1978)) (Figure 2.3). The lithology of the Karoo Group is dominated by an arenite conglomerate which produces dystrophic or mesotrophic soils. The tillite-arenite produces some rocky areas with miscellaneous soils. The Wilge River Formation consists almost entirely of sedimentary rocks such as sandstone, but in parts it is intruded by conglomerate and igneous rocks. The sandstone parent material is rich in iron oxides and consequently has a red to purplish colour. Its subsequent weathering has resulted in red beds that contain characteristically deep, red soils (South African Committee for Stratigraphy 1980). There are also small amounts of manganese oxide in these Waterberg sediments.

The slope of the Wilge River Formation is gentle to the south in the plains, but steep in the river valleys. The depositional characteristics of the conglomerate and shale are indicative of an alluvial environment, with transportational direction from the northeast. Cross-layeredness in the sandstone indicates the presence of a desert or dune-veld previously (Lurie 2001).

The red colour of the rocks represents oxidised hematite, which indicates that the atmosphere at the time of formation was strongly oxidising. In some areas diabase occurs, which either covers the formation as plates, or is interspersed with it. These plates are gabbroic to diabasic, with the most important minerals being plagioclase and hornblende (South African Committee for Stratigraphy 1980).

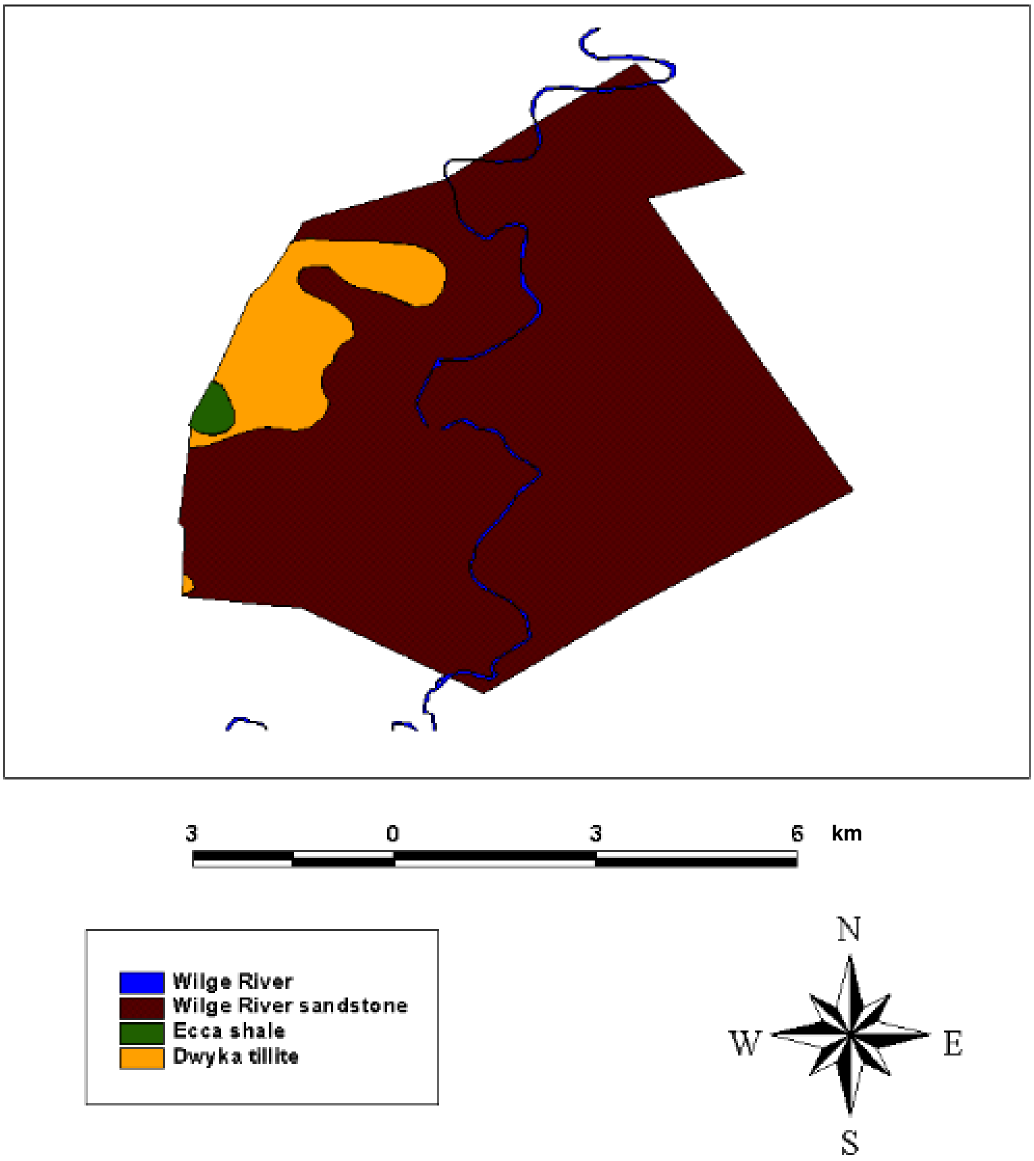


Figure 2.3: The geology at Ezemvelo Nature Reserve, South Africa. Adapted from the 1:250 000 geological series map sheet 2528 Pretoria (Geological survey staff 1978).

The soils include Hutton, Clovelly, Katspruit and Rensburg soil forms, and are highly weathered with diagnostic dystrophic (highly leached), red and yellow to brown, apedal characteristics (Soil Classification Working Group 1991). The soil texture is generally sandy to sandy loam with 10 to 20% clay, and with little structure except for in the bottomland areas. The sandy nature of the soils makes them susceptible to forces of water erosion especially under conditions of poor ground cover.

The red and brown soil colours indicate adequate drainage and aeration. Grey soils that occur along the drainage lines indicate waterlogged to wet conditions (Land Type Survey Staff 1987).

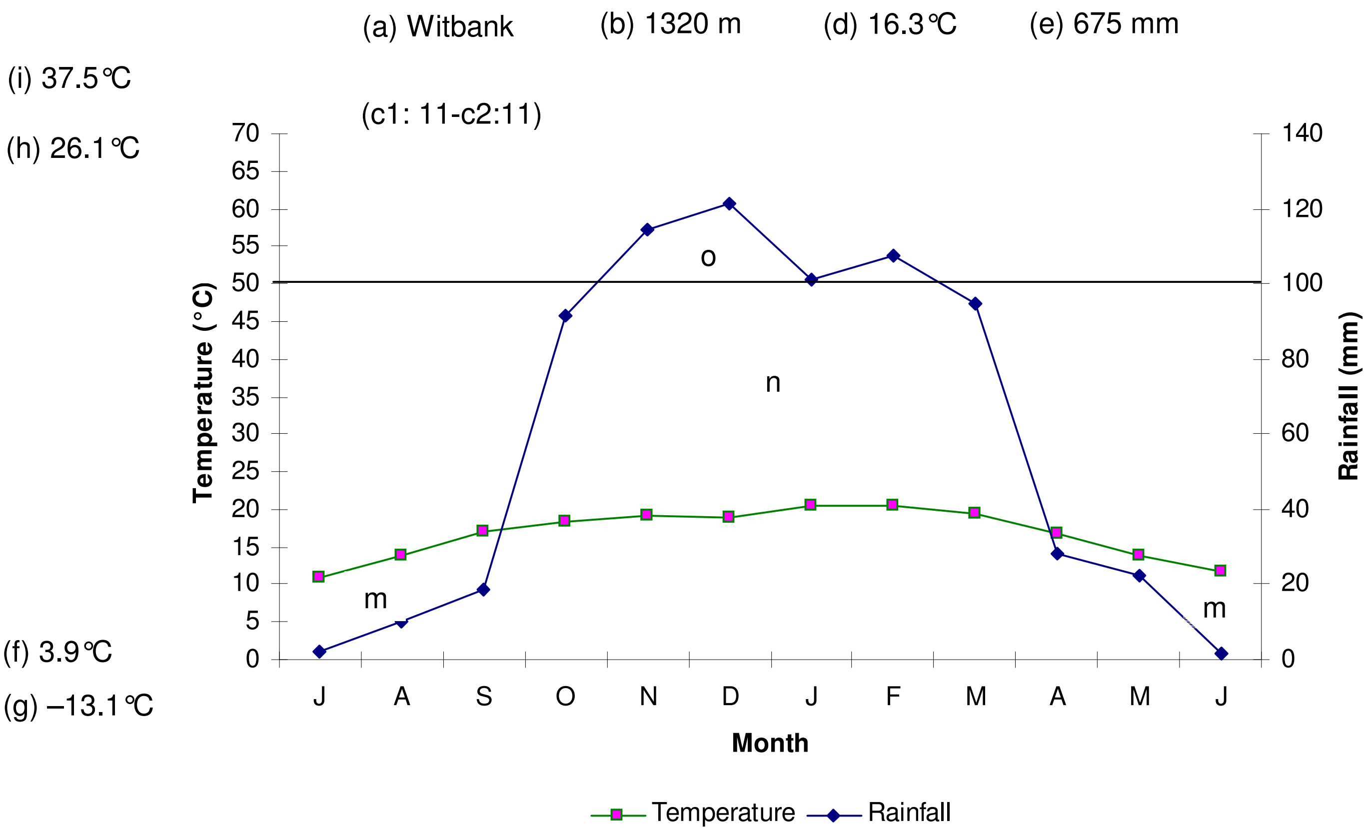
Although it is calculated that the earth is approximately 4.6 billion years old, relatively younger rock formations are found on the reserve. The red-brown, sandstone of the Wilge River Formation that is widespread in the reserve is approximately 1.9 billion years old (South African Committee for Stratigraphy 1980).

CLIMATE

Rainfall data statistics were calculated from the data for the Bronkhorstspruit Weather Station (0514408X) by using data from 1970 until November. Rainfall data from November 2003 data was obtained from the reserve records. The climate diagram for temperature and rainfall following Walter's convention (Walter 1979) (Figure 2.4.) gives an indication of the distribution of the temperatures and rainfall throughout the year taken from a mean of 11 years (1993 to 2003) for the Witbank Weather Station (05153208) as temperature statistics were not available from the Bronkhorstspruit Weather Station.

Temperature

According to the long-term records at the Witbank Weather Station, the highest temperature over the period between 1970 and 2003 was 37.5ºC while the lowest temperature recorded during the same period was –13.1ºC. The mean daily minimum temperature of the coldest month (July) and the mean daily maximum temperature of the hottest month (January) were 3.9 and 26.1ºC respectively, and the mean annual temperature was 16.3ºC. These values were similar to publications by the Land Type Survey Staff (1987) which indicated that the mean daily minimum temperature of the coldest month (June) and the mean daily maximum temperature



a = Weather station

b = Altitude

c1 = Duration of temperature data recording

c2 = Duration of rainfall data recording

d = Mean annual temperature

e = Mean annual long-term rainfall

f = Mean daily minimum temperature for the coldest month

g = Absolute minimum temperature

h = Mean daily maximum temperature for the warmest month

i = Absolute maximum temperature

m = Dry period

n = Wet period

o = Perhumid period (rainfall above 100mm)

Figure 2.4: Climate diagram for rainfall (mm) and temperature (℃) as determined following Walter’s convention (Walter 1979) from July to June based on data obtained from the Witbank Weather Station from 1993 to 2003.

of the hottest month (January) were –0.7 and 27ºC respectively . Frost occurs in the winter months from May to August.

According to data from the Land Type Survey Staff (1987), the mean duration of the frost period in the area in which Ezemvelo Nature Reserve is situated, is 115 days. In addition, the earliest frost date recorded for the area was 12 April and the latest frost date was 19 September.

Rainfall

According to the climate diagram, the wet period is from October to March and the dry period is from May to August (Figure 2.4). Figure 2.5 gives an indication of the rainfall pattern since 1970 as measured at the Bronkhorstspruit Weather Station. According to this data the wettest month was generally January and the driest month was generally July. The mean annual rainfall for the area in which the reserve is situated as calculated from the totals obtained from the Bronkhorstspruit Weather Station, was approximately 650 mm and ranging from 412 mm (1998) to 949 mm (1989). The rainfall data for Ezemvelo Nature Reserve, gathered from 10 regularly checked rain gauges, are available since November 2003. Reserve data before this time is not reliable and therefore could not be used. The actual rainfall that fell during the study period (January 2004 to August 2005) is presented in Figure 2.6. The annual rainfall that fell during the study period was 644 mm indicating that it was a normal rainfall period. The three years before the study was undertaken were below average rainfall years with a total annual rainfall of 556 mm, 506 mm and 531 mm for 2001, 2002 and 2003 respectively, as calculated from the Bronkhorstspruit Weather Station data.

Ezemvelo Nature Reserve falls in the summer rainfall region of South Africa. Conditions for rainfall in the study area, which is in the highveld region of South Africa, are most favourable when there is an anti-cyclone off the east coast of South Africa and a low-pressure system over the interior (Preston-Whyte and Tyson 1988). Moist air from the Indian Ocean that reaches the plateau is usually unstable. Such atmospheric conditions give rise to conventional destructive thundershowers of high intensity, creating a high potential for erosion. In the winter, the days are generally cool and cloudless and the nights are frosty. This is mainly due to a high-pressure cell over the interior and the influx of dry air over the plateau (Preston-Whyte and Tyson 1988).

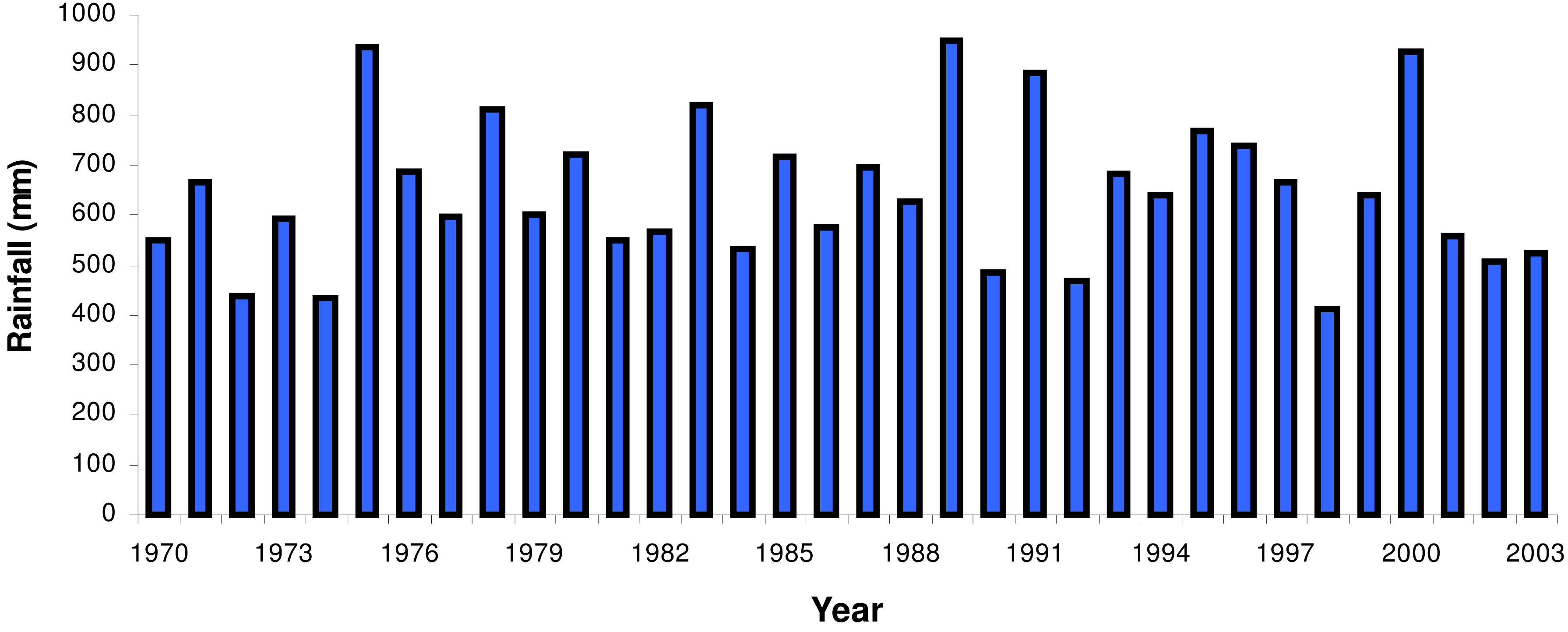


Figure 2.5: Long-term total annual rainfall (mm) for the Bronkhorstspruit Weather Station (0514408X), closest to Ezemvelo Nature Reserve in the Gauteng Province of South Africa from 1970 to 2003.

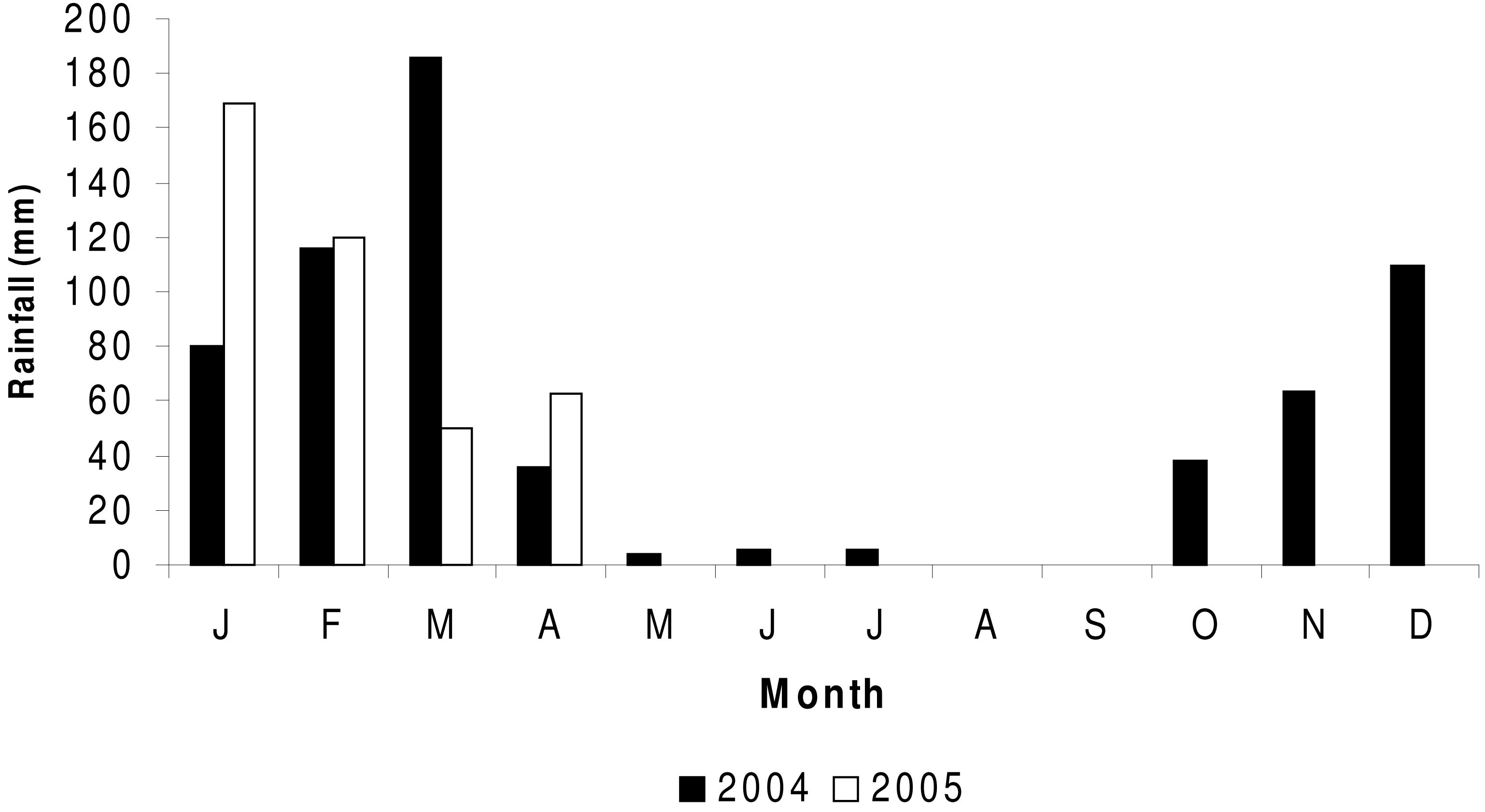


Figure 2.6: The actual total monthly rainfall (mm) received during the study period (January 2004 to August 2005) at Ezemvelo Nature Reserve, South Africa.

SEASONAL DIVISIONS

Three ecological seasons were identified at Ezemvelo Nature Reserve for the present study to mirror the effects of the phenological cycle of plants. Grasses often start to produce new leaves and emerge from dormancy before the onset of the first rains, indicating that a factor other than rainfall is responsible for the onset of the growth of dormant grass plants (Anslow 1966; Larcher 1995). Seasonal variation in grass leaf emergence largely appears to reflect changing temperatures (Tainton 1999). Light and temperature are the most important factors influencing leaf growth (Larcher 1995; Tainton 1999). It was assumed, based on studies of temperate plants that the cut-off temperature below which grass plants become dormant was 15°C (Larcher 1995; Tainton 1999). Mean daily temperatures for each month, based on the data from the Witbank Weather Station, were therefore used to determine the months when the mean daily temperature was below 15°C and when it was equal to or above 15°C (Figure2.4). This enabled making a division of the months of the year into a cold season (dormant season or winter) and a warm season (growing season or summer). The warm season was further delineated into an early growing season (early summer) and a late growing season (late summer) based on biomass accumulation rates (Grossman 1982), which are related to the mean rainfall during those months. Three seasons were therefore delineated.

The January to April period (late growing season) was characterised by abundant green forage, high temperatures and frequent thunderstorms. Wildebeest were in excellent condition at this time, having just calved during early December, allowing the calves to utilise the abundant forage available and keeping the cows in good condition to produce abundant milk. The May to August period (dormant season) was characterised by maturation and drying of grasses, low rainfall, and mean daily temperatures below 15°C. Forage was dry and low in nutrient content. The September to December period (early growing season) was characterised by increasing mean daily temperatures, increasing occurrence of rain showers, and the growth of grasses stimulated by the rising temperatures (sprouting) and the increase of rainfall (growth and flowering). The most critical period for wildebeest was at the end of the dormant season and the beginning of the early growing season due to low abundance of quality forage. Other factors beside temperature can also affect the onset of the growing season. The growing season can be accelerated by the occurrence of fire. At the same time the growing season can be delayed due to a paucity of fire where moribund material prevents new shoots from sprouting (Tainton 1999).

VEGETATION

The overall vegetation of the reserve can be classified as the eastern variation of the Bankenveld, which has been described by Acocks (1988). Low and Rebelo (1996) classify the vegetation in the area occupied by the reserve as a combination of the Moist Sandy Highveld Grassland, Rocky Highveld Grassland and the Moist Cool Highveld Grassland variations. More recent classifications have classified the vegetation of the area in which the reserve occurs as Rand Highveld Grassland and Loskop Mountain Bushveld (Mucina *et al*. 2005).

The Bankenveld is a transitional zone between the Savanna and Grassland Biomes. The grassland areas of the reserve cover approximately 4 688 ha and are characterised by large open plains that are interspersed with wetland areas, old lands, patches of alien vegetation and a few rocky outcrops. Savanna dominates the mountainous areas of the reserve, covering an area of approximately 3 780 ha and is characterised by the occurrence of a higher tree density than the grassland areas. The Wilge River that bisects the reserve is bordered by dense riverine bush.

The sandstones of the Wilge River formation is usually associated with the following indigenous trees in the rocky areas: *Englerophytum magalismontanum* (stem fruit), *Vangueria infausta* (wild medlar), *Faurea saligna* (Transvaal beech), *Burkea africana* (wild syringa), *Combretum apiculatum* (red bushwillow), *Cussonia paniculata* (mountain cabbage tree), *Strychnos pungens* (monkey orange), and *Protea caffra* (highveld protea). The diabase intrusions are characterised by thorn trees, among these the sweet thorn *Acacia caffra* and by *Gymnosporia* species. Vegetation in such diabase intrusions is easily seen from the air, as the areas are densely wooded, contrasting with the scattered vegetation on the sandstones. Intrusions of igneous rocks, especially diabase, are characterised by lowlands, wetlands, and the rockless strips through the hills of the reserve. Trees with thorns such as the *Acacia* species are found in these areas.

No detailed vegetation assessment had been conducted for the whole reserve at the onset of this project. A detailed vegetation classification is currently being compiled by A. Swanepoel at the University of Pretoria but was not available at the time of writing.

ANIMALS

Table 2.1 provides a list of the large mammals found at Ezemvelo Nature Reserve. Approximately 250 species of bird have also been identified on the reserve.

RESERVE HISTORY

The information for the compilation of this section was obtained through interviews with staff and management at Ezemvelo Nature Reserve as well as from the local inhabitants of the area. Although every care has been taken to ensure its accuracy based on these interviews, no responsibility will be taken for any errors or ommisions.

Ezemvelo Nature Reserve is privately owned by the Oppenheimer family and is made up of a number of farms that were purchased over the years (Figure 2.7). In 1974, the Oppenheimer family first purchased 1 640 ha from the owners of the magazine, Farmer’s Weekly, to build a house and develop an organic garden. This was done in the eastern section of the present reserve and the area involved was named Telperion Farm (Section 1).

In 1980 another 855 ha of land (Section 2), which already had a variety of wildlife species on it, including both black and blue wildebeest, was bought from Captain P. Grobler. This land bordered on the southern section of the land previously bought. The area was then incorporated into Telperion Farm and called Telperion Nature Reserve. In 1984, another 386 ha of land to the south of the nature reserve (Section 3) was purchased and the whole reserve became 2 881 ha in extent. Of this, 20 ha was used for planting lucerne to produce bales to sell to the public.

Another 913 ha (Section 4) were bought in 1988 to increase Telperion Nature Reserve to 3 794 ha in size. This new area was called the Tshuswane section (the name meaning ant) and the older part was called the Isipethu section (the name meaning little stream).

Table 2.1: Large mammals found at Ezemvelo Nature Reserve.

Common Name	Scientific Name
Herbivores	
Black wildebeest	*Connochaetes gnou*
Blesbok	*Damaliscus pygargis phillipsi*
Blue wildebeest	*Connochaetes taurinus taurinus*
Burchell's zebra	*Equus burchelii*
Common eland	*Taurotragus oryx*
Common reedbuck	*Redunca arundinum*
Common warthog	*Phacochoerus africanus*
Gemsbok	*Oryx gazella*
Giraffe	*Giraffa camelopardalis*
Greater kudu	*Tragelaphus strepsiceros*
Grey duiker	*Sylvicapra grimmia*
Impala	*Aepyceros melampus melampus*
Klipspringer	*Oreotragus oreotragus*
Mountain reedbuck	*Redunca fulvorufula*
Oribi	*Ourebia ourebi*
Ostrich	*Struthio camelus*
Red hartebeest	*Alcelaphus buselaphus caama*
Springbok	*Antidorcas marsupialis*
Steenbok	*Raphicerus campestris*
Waterbuck	*Kobus ellipsiprymnus*
White rhinoceros	*Ceratotherium simum*
Carnivores	
Aardvark	*Orycteropus afer*
Aardwolf	*Proteles cristatus*
African civet	*Civettictis civetta*
Black-backed jackal	*Canis mesomelas*
Brown hyaena	*Parahyaena brunnea*
Caracal	*Caracal caracal*
Leopard	*Panthera pardus*
Serval	*Leptailurus serval*
Primates	
Baboon	*Papio hamadryas*
Vervet monkey	*Chlorocebus pygerythrus*

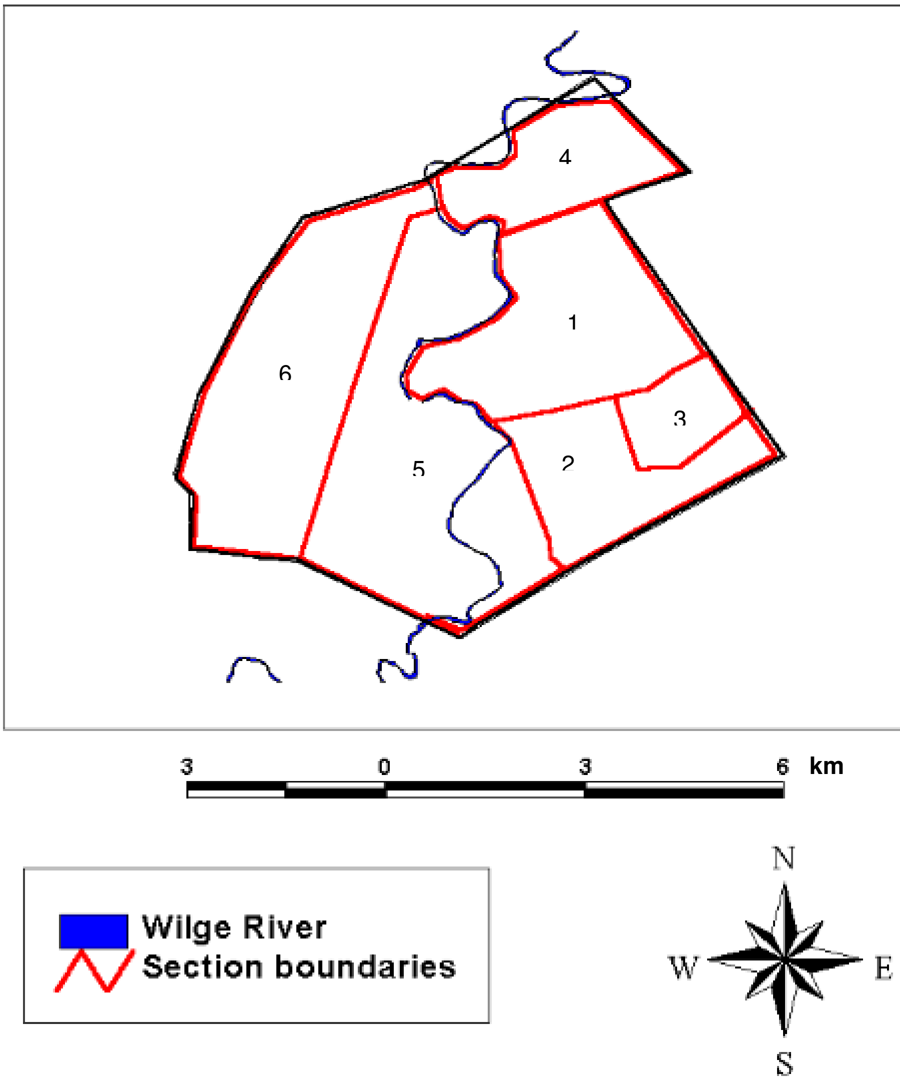


Figure 2.7: The distribution of the various sections purchased since 1974 by the Oppenheimer family to form the current Ezemvelo Nature Reserve, South Africa. The numbers on the map indicate Section 1 to 6 as described in the text.

In 1990 the planting of lucerne stopped and a breeding centre for Nguni cattle was started. A number of problems were experienced with the cattle as a result of the prevalence of malignant catarrhal fever caused by the intermingling of cattle and black and blue wildebeest on the reserve.

In 1993 the neighbouring cattle farm on the western side of the Wilge River burned down and the owner G. Britz sold it to the Oppenheimers in 1994. The 2 590 ha area was named Bohlokwa (the name meaning important) (Section 5). In a 15-year period prior to the incorporation of Bohlokwa into the Telperion Nature Reserve, two different owners had made use of the land. The first owner practised poultry production and maize was produced on the areas suitable for cultivation. Thereafter, a large portion of the cultivated area was re-established to permanent pasture by the second owner. Yellow maize, feed sorghum and lucerne were grown on a limited scale in the rest of the cultivated areas to provide conserved feed for the cattle. Mixed agriculture was also practised. Crops such as maize, sunflower, potatoes and groundnuts were produced with some success. Animal production systems were practised including cattle, wildlife, sheep, goats and chickens. Both the previous owners made use of inorganic inputs such as fertilisers.

The Oppenheimers practised only organic farming and the cattle on Telperion Nature Reserve were moved to the Bohlokwa section. In 1997 a peach production project was initiated at Bohlokwa. A population of 6 500 trees was cultivated in a peach orchard until 2003 when they were cut down.

In 1998 the Van Wyk family sold a 2 084 ha wildlife park on the western boundary of Bohlokwa known as eZemvelo to the Oppenheimers to increase the land owned by them to 8 468 ha (Section 6). This new section contained a variety of wildlife such as common eland *Taurotragus oryx*, greater kudu *Tragelaphus strepsiceros*, impala *Aepyceros melampus melampus*, white rhinoceros *Ceratotherium simum*, ostrich *Struthio camelus*, waterbuck *Kobus ellipsiprymnus*, blesbok *Damaliscus pygargus phillipsi*, and black wildebeest. The whole area was then renamed Ezemvelo Nature Reserve.

Initially eZemvelo was kept separate from the other areas by keeping the boundary fence in place. In 2000 a flood washed away the fenceline separating the Isipethu and Bohlokwa sections, allowing wildlife to cross the Wilge River and mix with the wildlife on the other side. In 2002 the Nguni cattle were removed from the reserve and the fence between Bohlokwa and eZemvelo was taken down. Ezemvelo Nature Reserve has been operating as a unit since 2002 with regard to wildlife movements. Wildlife are now free to move throughout the 8 468 ha reserve, only being restricted from crossing the Wilge River when it is in flood, something which occurs for a few weeks every two to four years.

HISTORY OF THE BLACK AND BLUE WILDEBEEST POPULATIONS

Since at least 1980 there were both black and blue wildebeest on the eastern side of the Wilge River in the Isipethu section. Records of the number of wildlife for this section only date back to 1991 and the black and blue wildebeest numbers since that time up until 2000 when the fence separating the two sections was washed away appear in Figure 2.8. It is clear that there was a small number of black wildebeest on the Isipethu section that struggled to reproduce since 1991. The blue wildebeest were, however, successful and their numbers increased over the years. No culling or wildlife capture has ever taken place on the Isipethu section since it was taken over by the Oppenheimer family.

However, wildlife capture and hunting operations were a regular feature in the eZemvelo section over the years, but these records along with wildlife census data are not available for this section before 1998.

Before 2000 the black wildebeest population on the eZemvelo section had not come into contact with blue wildebeest. The results of the wildlife counts conducted on this section between 1998 and 2001 are shown in Figure 2.9.

During the time of the study, there were five main herds of black wildebeest occurring on the western side of the Wilge River. There were only seven black wildebeest left on the Isipethu section of the reserve on the eastern side of the Wilge River. There were four large herds of blue wildebeest on the eastern side of the Wilge River and at least three more large herds on the western side of the river in 2004. At the start of the study there were 98 black wildebeest and 256 blue wildebeest on the entire reserve of 8 468 ha (Tau 2004 pers. comm.)[1].

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[1] Mr. M. Tau. Manager, Ezemvelo Nature Reserve. P.O. Box 599, Bronkhorstspruit, 1020, South Africa. ezemvelo@telkomsa.net

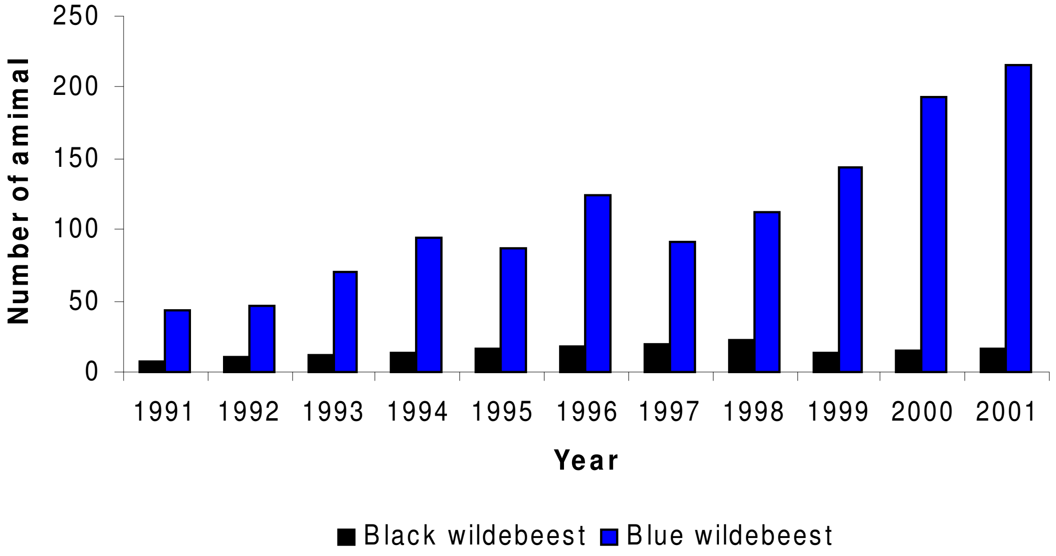

Figure 2.8: The number of black and blue wildebeest on the Telperion Nature Reserve from 1991 to 2001.

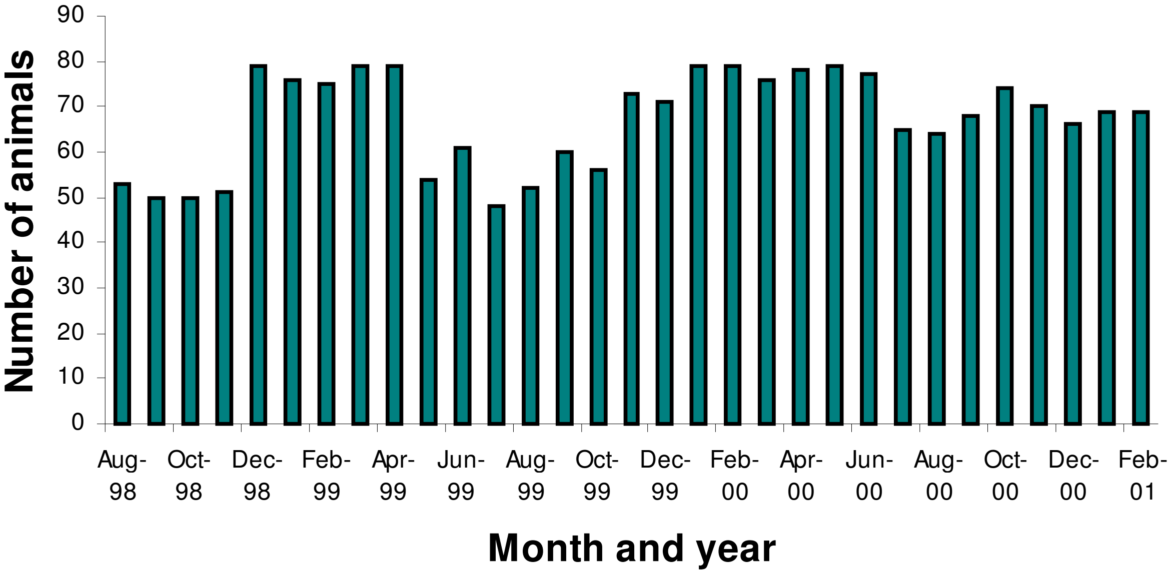

Figure 2.9: The number of black wildebeest on the eZemvelo section of Ezemvelo Nature Reserve from 1998 to 2001.

All the blue wildebeest occurring on the western side of the Wilge River during the time of the study had migrated there from the Isipethu section after the fence along the Wilge River was washed away in 2000.

CHAPTER 3: THE BLACK AND BLUE WILDEBEEST

TAXONOMY OF THE GENUS *CONNOCHAETES*

Both types of wildebeest belong to the Kingdom Animalia, the phylum Chordata and the class Mammalia. They are placed in the order Artiodactyla, which contains all the even-toed animals. They are grouped into the family Bovidae due to them being in possession of horns. All African antelope species are grouped into this family as well as the various species of buffalo *Syncerus caffer*. The wildebeest are placed in the subfamily Alcelaphinae, which comprises three genera namely *Connochaetes* (wildebeest species), *Alcelaphus* (hartebeest species) and *Damaliscus* (tsessebe species, blesbok and bontebok *Damaliscus pygargus dorcas*). The Alcelaphinae subfamily is characterised by both sexes having horns, well-developed pre-orbital glands and pedal glands on the front feet, which are rudimentary or absent on the hind feet, and no inguinal glands. The females of this subfamily have a single pair of mammae (Smithers 1986). Both wildebeest species belong to the genus *Connochaetes* due to the horns being smooth throughout and directed downwards initially. Prominent facial tufts of hairs, a neck mane and a fringe of hairs either on the throat or on the chest between the fore limbs further characterise this genus (Ansell 1974).

Five subspecies of the blue wildebeest occur on the African continent, but *Connochaetes taurinus taurinus* is the only one naturally occurring in South Africa. There are no subspecies of the black wildebeest and the only existing species is endemic to South Africa.

DESCRIPTION OF THE *CONNOCHAETES* SPECIES

Field characteristics

Black wildebeest

Also called the white-tailed gnu, the males of the black wildebeest stand approximately 120 cm at the shoulders and weigh from 147 to 193 kg whereas the females are lighter and smaller being from 120 to 160 kg and standing approximately 110 cm at the shoulders (Smithers 1983; Furstenburg 2002a). Both sexes carry horns arising from expanded bases, sweeping downwards and forwards and then curving upwards. Males have thicker and heavier horns than females. Buffy brown is the general coat colour with darker faces. The males become darker brown, almost black as they age. Juveniles have shaggy fawn-coloured coats and straight horns that only start to curve at about 1 year of age. The tail is dark at the base, becoming off-white toward the tip and reaching almost to the ground. The manes are high and erect with the hairs at the base a creamy colour becoming black at the tips. A distinct beard of long hair is present, as well as a brush of long hair between the eyes and the nostrils (Smithers 1983; Furstenburg 2002a). Territorial bulls utter a loud call often described as an 'oink' (Mills and Hess 1997). Life expectancy is about 16 years for males and 18 years for females and the natural population growth rate is approximately 28 to 33% annually (Furstenburg 2002a).

Blue wildebeest

Also called the brindled gnu, adult males of the blue wildebeest stand approximately 150 cm at the shoulder and weigh from 210 to 260 kg, while females are smaller standing 135 cm tall and weighing from 170 to 200 kg (Attwell 1977; Furstenburg 2002b). Their heads are massive and elongated, broadening out at the lips and nostrils. A distinct beard of long black hair occurs on the chin. The overall coat colouring is dark grey tinged with brown and with a silvery sheen. A series of dark coloured bars occur on the neck and shoulders, extending to about the middle of the body to give a brindled appearance. Juveniles and females are browner than the adult males and may have more of a russet colour on the forehead, extending from the forehead to between the eyes. Manes of long black hair, long whisks of black hair on the ends of their tails and a fringe of long black hair occurs down the throat. Both sexes carry horns which sweep outwards and slightly downwards and then rise upwards to the inwardly pointing tips often directed slightly backwards (Smithers 1983). The mean life expectancy is the same as for the black wildebeest (Furstenburg 2002b).

Morphological separation

Morphological separation of the two types of wildebeest is based on horn direction and tail colour. The black wildebeest has horns that are directed downwards before curving up, with the muzzle not noticeably elongated and a white tail. The blue wildebeest has horns directed outwards and slightly downward before curving upwards, a muzzle and nasals noticeably elongated and a black tail. The blue wildebeest also has rudimentary pedal glands on the hind feet (Ansell 1974), which are absent in the black wildebeest. The black wildebeest is generally smaller than the blue wildebeest, with the males of black wildebeest weighing approximately 180 kg, whereas the males of blue wildebeest weigh approximately 250 kg (Smithers 1983; Furstenburg 2002a and b). Brindles on the neck and shoulders are present in the blue wildebeest but not in the black wildebeest.

Distribution and status

Black wildebeest

The natural occurrence of the black wildebeest is limited to the central inland plateau of South Africa (Figure 3.1). Therefore, it is endemic to South Africa. It was specifically known to have occurred in the Free State province, the highveld regions of the southern, central and northern Cape region, the southern parts of Gauteng, the southeastern parts of North West province and marginally in the grassland regions of KwaZulu-Natal province in the foothills of the Drakensberg Range (Von Richter 1974). The distribution coincides with the extension of the grassland and Karoo vegetation types as delineated by Acocks (1988). It therefore occupied the central grass and shrublands from south of Pretoria to close to the Swaziland border in the east and the Botswana border in the west. Its distribution southwards included the region south from the Kgalagadi Transfrontier Park in the west, south to and including the central Karoo (Plug and Badenhorst 2001). The black wildebeest is currently categorised as being of least concern on the Red Data List of Threatened Animals as compiled by the International Conservation Union (IUCN) (Friedman and Daly 2004).

Blue wildebeest

In the southern African subregion the blue wildebeest has a restricted distribution in Namibia but it is widespread in Botswana. It occurs in parts of the North West and Limpopo provinces, and throughout Mpumalanga province all the way south to near the Swaziland border (Smithers 1983). It also occurs southwards in the Hluhluwe-Imfolozi Park in KwaZulu-Natal and has a marginal occurrence in the Northern and Western Cape provinces (Figure 3.2).

It is particularly associated with open woodland where there is water (Smithers 1986). This type of wildebeest occurs in large numbers in Africa but due to loss of habitat and illegal hunting, numbers are declining drastically throughout Africa. Approximately 35 660 animals reside in South Africa, the largest populations existing in protected areas, while other large populations are present on privately owned

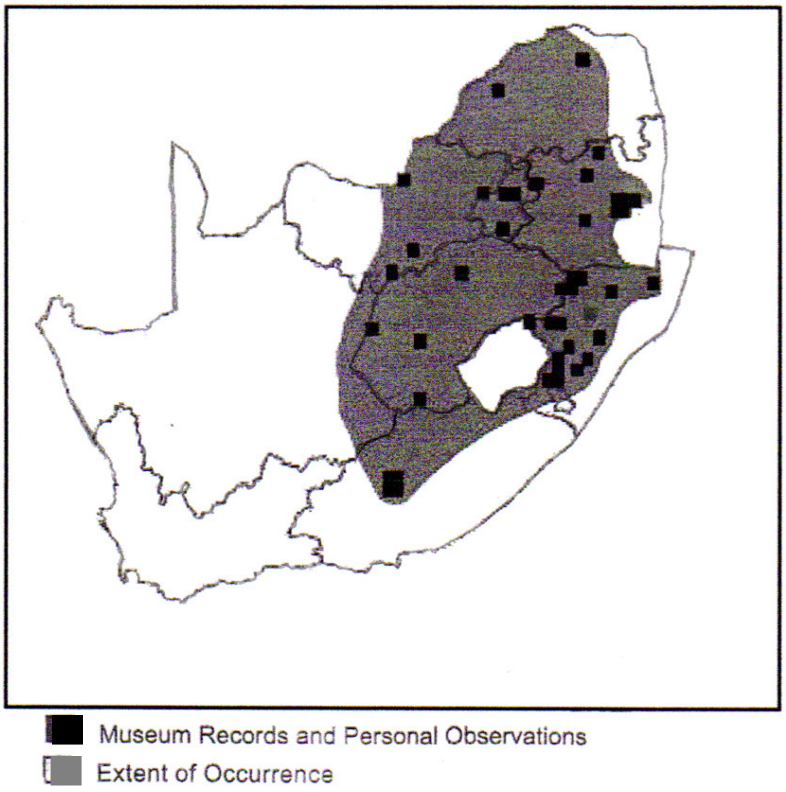

Figure 3.1: Current distribution of the black wildebeest in South Africa. Adapted from Friedmann and Daly (2004).

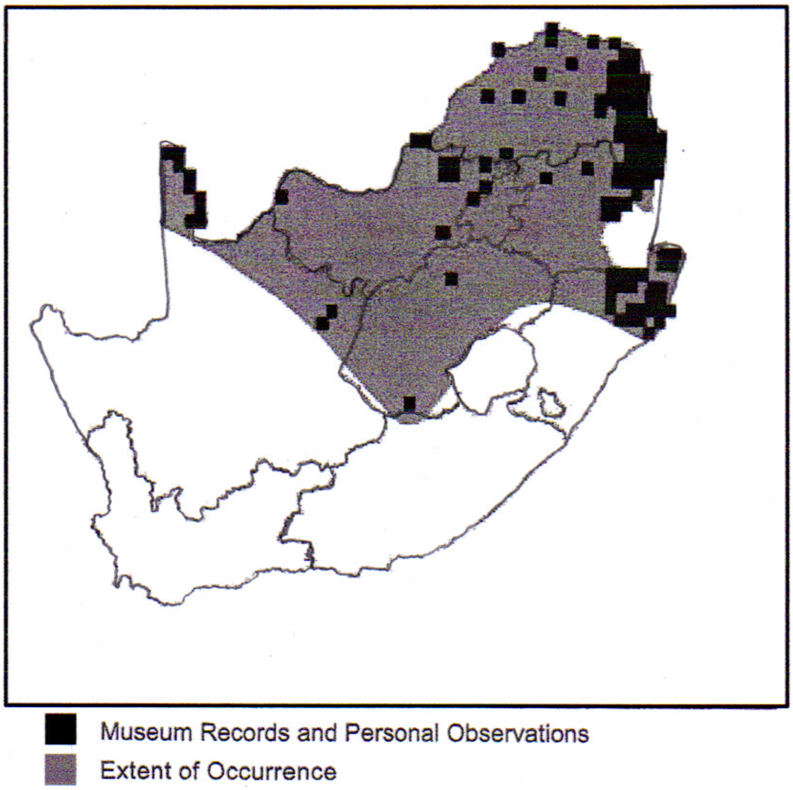

Figure 3.2: Current distribution of the blue wildebeest in South Africa. Adapted from Friedmann and Daly (2004).

wildlife ranches (East 1998). The species is not under threat in South Africa and is classified as of least concern in the latest IUCN Red Data List (Friedman and Daly 2004).

Du Plessis (1969) stated that the past geographical ranges of the black and blue wildebeest must have overlapped in parts of the Gauteng, Free State, and Northern and Western Cape provinces, at least seasonally. In these areas of overlap differences in the habitat preference of the two types of wildebeest would have kept them separate, as black wildebeest prefer short open grassland or karroid shrubland, whereas blue wildebeest prefer grassland associated with open woodland. Today, however, the black and blue wildebeest are confined together on many private properties throughout South Africa.

Ontogeny and reproduction

Black wildebeest

The black wildebeest has a gestation period of 250 to 260 days and is strictly seasonal in its calving time. The precise time of calving varies in different localities from the middle of November to the end of December (Smithers 1983; Furstenburg 2002a). A single calf is born, usually during the morning and is able to stand on its own within minutes of birth. They are weaned from six to nine months of age depending on the range condition. Sexual maturity is reached by the females from 16 to 18 months and they give birth for the first time at about two years of age (Furstenburg 2002a). Sexual maturity is reached by the males at about three years of age, but usually only the older males can procure a territory and thus partake in the rut (Von Richter 1974). The bond between a mother and her single calf is strong and the calf remains close to its mother for the early part of its life, but with the birth of her next calf the female drives it away (Smithers 1986). Day-length is the proximate factor influencing the breeding cycle of this species (Smithers 1983).

Blue wildebeest

Gestation is about 250 days and the main calving season is from mid-November to the end of December, with some births in May (Smithers 1983; Furstenburg 2002b). Although there may be an inherent rhythm in the breeding activities, such activities may be more influenced by prevailing climatic conditions (Fairall 1968). A single calf is born, weighing about 22 kg at birth. It can run with the herd within five minutes after birth (Smithers 1983).

Habitat

There are still large gaps in the literature regarding the habitat preferences of the black and the blue wildebeest on small nature reserves under artificial circumstances where predation is not a population control factor. Furthermore, no study has to date compared the two types of wildebeest ecologically on the same property.

Weaver (1995) conducted a study on the habitat utilisation of selected herbivores in the Klaserie Private Nature Reserve. In the dry season, a strong positive correlation between the number of blue wildebeest and distance from riparian vegetation, as well as distance from an established graded road was found. Habitats with good visibility in all directions and with 10 to 40% bare ground were preferred. It was also found that blue wildebeest had a clear affinity for habitats where *Aristida congesta* was the visually dominant grass species, and that there was a dry season preference for habitats where the visually dominant woody plant was a *Grewia* species. During the wet season the blue wildebeest was most often found in areas where there was heavy utilisation of the available grass biomass. These habitat preferences reflect the dependence of the blue wildebeest on water, as well as its affinity for semi-open to open grassland habitats and for areas that are dominated by increaser grass species.

Fabricius (1984) found that the most important abiotic factors affecting black wildebeest distribution in the Golden Gate Highlands National Park were slope, aspect and grass height, with moderate slopes, northerly aspects and short grasses being preferred. Schmidt (1988) described the habitat utilisation of black wildebeest in the Suikerbosrand Nature Reserve, and found that it tended to aggregate on northern slopes with an incline of 2 to 7º. Moreover, they especially concentrated on such areas in the winter. The preference for northern slopes was related to temperature. The black wildebeest was also found to concentrate on high-lying areas and on plateaus, probably because of behaviour such as territory defence and sighting predators. No study to date has found a relationship between the availability of surface water, with the distribution of black wildebeest. A preference for open grassland is probably associated with predation, as black wildebeest rely more on speed than on camouflage to escape predators. Open areas do not allow for concealment of approaching predators and this also relates to a preference for slopes and high-lying areas where the visibility over the surrounding terrain is high.

Food

Black wildebeest

Black wildebeest are predominantly grazers, although they may also make use of karroid shrubs. Their preferred habitat is the treeless, sweet grassveld and Karoo of the central South African plateau. Sour grass species that mature quickly and become unpalatable are only taken when fresh. Short grass veld is preferred and areas of tall, matured grass are avoided (Von Richter 1974). The species conditions its own preferred habitat by the tendency of herds to stay for prolonged periods in the same areas, thereby keeping the grass in the preferred short state (Von Richter 1971a). Utilisation percentages of the different components of the veld have been found to include 94% grass, 3% karroid shrubs and 3% herbs (Mills and Hess 1997). Black wildebeest turn to the karroid browse after the first winter frosts when the grass starts to lose its nutritional value (Mills and Hess *op. cit.*). Among the grasses *Sporobolus* spp., *Themeda triandra* and *Cynodon dactylon* are important as food. The karroid shrubs that are used as food include *Nenax microphylla, Salsola rabieana, Osteospermum leptolobum, Nolletia ciliaris* and *Pentzia* spp. (Smithers 1983). The black wildebeest practises an extreme form of area selection in reserves where migration is prevented (Von Richter 1971b).

Blue wildebeest

The blue wildebeest is virtually a pure grass eater. Attwell (1977) found that 96% of the rumen content was grass with the other 4% being negligible amounts of bark and browse. It is highly selective for leaf blade and sheaths throughout the year, taking a higher percentage of stems during the dry season than the wet. It prefers short grass (30 to 40 cm tall) and together with Burchell's zebra *Equus burchellii*, is the first herbivore species to appear on burnt veld (Grunow 1980). They are partial to fresh sprouting grass on burnt areas and will move in search of fresh green grass sprouting after rain (Smithers 1983).

Panicum spp., *Digitaria argyrograpta* and *Themeda triandra* are important in the diet in KwaZulu-Natal, and *Cynodon dactylon* is utilised when other grass species are heavily grazed (Attwell 1977). The habitat of the blue wildebeest can be described as open grassland, floodplain grassland, open bush savanna and light, open woodland (Smithers 1983).

Both types of wildebeest are dependent on water and their daily consumption is about 8.3 litres with a drinking interval of 47 hours (Du Toit 1991). Black and blue wildebeest also prefer natural water points to artificial waterholes.

Behaviour

Black wildebeest

This type of wildebeest is gregarious, with a social organisation involving territorial males, female herds and bachelor groups (Smithers 1983). Territorial males alone take part in the rut, and territories are marked by scent-marking with faeces and urine and the various glands on the body, including the preorbital and the interdigital glands (Furstenburg 2002a). The female herds consisting of females and their offspring wander freely over their territories. The bachelor herds are loose associations made up of adult, subadult and yearling males, with a lack of aggression between the members of this herd (Von Richter 1971a). The black wildebeest is most active in the early morning and late afternoon, resting in the middle of the day. Unlike most animals, it does not seek shade during midday. The open grassland habitat, which this species occupies, provides little shelter from the elements, as well as little cover from predators. Therefore, the black wildebeest needs to be constantly vigilant and relies on its speed when chased, rather than on camouflage to escape from predators.

Blue wildebeest

This type of wildebeest is also gregarious and occurs in herds of up 30 animals. It also has territorial males, female herds (nursery herds) and bachelor groups (Estes 1969). Territorially and sexually active bulls employ a number of ritual displays for different circumstances (Smithers 1983). Young males are evicted from the nursery herd at about 2 years of age. The social organisation of this species is much more fluid than that of the black wildebeest, and only becomes rigid during the breeding season. However, the males are not as territorial as they are in the black wildebeest.

Diseases

Wildebeest are prone to rinderpest, anthrax, bovine malignant catarrhal fever (snotsiekte / BMCF), foot-and-mouth disease and heart water (black wildebeest), amongst others. Snotsiekte and foot-and-mouth are the most important diseases affecting wildebeest distribution and movement.

Snotsiekte is a viral disease that is sustained in its reservoir host, the wildebeest, and has important consequences for the distribution of both black and blue wildebeest. This is because the disease can be highly destructive to susceptible cattle populations that may come into contact with infected wildebeest. Both black and blue wildebeest (also including all members of the subfamilies Hippotraginae and Alcelaphinae) are susceptible to the virus. Primarily the wildebeest calves excrete the virus, which may be the main reason why outbreaks of the disease occur mostly during the calving and weaning seasons (Du Toit *et al.* 1996). The virus has been isolated from nasal and occular secretions of wildebeest calves up to 3 months of age. It has been suggested that the virus replicates in the cornea and turbinates of young wildebeest calves (Mushi *et al.* 1981). The vector is currently unknown, therefore the mechanism of the transmission of the disease from wildebeest to cattle is still poorly understood. Both cattle and exotic ruminants show signs of the disease, whereas wildebeest are merely carriers of it.

Even though cattle and wildebeest graze in close proximity in many parts of South Africa, only sporadic outbreaks of snotsiekte are recorded. For example, during 2002 only two outbreaks were recorded in the KwaZulu-Natal province resulting in the death of nine head of cattle (Cooper 2003). This is due to the fact that although wildebeest are continual carriers of the disease, they do not necessarily excrete the virus and are therefore not always infectious to cattle.

Calves excrete the virus just after birth and during the stressful period of weaning. However, any form of stress such as capture, hunting and aerial counts will promote virus excretion, even in adult wildebeest.

The disease is limited to certain districts in South Africa (Du Toit 1991):

- High-risk districts are Pilgrims Rest, Bela Bela, Waterberg, Thabazimbi and Soutpansberg.
- Medium-risk districts are Brits, Mokopane, Letaba, Lydenburg, Barberton, Lephalale, Musina and Phalaborwa.
- Low-risk districts are all other districts in South Africa.

Therefore the study area falls within a low risk area for snotsiekte.

Control of the disease involves the prevention of contact between wildebeest and cattle, farm registration and the threat of litigation. However, it is realised that there are no scientifically proven control measures for BMCF, except the separation of cattle and wildebeest by wide distances and possibly the reduction of stress in wildebeest if cattle are kept in the vicinity (Cooper 2003). Wildebeest are crawlers and may be able to crawl under many types of game fencing. It is, therefore, recommended that electrified fences be erected in areas where wildebeest are on farms adjoining cattle ranches and that a separation distance of over 1 km is used as the minimum between wildebeest and cattle (Du Toit 1991).

The smaller the farm the higher the risk of outbreaks or contacts, and the lower the veld condition the greater the number of outbreaks (Du Toit 1991). Therefore, certain minimum farm sizes should be set for keeping wildebeest and the veld needs to be kept in a good condition.

Heart water is an indigenous bacterial disease that is a significant natural restrictor of the distribution of the black wildebeest in South Africa (Du Toit *et al.* 1996). The black wildebeest, like the springbok, is not indigenous to areas where the vector, the *Amblyomma* tick species, occurs naturally and are thus susceptible to the disease. Indigenous inhabitants of such areas are, however, immune.

Black wildebeest have also been found to be prone to swayback disease in areas with copper deficiency in the soil (Penrith *et al.* 1996). Copper deficiency can result directly from low dietary copper, or it can be induced in spite of adequate dietary copper by interactions with other minerals. This can be prevented by adequate copper supplementation in the form of licks or oral dosing. Swayback disease usually causes death in calves, and ataxia and microscopic lesions of myelopathy in adults (Penrith *et al.* 1996). This disease can have serious consequences for the survival of isolated populations on wildlife ranches in areas where the soils are prone to leaching and thus will have a copper deficiency.

Parasites

Parasite burdens are susceptible to wide seasonal fluctuations and in wild populations it can be one of the main causes for declines in population size. In a study of the blue wildebeest in the Kruger National Park and the black wildebeest in the Golden Gate Highlands National Park in South Africa, it was found that only *Haemonchus bedfordi*, a nematode and *Gedoelstia hässleri*, an oestrid fly larvae, were recovered in large numbers in both types of wildebeest (Horak *et al.* 1983).

Black wildebeest appear to be fairly resistant to parasitic infections and were found to have a much lower parasite load than the blue wildebeest. According to Horak *et al.* (1983), blue wildebeest harboured 13 nematode species, four cestode species, one trematode species, the larvae of five oestrid fly species, three lice species, seven ixodid tick species and one mite species. Black wildebeest on the other hand carried burdens of four nematode species, one cestode species, the larvae of five oestrid fly species, two lice species, four ixodid tick species and one mite species. The lower temperatures experienced by black wildebeest in their distributional range may be a significant contributor to the lower parasite burden of the black wildebeest.

HYBRIDISATION

Threats of hybridisation

Hybridisation is possible if the two taxa in question have not diverged too far, but the final outcome is unpredictable. It is widely believed that hybridisation is ephemeral, leading ultimately to either speciation or to fusion of two races by introgressive hybridisation (Moore 1977). This means that either a new species can be produced by hybridisation or two species can be fused into one.

The black wildebeest is endemic to South Africa and hybridisation with blue wildebeest poses a serious threat to the genetic integrity of the black wildebeest. Hybridisation may eventually also pose a significant threat to the genetic integrity of the blue wildebeest (Vrahimis 2003b). Black wildebeest numbers are still relatively low in South Africa and therefore, the risk of extinction remains, which if allowed to occur would result in a loss of endemic biodiversity (Anon 2003a).

Presently, with the large-scale increase in the number of wildlife ranches throughout South Africa, landowners are keeping a wider range of wildlife on their properties (Bothma 2002a). This is being done mainly to cater for local and overseas hunters and ecotourists. The result is more and more areas accommodating both types of wildebeest, with a concomitant potential increase in hybridisation.

Hybridisation is not only a threat to the types of wildebeest, but also to the livelihood of wildlife producers (Vrahimis 2003b). Blesbok *Damaliscus pygargus phillipsi* and bontebok *Damaliscus pygargus dorcas* hybridise freely, and only certified pure bontebok and blesbok are recognised in the Safari Club International Record Book.

Wildlife producers would have to go through costly procedures to ensure that their wildebeest populations are pure and if there is any possibility of hybridisation having occurred, their animals may have reduced value. They may not even be able to sell live animals. The only market for the hybrids may be in their meat and maybe for hunters who would like to hunt a strange variation of the wildebeest, namely the so-called red wildebeest. This translates into serious economic implications for the value of both types of wildebeest.

The extent of crossbreeding between black and blue wildebeest throughout South Africa is presently unknown. However, the hunting community is reporting more and more cases of hybridisation in different parts of the country. In order to remedy this situation, it is of the utmost importance to impose drastic measures on a national level (Anon 2003a).

Description of the hybrid

First generation hybrids are easily identified, but the offspring of hybrids that have interbred with pure stock black or blue wildebeest are difficult to recognise on appearance alone (Vrahimis 2003b). The most obvious deviation is in the shape of the horns. Table 3.1 compares morphological features of the two types of wildebeest and the hybrid. These features are in no way an absolute description of the hybrid and probably only pertain to the hybrids studied by Fabricius *et al.* (1988). Morphological features may vary according to the original black to blue wildebeest ratio and the generation of the hybrid. According to Fabricius *et al.* (1988) the hybrids appeared to have the same social organisation as the black wildebeest. Vocalisation was found to consist of the grunting sound characteristic of the blue wildebeest and the hybrid has been shown to be fecund. Conditions affecting the fertility of the hybrids still need to be assessed. Evolution and speciation knowledge can be improved by further study of the hybridisation process. Further studies also need to be made on established hybrid herds in order to obtain information on the hybrid ecology and the effects that the parentage would have on this ecology.

Factors leading to hybridisation

It is clear that the social behaviour of wildebeest, especially the habit of male blue wildebeest to associate with animals of other species, predisposes them to opportunities of hybridisation when confined with black wildebeest (Vrahimis 2003b).

In most recorded cases it appears that disruption of the normal demographic or social structure was involved, as was seen at the Spioenkop Nature Reserve in 1995 (Langley 1995). According to Langley (*op. cit.*), the water level of the Spioenkop Dam dropped during a dry period in the reserve. This allowed several blue wildebeest bulls to cross the dam and establish territories in an area favoured by black wildebeest. It is suspected that the larger blue wildebeest dominated the smaller black wildebeest males during the rut and mated with black wildebeest females. It is believed, however, that hybridisation is only likely under artificial conditions, where the two types of wildebeest are forced together in a confined area. Hybridisation in such areas occurs primarily as a result of the similar behaviour and the synchronised breeding seasons of the two types of wildebeest, and due to their relatively recent phylogenetic divergence (Anon 2003a).

Methods for identifying hybrids

The study by Corbet (1991) represented the first attempt to determine the extent of genetic divergence between the blue and black wildebeest. A variety of molecular and cytogenetic techniques were used to study the divergence between the two types of wildebeest and to assess the status of the South African populations of wildebeest with regards to inbreeding and hybridisation.

Table 3.1: Comparison of the morphological features of the hybrids and pure types of wildebeest as studied by Fabricius *et al.* (1988)

Black wildebeest	Blue wildebeest	Hybrid
Horns curl down for half of their length and then curl upwards.	Horns horizontal for half of their length and then curl inwards towards the head.	Horns curl down at an angle of 30 degrees and then curl outward, away from the head.
Colour buff brown.	Colour dark grey.	Colour dark brown.
Tail white.	Tail black.	Top half of the tail black, bottom half white.
Mane stiff and erect, black and white.	Mane shaggy and black.	Mane stiff and erect, black and white.
No brindles.	Brindles on neck.	Brindles on neck.
Nose not elongated with a tuft of hair.	Nose smooth and elongate.	Nose not elongated with a tuft of hair.
Shoulder height of males 1.2 m.	Shoulder height of males about 1.5 m.	Shoulder height of males about 1.2 m.

The study included cytogenetics, which included chromosome number and shape (karyotypic) comparisons between taxa based on G- and C-banding techniques (involving the staining of chromosomes). This gives an indication of whether stable meiosis was possible in cases of hybridisation. Both types of wildebeest have the same number of chromosomes (diploid number: 2n = 58) and it was not possible to distinguish between the two by using staining techniques, indicating that meiosis would be stable and not impair hybrid fertility (Corbet 1991). Analyses of mitochondrial deoxyribonucleic acid (mtDNA) restriction fragment length polymorphisms were also performed. The mtDNA analysis showed that there was a 2% divergence between the black and blue wildebeest, which roughly corresponds to 1 million years of divergence, a similar estimate to what has been suggested based on the fossil record (Brink 1993). The mtDNA also showed important differences between the two types of wildebeest with respect to the amount of within species genetic variability.

Examination of protein variation by using one-dimensional gel electrophoresis (allozyme or protein electrophoresis) and of variation in the nuclear genome by utilising ribosomal DNA and DNA fingerprinting probes was also performed, but did not reveal a diagnostic test for hybrids (Corbet 1991).

The use of DNA fingerprinting has recently been, to a large extent, replaced by micro-satellite markers (Grobler 2003). These are short DNA repeats (of two to five bases) that are highly variable and have the advantage that each locus is studied independently, therefore allowing the assignment of heterozygosity. Alais (2000) and Grobler (2003) used micro-satellite markers to address genetic variability within black wildebeest and in the hybridisation between the two types of wildebeest. Four potentially diagnostic markers were found and now need to be tested on known hybrids and the two pure forms.

Grobler (2003) listed a few priorities for future research on the topic:

- Assess the genetic diversity of the pure species by using carefully selected reference populations.
- Test the diagnostic loci on known hybrids (preferentially F1 hybrids and backcrosses).
- Assess fitness related traits (such as sperm quality) of pure forms and their hybrids and assess adaptive genetic variation.

Osteological work is also being conducted, and potential markers are in the process of being identified (Anon 2003a).

Prevention of hybridisation

It is currently thought that the only way in which to ensure that hybridisation does not occur, is to prevent any contact between the two types of wildebeest. This is because conservationists and scientists cannot clearly identify the factors that result in hybridisation, and whilst there is much speculation, there are insufficient, adequately documented cases. In order to identify these factors it is necessary to understand the ecological and behavioural differences between the two types of wildebeest.

CONSERVATION

Historical conservation status of the black wildebeest

As a result of heavy, indiscriminate hunting pressure by travellers, hide hunters and settlers, as well as the allocation of the best fertile land to farming in the previous century, the number of black wildebeest had dwindled to the brink of extinction by the 1940s (Fabricius and Oates 1985). Conservation programmes were then set up to conserve and breed this endangered species for relocation to those areas where it had previously occurred.

At the turn of the 20th century the population of black wildebeest in South Africa had fallen to below 1 000 (Fabricius and Oates 1985). A survey performed by Bigalke (1947) revealed that there were approximately 1 048 black wildebeest in the Union of South Africa in 1946. Eighteen years after the publication of the first survey by Bigalke (1947), another survey was performed by Brand (1965) yielding a total of 1 808 black wildebeest in South Africa. In 1970, when a third survey was done by the Orange Free State Directorate of Nature and Environmental Conservation, the population size had risen to 3 220 animals. A survey done in 1979 showed that there were 1 532 black wildebeest in the Transvaal alone. In 1981 another survey revealed a population size of 6 493, and in 1988 the count revealed a total of 6 685 animals in South Africa (Kay 1992). By 1997 the numbers of black wildebeest in South Africa had increased to approximately 12 000 animals (Mills and Hess 1997). Presently, the total black wildebeest population is estimated at more than 18 000 animals, of which

80% occur on private land and 20% in formally protected areas (Anon 2003a). This steady increase of animals was the direct result of the intensive conservation programmes put into place to conserve the species, as well as the dedication of a few Free State farmers who were intent on conserving the species (Weaver 1992).

The species has been widely re-established within its former distribution range and more recently introduced into other parts of the country and into neighbouring countries outside its historical range (Mills and Hess 1997). On private farmland in Namibia, importations from South Africa have led to a dramatic rise in the estimated total numbers of black wildebeest, from 150 in 1982 to more than 7 000 in 1992 (East 1998). The megapopulation size is therefore, steadily increasing, especially on private land. This has been a major reversal in status for this species and reflects favourably on the conservation efforts of the past.

Regulations and policies in South Africa

Past policies in the former provinces of South Africa did not provide any regulations on the housing of the two types of wildebeest on the same property. Recently it has been recognised that black wildebeest are an important endemic South African species and that hybridisation with the blue wildebeest is undesirable and a threat to both types of wildebeest. It is suspected that with the ever-increasing number of wildlife ranches being developed throughout South Africa, more and more properties are keeping the two types of wildebeest together. At present, in the Free State, Northern Cape and KwaZulu-Natal provinces alone, it is estimated that there are more than 120 private properties that are housing black and blue wildebeest together (Anon 2003a). This means that the hybridisation problem in South Africa can already be far advanced.

The present policies in the various provinces of South Africa are described below, keeping in mind that a National Translocation Policy is about to be released, which will hopefully streamline the policies in the current nine provinces and address the hybridisation problem.

Gauteng

Information for this province was supplied by Buijs 2003 (pers. comm.)[2]. The policy is not to allow both types of wildebeest on one property. In addition only black wildebeest are allowed on highveld grassland properties and blue wildebeest in the savanna regions of Gauteng. When it is a borderline case, it is treated on merit through the use of historical data and an ecological assessment. The species that occur on other farms in the region are also looked at and the species most common in the area is recommended. This attempts to prevent complications in the future when landowners decide to amalgamate their properties. Where permits for both species have been issued in the past, permits for the removal of live animals from such farms will not be allowed. The only legal way to remove them will be to shoot them.

As far as the records at Gauteng Nature Conservation go, only seven properties in Gauteng house both types of wildebeest. It is not apparent whether they are separated by a fence or not. Considering the size of Gauteng in relation to the other provinces this indicates a high density of properties possessing both types of wildebeest.

KwaZulu-Natal

Information for this province was supplied by Rushworth 2003 (pers. comm.)[3]. Black wildebeest have protected status in KwaZulu-Natal. Their policy is to ensure that both types of wildebeest do not occur in the same protected area, even where a fence or other barrier may separate them. They also aim to maintain wildebeest in protected areas in accordance with historical distribution and habitat suitability, with preference being given to black wildebeest in areas of overlap in distribution and where habitat is suitable for both types. Only certified genetically pure wildebeest are to be introduced into protected areas. They plan to adopt a certification process for all black wildebeest populations in the province and hope that this will be copied by the other provinces in the country. The policy is also to prevent the introduction of both types of wildebeest to any property in the province through permit controls.

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Excess wildebeest of any type will only be sold to landowners who either have certified pure populations or no wildebeest on their properties. Only landowners who have adequate fencing to contain these animals and have made a commitment to maintaining these herds as pure in the long-term will be able to purchase such wildebeest. KwaZulu-Natal promotes and facilitates, with compensation where necessary, the removal of hybrids or of one type of wildebeest where both have already been introduced to a property under permit.

Northern Cape

Information for this province was obtained from Jonk 2003 (pers. comm.)[4]. New translocation policies for wild animals within the Northern Cape have been approved, which state that black and blue wildebeest are not allowed on the same property unless they are separated by a game fence that meets the specifications of the province for antelope. Fence specifications for the wildebeest are either a stock proof fence or a jackal proof fence that is 1.4 m high.

Western Cape

Information for this province was supplied by Lloyd 2003 (pers.comm.)[5]. Originally the mammalian translocation policy in the Western Cape did allow for the two types of wildebeest to be kept on the same property. This was in order to cater for those properties in the former Cape Province where the two types of wildebeest occurred sympatrically. Once it became known how serious the hybridisation problem was, such permission was no longer given. However, there are several properties in the Western Cape that still have both. It is simple to deal with those that are covered by certificates of adequate enclosure. However, there are cases of people having them illegally without such certificates.

Other provinces

It was not possible to obtain information from the remaining provinces in South Africa. However, it is clear that most provinces are taking the hybridisation threat seriously and are attempting to implement regulations, which will prevent the two types of wildebeest from occurring together on the same property. Some provinces are stricter than others in their policies. The development of the National

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Translocation Policy will hopefully address these differences and incorporate wildebeest hybridisation.

Evidently, the existing regulations to prevent keeping blue and black wildebeest together should be retained and enforced as vigorously as possible. All possible hybrid herds on private properties and nature reserves should continue to be regarded as such, until proven otherwise by using a molecular genetic approach (Anon 2003a).

National conservation plan

A National Conservation Plan for the two types of wildebeest is being developed by the Free State Department of Tourism, Environmental and Economic Affairs, the University of Pretoria, the Animal Genetics laboratory at the Agricultural Research Council and provincial parks' boards and nature conservation agencies throughout South Africa (Vrahimis 2003b). The aim of the National Conservation Plan is to investigate the extent of hybridisation between black and blue wildebeest in South Africa, by involving all role-players and to develop a national strategy and action plan, which will be aimed at ensuring the genetic integrity of both these wildebeest types (Anon 2003a).

It is important to understand that the problems being experienced with black and blue wildebeest hybridisation are symptomatic of larger problems pertaining to conservation and trade in wildlife and cannot be addressed in isolation. Addressing some of the broader problems will automatically assist in addressing some of the wildebeest issues.

A workshop on black wildebeest hybridisation was held in June 2003 at the Florisband Quaternary Research Station in the Free State (Anon 2003a). This workshop was the starting platform for the development of the national conservation plan. Participants worked in two groups by focussing on the research aspects of the hybridisation process and the regulatory and policy mechanisms that are necessary to manage the situation (Anon 2003a). The policy and legislation working group and the research-working group identified problems covering the core issues. The problems were addressed and possible solutions sought (Table 3.2).

One of the main problems identified was the lack of uniform national legislation in South Africa (Problem 1). Therefore, South Africa was considered not to be complying with its obligations in terms of the Convention on Biodiversity, which this country ratified in 1995 (Anon 2003a).

The National Translocation Policy, which is about to be released, includes specific mention of the issue of wildebeest hybridisation and may be able to provide a solution to this problem. Current market forces in wildlife ranching are promoting large diversity of animals on small properties (Problem 2). These forces are not only favouring hybridisation but also the breeding and hunting of colour variations such as those of springbok, blesbok and impala, as well as the housing of species outside of their natural distribution range (Anon 2003b). This is a difficult problem to tackle as it involves the changing of attitudes among members of the wildlife ranching industry. An incentive-disincentive scheme has to be compiled to address this problem.

Table 3.2: A list of the problems and their proposed solutions for the black and blue wildebeest hybridisation problem in South Africa as stipulated in a workshop on black wildebeest hybridisation held in June 2003 at the Florisband Quaternary Research Station in the Free State province (Anon 2003a)

Number	Problem	Proposed Solution
1	The lack of uniform national legislation, policy and strategy is resulting in the inability of the state to control existing problem areas and prevent further problems.	Support current initiatives to develop and fast-track the publication of the National Translocation Policy, ensuring that this addresses all the wildebeest issues.
2	Current market forces promote landowners to stock many species, often on relatively small areas, thereby encouraging hybridisation.	1). Consult/work with hunting organisations to get their support for not recognising trophies hunted out of natural distribution, hybrids/potential hybrids, or colour variations. 2). Consult with zoological organisations to prevent inappropriate ‘dumping’ of exotic/hybrid animals. 3). Conservation Extension staff have to be trained/re-trained to discourage the desire among landowners for stocking as many species as possible. 4). Investigate the development of certification/registration system for pure herds. 5). Reduce cost to individuals of rectifying problem areas by exchanging hybrids or swapping for one type of wildebeest where both exist. 6). Advisory service by conservation agencies at auctions to prevent the unintentional spread of problems and discourage deliberate problem creation. 7). Auctioneer incentives through developing a code of conduct and providing conservation ‘Stamp of Approval’/accreditation – will assist in controlling the live trade.
3	There is uncertainty as to the genetic purity of existing wildebeest populations.	1). Conduct a national survey and develop a database of all properties with one or both species of wildebeest, with tentative status i.e. not confirmed by genetic tests. Database must: -Include details of landowners. -Must be available to all provinces to assist with permitting. -Will highlight specific, immediate problem areas. 2). Support genetic and osteological research, including financial support by the state.

Table 3.2 (Continued):

Number	Problem	Proposed Solution
4	Lack of capacity within conservation agencies to implement existing legislation i.e. reducing effectiveness of the state to regulate, control and be aware of movement of wildebeest.	No solutions were formulated due to time constraints.
5	Failure by South Africa to comply with the requirements of the Convention on Biodiversity.	No solutions were formulated due to time constraints
6	Different organs of state are enacting legislation in an uncoordinated manner and that often results in contradictory/conflicting approaches.	No solutions were formulated due to time constraints
7	There is no integration of the existing genetic benchmarks or in determining the potential gaps in the existing data.	Establish the genetic benchmarks for identifying black and blue wildebeest and hybrids.
8	Lack of understanding of the natural distribution range and origin of wildebeest within that range.	Collation and verification of existing information on: fossil evidence-records; historical records; indirect indications – habitat requirements as a proxy.
9	There is a lack of national information on the extent of the hybridisation problem (number of farms and nature reserves with one or both type).	Collate existing information and develop a national database on wildebeest data.
10	There is insufficient understanding of the hybridisation process (herd dynamics and farm practices for possibly keeping the two species).	Collate all existing information on the hybridisation process and formulate methods to fill in knowledge gaps.
11	There is no clear understanding of black wildebeest or hybrids as potential vectors for snotsiekte.	Consult Onderstepoort on existing research, or anybody else working on the problem, to find out what they know on the issue.

Table 3.2 (Continued):

Number	Problem	Proposed solution
12	There is insufficient dissemination of information to relevant stakeholders.	1). Disseminate information on the problems and possible solutions to a wide range of stakeholders, including wildlife ranch owners and managers, scientists and the public. 2). Publish information in scientific journals, write reports and hold training workshops for nature conservation scientists and managers.
13	There is no general, easily implementable identification system for pure individuals.	Develop a cost-effective, rigid and easily implementable ID system.

CHAPTER 4: HABITAT SELECTION AND SEPARATION: GENERAL METHODOLOGY

INTRODUCTION

Habitat selection is one of the major components of any general ecological study of a species (Penzhorn 1982). Understanding black and blue wildebeest habitat selection is vital for assessing the ecological separation between the two types of wildebeest at Ezemvelo Nature Reserve. A habitat can broadly be defined as the area that contains all the biotic and abiotic components necessary to an animal to sustain all of its basic life requirements (Fabricius 1989; Joubert 2002). Therefore, the presence of an animal in a certain habitat indicates that the minimum requirements for its existence have been met by that habitat (Riney 1982).

Habitats are selected by a species according to the specificity of its niche and the extent of the special physical adaptations that the species has developed to successfully exploit that niche (Ben-Shahar 1986). The Hutchinsonian concept of a niche was used in the present study, which states that a niche is the totality of the environmental factors in n-dimensional hyperspace acting on a species (Hutchinson 1957).

Differences in body size, mouth morphology, feeding style, and digestive systems are usually the main reasons cited for differential niche use between sympatric African grazing herbivores (Gordon and Illius 1989; Voeten and Prins 1999). However, when two types of wildlife are morphologically, physiologically and behaviourally similar, such as is the case with black and blue wildebeest, their niches would also be expected to be similar. Consequently their habitat preferences should be similar.

Given these similarities, the question arises as to if and how these two types of wildlife would be able to co-exist without competing for their basic resources? The occurrence of both black and blue wildebeest in the same area provides an ideal opportunity to provide some information which may allow deductions to be made as to whether the two types of wildebeest have inherent niche differences, which cannot be directly deduced from their overall morphology, physiology and behaviour.

If no niche differences exist between the two types of wildebeest, alteration of the normal foraging and habitat use patterns by one or both types may have to occur in order to avoid competition. Such adaptations in behaviour may have negative impacts on the long-term viability and survival of an animal in an area (Rubin *et al*. 2002). However, evidence for such adaptations may only be found in studies where the habitat use of the two types of wildebeest is studied in isolation, as well as where they occur together and thus, if they are being made, the present study will only be able to infer such adaptations, not prove them. However, if the adjustments mentioned above are being made, then it may result in the long-term decline in one of the two types of wildebeest that presently occur at Ezemvelo Nature Reserve.

Blue wildebeest habitat selection has been extensively studied in savanna ecosystems in the eastern parts of South Africa (Whyte 1985; De Wet 1988; Wentzel *et al*. 1991; Weaver 1995). Black wildebeest habitat selection has been studied in detail in the Golden Gate Highlands National Park (Fabricius 1984; Kay 1992) and at the Suikerbosrand Nature Reserve (Schmidt 1988) in South Africa. No habitat selection studies on either type of wildebeest have been conducted on populations inhabiting the grasslands of the highveld where Ezemvelo Nature Reserve is situated.

Habitat separation has been demonstrated by a number of studies on niche partitioning in sympatric species (Van Horne 1982; Dueser and Shugart 1978; Rushworth 1992; Forsyth 2000; Wei *et al.* 2000; Namgail *et al.* 2004). A decision on what aspects of a habitat to measure in order to determine the factors that separate the habitat choices of two species is a complicated one. The habitat of a species consists of both biotic (wildlife and vegetation) and abiotic (physical) factors (Joubert 2002), and an analysis of both factors is equally important. The scale of analysis is also important. Habitat selection within a reserve context can take place at a number of scales. The scales most commonly analysed is the broad habitat type level (macroscale) and the feeding site level (microscale) (Novellie 1990). In addition habitat selection can also be analysed at a scale that would incorporate all the abiotic and biotic habitat factors such as slope, aspect and woody vegetation cover at the sites of occupation of the species under study (mesoscale). Analysing habitat selection at multiple levels can allow for observation of influences that may be masked within a single level analysis (Lyons *et al*. 2003). Various authors have recommended hierarchical approaches to the analysis of habitat utilisation in order to examine habitat selection operating on different levels (Johnson 1980; Manly *et al.* 1993).

Therefore in the present study, habitat selection was firstly examined at the broad habitat type scale to determine which broad habitat types and their associated vegetation characteristics were preferred by which type of wildebeest (macrohabitat scale) (Chapter 5). Secondly, habitat preferences of the black and blue wildebeest were examined at the mesoscale incorporating both the abiotic and biotic components of the habitat (Chapter 6). This was achieved with the creation of logistic regression models. These models allowed for the delineation of the important separating mechanisms operative in the habitat preferences of the two types of wildebeest. Finally, the vegetation characteristics of the feeding sites (irrespective of habitat type) of the two types of wildebeest were then examined to determine whether they differed in terms of forage quality and quantity (microhabitat scale) (Chapter 7).

In addition to the above, examination of habitat utilisation within a seasonal context is an important component of habitat separation analysis (Fabricius and Mentis 1990; Heitkönig and Owen-Smith 1998; Traill 2004). Many studies have investigated habitat separation and resource overlap in only one season, usually at the time when resources are most abundant. However, the critical season when resources are most limiting would be expected to result in higher competition for shared resources (Gordon and Illius 1989). For continued coexistence, mechanisms, if they exist, to reduce this competition would be most evident during the critical season. In addition, habitat features and requirements of herbivores may change within a daily context and thus the time of day may impact on habitat separation between the two types of wildebeest and provide further opportunity to avoid competition for shared resources (Hemami *et al*. 2004). Certain weather conditions may also influence the habitat preferences of a species, especially when these conditions become extreme (Pianka 1973). Different social groups may also exhibit different habitat preferences (Geist and Petocz 1977; Przybylo and Merila 2000).

Taking the above into consideration, habitat selection and separation of the two types of wildebeest was examined also within a seasonal context, and where possible, a daily, weather and social group context.

It was expected that the habitat preferences of the two types of wildebeest would be too similar for ecological separation to occur in terms of habitat use and therefore the objective of this part of the present study, which has been detailed in Chapters 5 to 7, was to answer the following key question:

- Is there any evidence of ecological separation between the black and blue wildebeest being achieved by segregation in habitat selection?

METHODS

The basic survey method utilised to determine habitat preferences of the two types of wildebeest has been described in detail in this chapter. Any variations to this method and additional methods that were applied exclusively when examining the vegetation characteristics of the habitat types and feeding sites have been described under the relevant chapters.

Field collection of the data

Numerous methods exist to determine the habitat preferences and interactions of herbivores with each other and their respective habitats. The specific method chosen is usually determined by local circumstances such as available resources and time. The level of the investigation is important and studies can be conducted at the population or individual level (Thomas and Taylor 1990). The present study investigated habitat selection at the population level as individual animals were not identified.

The most widely used method for assessing habitat selection in Africa is that of observing the species under study by traversing road transects that are established to incorporate all the plant communities and habitat types in the area (Weaver 1995; Dörgeloh 1998; Von Holdt 1999; Strauss 2003; Cromhout 2006). This method requires the measurement of certain variables at each sighting of the animals concerned. The variables chosen for incorporation in a study are based on prior observation of the species under study and from other relevant studies.

The method selected for the present study was that of systematic sampling in all possible wildebeest habitats and the recording of site attributes wherever wildebeest were located. According to Fagen (1988), ecological habitat selection theory suggests that population densities are an indication of habitat quality. The procedures used here were primarily those of Ferrar and Walker (1974), Melton (1978) and Reilly (1989).

To avoid sampling bias, a methodical search pattern was laid down to cover the entire study area as suggested by Pettifer and Stumpf (1981). The study area was divided into ten blocks, each of which could be conveniently searched within 2 to 3 hours. Two or three adjacent blocks were systematically searched each day on foot or by vehicle, following a standard route. This standard route was devised and formalised after a ground reconnaissance session that aimed to determine the areas on the reserve where both types of wildebeest were most likely to occur and the areas that were inaccessible to them. This resulted in some areas of the reserve being excluded from analysis as the terrain in these areas was found to be inaccessible to both types of wildebeest. The route was reversed on every alternate search to minimise observer bias (Von Holdt 1999). All wildebeest encountered within that block were recorded. An attempt was made not to measure the habitat of the same individuals on the same day (Manly *et al*. 1993). The blocks were searched in an orderly manner from one to ten to ensure independent observations. No block was therefore surveyed more than once in 3 days. Each block was surveyed at least twice a month and not more than five times a month. Data collection lasted from January 2004 to August 2005 allowing for seasonal differences to be explored.

The objective of this type of sampling was to achieve an even intensity of sampling in all wildebeest habitats so that species frequencies would reflect abundance, distribution and habitat preferences (Ferrar and Walker 1974; Reilly 1989). This method was chosen over the fixed transect method utilised by many other studies (Weaver 1995; Von Holdt 1999; Traill 2004), due to the relative seasonal stability of the distribution of the two types of wildebeest within the study area and due to certain areas consistently not being utilised by the wildebeest (pers. obs.). This observation may have been due to the territoriality of both types of wildebeest (Von Richter 1971a). In addition, the road system in the reserve did not cover all the areas where wildebeest were known to occur and the road transect method would have under-sampled the entire population of both types of wildebeest.

Once an animal or group of animals was located, the point where an individual occurred or the centre point of the herd was determined. This position was recorded with a Global Positioning System (GPS) instrument. During approach, the dominant activity was recorded and the site size or area of occupation of the group was noted for the purpose of subsequent vegetation sampling. A standard site size of 5 m radius was used for single stationary animals where all subsequent vegetation variables were recorded (Ferrar and Walker 1974).

A fixed set of habitat variables was measured and their values recorded on a field data sheet (Appendix 1). A broad-based holistic approach was considered most valuable for this part of the present study and it was therefore decided to reduce the accuracy of data collection, and thus the time spent at each site, rather than the area or number of habitat factors considered (Ferrar and Walker 1974). As a result, many of the variables were visually estimated rather than measured. Since it is expected that the choice of a site by a type of wildebeest is likely to include variability of the same order of magnitude as would result from such visual estimates (Ferrar and Walker 1974), the use of this level of accuracy (visual estimate, rather than the quantitative measurement) was considered appropriate to the conditions of the present study.

The following variables were recorded at each sighting:

Type of wildebeest

- Black wildebeest
- Blue wildebeest

Date and time of observation

The date was noted to determine seasonal habitat preferences and the time was recorded to determine whether the time of day affected habitat selection.

The seasons were categorised as follows:

- Late growing season: January, February, March and April
- Dormant season: May, June, July and August
- Early growing season: September, October, November, December

The time of day was categorised into three categories:

- Morning: >05:00 – 10:00
- Midday: >10:00 – 14:00
- Afternoon: >14:00 – 19:00

No night-time observations were made due to logistic constraints.

Location

The position at the middle of the herd or where the individual was standing was determined by using a Garmin Global Positioning System (GPS) instrument. These co-ordinates were used to plot wildebeest distribution on a map of the study area.

Group composition

- Males: identified by distinct male characteristics
- Females: identified by distinct female characteristics
- Subadults: young animals, ≥1 year old but not having reached reproductive maturity determined through horn development patterns
- Calves: <1 year old.
- Total herd size: number of animals in the herd.

Social group

Three social groups were recognised based on Von Richter (1971a):

- Bachelor herds: Herd of at least three individuals consisting of only males of all ages
- Female herds: Herd of at least three individuals consisting of adult females, subadults and/or calves.
- Territorial bull: Single dominant bull occupying a territory.

For those observations that did not fit into these three categories, no attempt was made to classify that particular observation into a social group category and these were omitted from any further social analyses.

Habitat type

No formal vegetation classification had been done before this study for the entire reserve. A number of physiognomic classifications had been performed (Bancroft 1989) and portions of the reserve had been surveyed for phytosociological classification (Grobler 1999). A phytosociological classification of the entire reserve was initiated half-way through the present study, but the results were not available for use in the present study (Swanepoel 2006 pers. comm.)[6]. Five broad habitat types or homogeneous units, all utilised by the wildebeest, were identified subjectively from

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stereo aerial photographs and ground reconnaissance as described by Barrett (1982):

- *Burkea* woodlands
- Moist grasslands
- Old lands
- Rocky grasslands
- Sandy grasslands.

The boundaries for these habitat types were based on overall physiognomy, rock cover, moisture regimes, dominant plant species and previous land use, incorporating overall vegetation composition to a lesser extent. *Burkea* woodlands were defined as habitats where even height stands of *Burkea africana* occurred in open to moderately dense woodlands and were dominated by deep, red sandy soils predominantly on northerly slopes. Moist grasslands were defined as habitats occurring in wetland areas or along drainage lines with dense herbaceous vegetation and dominated by plant species such as: *Imperata cylindrica, Aristida junciformis, Eragrostis nindensis* and *Paspalum urvillei*. Old lands were defined as habitats occurring on relatively flat plains, with no rock cover and where crops were cultivated in the past. The dominant plant species in this habitat were: *Digitaria eriantha, Cynodon dactylon* and *Eragrostis curvula*. Rocky grasslands were defined as habitats predominantly occurring on slopes with shallow soils and with the occurrence of the plant *Xerophyta retinervis.* The rock cover was ≥30%. Sandy grasslands were defined as habitats occurring on rolling plains and on the plateaus of the study area (natural grassland) where the soils were deep and red and rock cover was <30%. The areas and locations of these broad habitat types and those areas not utilised by the black and blue wildebeest are discussed in more detail in Chapter 5.

Topography

Aspect

The major direction towards which a slope faced was measured with a compass and categorised into the following categories: North (≥270º - 90º) and South (≥90º - 270º).

Landscape position

The landscape unit where an individual or group was sighted was recorded. These included plains, gentle slopes, valleys (including drainage areas), and plateaus.

Slope

An area that is inclined at an angle of more than 2º, but <45º from the horizontal, is defined as a slope. The slope of the land was visually estimated and the following broad categories were used: flat (0º), gentle (>0º - 10º), moderate (>10º - 20º) and steep (>20º).

Erosion

The degree of erosion in the area of occupation was categorised as follows (adapted from Theron 1991):

- Low: Small areas with exposed soils, but with the soil mantle generally intact
- Moderate: Larger areas with exposed soils, signs of sheet erosion, with a low plant cover
- High: Distinct signs of dongas and a high degree of soil loss.

Rock cover

The proportion of the surface covered by rock within the area of occupation was estimated visually as a percentage.

Altitude

The height above sea level in metres at the site was determined from a topocadastral map with the GPS recording used for verification.

Geomorphology

Geomorphology described the shape of the landscape and has an influence on the drainage and erosion in an area. Three categories were used: flat, concave and convex.

Other physical factors

Time since last burn

Records of the reserve management for accidental and block burns were used to determine the time since last burn at the location.

Distance from water

The available water sources were noted throughout the year. The distance in metres from the site to the nearest water source was determined from a topocadastral map.

Exposure

The exposure to the sun at the site was categorised as: shade, partial shade and full sun.

Distance to shade

The distance from the position of a wildebeest to the nearest suitable shade was estimated visually in metres.

Weather

Temperature

The screened ambient temperature (not exposed to rays of the sun) was measured by using a digital thermometer and categorised into three classes: <15°C, ≥15 - 25°C, and >25°C.

Cloud cover

The percentage cloud cover was visually estimated and categorised into three classes: 0% (Clear skies), >0 – 50% (Partly cloudy), >50% (Overcast).

Wind velocity and direction

Wind velocity was assessed from an adapted Beaufort scale as: none: 0 - 2 km/h (smoke rises vertically); slight: >2 - 5 km/h (direction of wind shown by smoke drift, wind felt on face, leaves rustle); moderate: >5 - 13 km/h (leaves in constant motion, raises dust, a moderate breeze); severe: >13 km/h (trees begin to sway, fresh to strong breeze). The wind direction was measured with a compass in degrees and classified into the following categories: North; Northeast; East; Southeast, South; Southwest; West; and Northwest.

Vegetation structure

Vegetation structure is the organisation in space of the plant individuals that form a vegetation type, the primary elements of which are growth form, stratification (height class) and cover (canopy cover).

Woody plant cover

The woody plant cover was assessed visually and categorized into the following classes:

- No woody vegetation: 0% cover
- Sparse: > 0-10% cover

- Open: > 10-20% cover.

Grass cover

The horizontal herbaceous structure was assessed visually and categorised into the following classes:

- Sparse: Grasses sparsely spread in areas, with annual grasses and forbs
- Medium: A moderate grass canopy cover with occasional open areas
- Dense: High grass canopy cover with little or no open areas.

Grass height

The vertical herbaceous structure was assessed at two levels. The first level was the height of the entire grass plant, including the inflorescence, and the second level was the height of the top grass leaves excluding the inflorescence. The mean height of the dominant vegetation within the site of occupation was recorded with a tape measure. The grass leaf height was categorised into four classes namely: 0 - 50 mm, >50 - 100 mm, >100 - 400 mm and >400 mm. The total grass height was categorised into three classes namely: 0 - 50mm, >50 - 500 mm and >500 - 800 mm.

Plant species composition

The dominant and sub-dominant plant species within the site of occupation were identified, and specimens not identifiable in the field were collected for later identification in the Schweickerdt Herbarium at the University of Pretoria or the herbarium of the National Botanical Institute in Pretoria. All non-grass herbaceous species were grouped under the category forb, and all woody species under the category woody.

Forb: grass ratio

The mean forb: grass ratio was visually estimated on the site of occupation.

Plant utilisation

Utilisation was defined by the presence of any partially or totally eaten grass plants. The degree of utilisation of the herbaceous layer by herbivores was subjectively estimated and classified as follows:

- Low: Tufts of grass recently grazed were wide apart and 1 - 10% of the current season’s grass biomass had been utilised.

- Moderate: Tufts of grass recently grazed were close together and >10 - 50% of the current season's grass biomass had been utilised.
- High: Tufts of grass recently grazed were close together and >50 - 60% of the current season's grass biomass had been utilised.
- Excessive: Tufts of grass recently grazed were extremely close together and >60% of the current season's grass biomass had been utilised.

Visibility

Visibility was determined by the mean visibility of an animal the size of a wildebeest into each of the four main compass directions. Visibility into four directions was done at just above the shoulder height of an average mature wildebeest. For the black wildebeest this height was taken at 110 cm and for the blue wildebeest it was taken at 130 cm (Smithers 1983). Visibility distances in metres were taken as the distance from the position of the wildebeest to where visibility was first obscured. Distances were estimated in metres.

Activity

At each observation the dominant activity of the individual or the group was recorded and categorised based on a modification of Engelbrecht (1986), Wentzel (1990) and Von Holdt (1999):

- Grazing: More than half the group was grazing.
- Lying down: More than half the group was lying down.
- Walking: More than half the group was walking.
- Standing: More than half the group was standing.
- Other: Any activity that is not part of the above activities, including drinking, running and grooming.

Association

Whenever any other animals were in the vicinity of a wildebeest and were closer than 100 m to it, the species was recorded.

Application of the methods

When applying these methods a number of assumptions were made based on those suggested by Fagen (1988):

- Wildebeest locations are representative of the entire population
- Wildebeest are able to move freely to and between preferred habitats
- Wildebeest will select habitats that provide the highest returns in terms of energy investment
- Natural resource availability is predictable and equal for both types of wildebeest
- Moving within each habitat costs the same in terms of energy expenditure.

This chapter serves as an introduction to Chapters 5, 6 and 7 and therefore no results or discussion have been presented here. The results and discussion have been incorporated under the relevant chapters for the various levels and components of the habitat that have been examined in the present study.

CHAPTER 5: HABITAT SELECTION AND SEPARATION: MACROHABITAT SCALE

INTRODUCTION

It is evident that large vegetation units such as savannas and grasslands form the macrohabitat for different animal species over a broad geographical scale. However, large vegetation units may have significant variation within their boundaries. Although grasslands have an overall homogeneous nature, being defined as consisting of grass species of about 0.3 to 1.5 m tall, there is substantial variation in plant species composition, functional attributes of the plant species, productivity and vegetation dynamics (Bredenkamp and Van Rooyen 1998). Where different structural habitat types occur in the same region, the presence of a variety of herbivores with different habitat preferences, may result in a broad spectrum of utilisation and allow for a higher biodiversity and production per unit area (Van Rooyen *et al.* 1996).

At least two apparently functional habitat types have long been recognised in the African grasslands (Cromsigt 2006): grasslands that are dominated by tall, bunch grass communities with a caespitose growth form, and grasslands that are dominated by short, stoloniferous lawn grass species, commonly referred to as grazing lawns (McNaughton 1984; Archibald *et al.* 2005). Any variation between these two extremes may also be found. Mixed grasslands consist of a combination of patches of bunch grasses with patches of grazing lawns (Cromsigt 2006).

Grazing lawns have been described as areas where grazing promotes forage quality in terms of increased nitrogen content (Ruess *et al*. 1983) and forage quantity in terms of primary production (Hik and Jeffries 1990). They are defined as an expanse of short grass in an immature state and have grass with a higher leaf to stem ratio and a higher bulk density than that of tall grass stands (Verweij *et al*. 2006). Compared with grazing lawns, the grass species that dominate the bunch grasslands are of a relatively low forage quality (low protein and high fibre content), but offer a high quantity of food in terms of standing grass biomass. Due to the high rainfall in the study area, plant biomass increases during the growing season and the nutritive value and digestibility of the forage decreases (McNaughton 1979). Therefore, herbivores need to feed on grass swards kept in a favourable condition by repeated grazing in order to optimise their intake (Fryxell 1991). This results in the creation of patches within the tall grasses that can be referred to for the purposes of this study as grazing sites, which have some of the characteristics of grazing lawns. No areas in the study area could be described as pure grazing lawns as the grazing sites referred to here were interspersed with taller grasses at varying intervals. A number of areas in the study area could be classified as grazing sites due to the repeated grazing by herbivores in these sites. It was therefore thought appropriate to use the term mixed grasslands for those areas that were consistently utilised by the herbivore species creating a patch mosaic of mostly short immature grasses and some tall unpalatable grasses. These areas occurred throughout the study area and were extremely patchy in extent. They could therefore not form a basis for habitat delineation. The grazing sites (or feeding sites) within the mixed grassland areas were, however, analysed in more detail in Chapter 7.

It has been pointed out that the *a priori* decisions necessary in defining habitat boundaries can result in spurious inferences (Porter and Church 1987). Therefore habitat division decisions should be based on overall functional differences that have already been proven in the particular vegetation type under study.

It was therefore decided in the present study to divide the study area into broad habitat types (hereafter referred to as habitats) based on soil moisture regime, soil type, physiography (rock cover) and past land use. Within the grassland vegetation type there may also be areas with localised growth of woody vegetation due to particular environmental conditions such as rocky outcrops and the occurrence of certain soil types and such areas could also be considered as separate habitats. Once these habitats have been identified, a habitat utilisation study at the macrohabitat level could be conducted to indicate which of these habitats may have been preferred by a particular herbivore species (Novellie 1990).

Studies of the detailed vegetative characteristics of the delineated habitats could further provide the mechanisms leading to the reasons why certain habitats are preferred by a certain species and why others are utilised to a lesser degree than expected. Therefore ecological separation between the black and blue wildebeest may be shown by the differential utilisation of the different habitats that are present at Ezemvelo Nature Reserve, which may be caused by differences at various levels in the characteristics of their vegetation and physical character. In addition, the identification of those habitats on which there is a potential for conflict between two wildlife species may also be possible from such a study (Barrett 1982).

When a habitat is used disproportionately to its availability, use of that habitat is said to be selective (Johnson 1980). A number of biological factors may affect habitat selection studies, including variations among subpopulations (sex and age groups), fluctuations in population size, lack of independence of individuals due to territoriality or aggregation, traditional use of resources and/or the local occurrence of competitors and predators (Thomas and Taylor 1990). An understanding of these influences is fundamental to the interpretation of the results of such a study.

Some portions of a habitat may not be used or underutilised while others may be selected and overutilised (Van Rooyen *et al.* 1996). Management practices could be used to reduce this impact. Fire and salt licks could be used to attract animals to underutilised areas and the opening and closing of waterpoints could be a way to attract wildlife away from overutilised areas. Patterns of habitat use by both types of wildebeest at Ezemvelo Nature Reserve would therefore also aid in developing management proposals for the future of the two types of wildebeest present on the reserve. In order to determine whether a habitat is underutilised or selected by a particular type of wildebeest, information on the availability of the habitat in question must be obtained (Manly *et al.* 1993). Even if a type of wildebeest occurs within a habitat, this does not necessarily imply that the habitat in question is being selected for. When comparing the occurrence of any type of wildlife and the availability in terms of surface area, information on positive or negative selection may be obtained.

Both the physical structure and the vegetation of a habitat may influence its selection by an animal species. By analysing the vegetation of the various habitat types in an area, the relationship between the habitat preferences of an animal species and the characteristics of the vegetation of that habitat may become clear (Reilly 1989). If few species differences in the vegetation of two habitats can be discerned, physical feature differences may be the governing factor for selection of one or the other habitat by an animal species.

Species composition and structure are the two most important components of the vegetation that form part of the habitat of an individual animal (Von Holdt 1999). The species that constitute the vegetation type will determine whether or not the food resource is potentially sufficient for herbivores (Wentzel *et al.* 1991). The structure of the vegetation will determine the availability of food at certain height classes (Bothma and Van Rooyen 1996) as well as the availability of shade for daytime resting. The availability of shade may in turn provide opportunities for escape from climatic extremes (Cromhout 2006). Plant phenology may also be an important factor governing habitat selection as deciduous trees lose their leaves in winter and hence less protection against extreme environmental conditions may be experienced by a species (Krüger 1996; Cromhout 2006). Habitat selection may therefore change through the seasons due to the availability of certain plant parts or nutrients within the plants eaten. A survey of the herbaceous characteristics of the preferred habitat of each type of wildebeest on Ezemvelo Nature Reserve could therefore be used to determine if the two types of wildebeest present selected habitats that are characterised by certain plant species or vegetation structure or not (Reilly 1989).

The null hypothesis to be tested in this part of the present study was that the black and blue wildebeest at Ezemvelo Nature Reserve would utilise the available habitats in proportion to their occurrence.

The following key questions were therefore addressed:

- What are the broad habitat preferences of the two types of wildebeest present, and what are the associated herbaceous characteristics of each habitat?
- Are there any seasonal differences in the broad habitat choices of the two types of wildebeest?
- Are there any social group differences in the broad habitat choices of the two types of wildebeest?

MATERIALS AND METHODS

Habitat delineation

The five broad habitats described in Chapter 4 were used to assess habitat use by the two types of wildebeest at Ezemvelo Nature Reserve. These habitats are mapped in Figure 5.1.

The approximate areas covered by each of these broad habitats was 2 933 ha (sandy grasslands), 2 540 ha (rocky grasslands), 744 ha (old lands), 658 ha (moist grasslands), and 123 ha (*Burkea* woodlands). Of the surface area available to both types of wildebeest, the sandy grasslands formed 42% of such area, the rocky grasslands formed 36%, the old lands formed 11%, the moist grasslands formed 9% and the *Burkea* woodlands formed 2% of the area. The availability of each habitat on

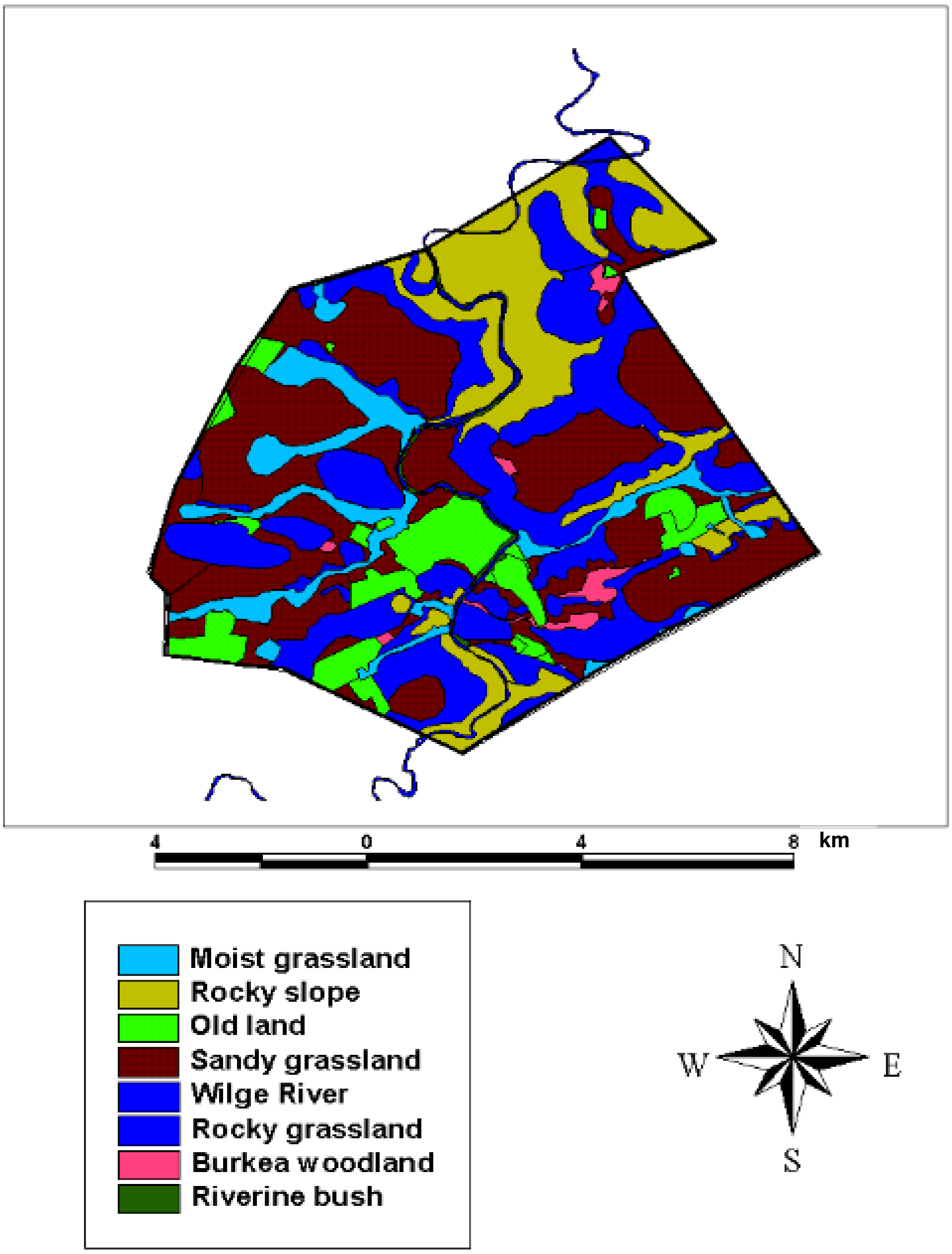

Figure 5.1: The broad habitat types found at Ezemvelo Nature Reserve, South Africa.

the study area was determined from recent stereo aerial photographs and topographical maps by using Arc View 3.2®.

The old lands consisted predominantly of short stoloniferous lawn grass species interspersed with tall unpalatable grass species at wide intervals. This habitat was thus considered to be structurally most similar to grazing lawns but was classified as mixed grasslands for the purposes of the present study due to the reasons mentioned in the introduction to this chapter. The rocky grasslands, sandy grasslands and moist grasslands represented the bunch grass communities on Ezemvelo Nature Reserve. Spatial heterogeneity within the bunch grass community included differences in rock cover, soil type and soil moisture regime. Certain areas within these bunch grass communities consisted of patches of heavily grazed grasses and could hence also be considered as mixed grassland. Given the mobility of both types of wildebeest in the study area, it was assumed that all these habitats were equally available physically to all wildebeest.

Two other habitats were identified at Ezemvelo Nature Reserve, ie. rocky slopes and riverine bush (Figure 5.1). The rocky slopes were dominated by woody vegetation and the slopes were >20°, making it inaccessible to both types of wildebeest. The rocky slope vegetation type was evident on the rocky outcrops and the rocky areas near the Wilge River. It comprised 15% of the surface area of the reserve. Riverine bush comprised only 5% of the surface area of the reserve and was restricted to the banks of the Wilge River. The riverine bush habitat did not form part of the area utilised by either type of wildebeest except for the dry parts of the year when it was visited for drinking water when the other watering holes were dry. It was also excluded from the present study, as it was not found not to be an important component of the overall habitat utilisation of the black and blue wildebeest at Ezemvelo Nature Reserve.

The present study followed Study Design I of Thomas and Taylor (1990) where analysis at the population level was conducted (no individuals were identified) and where the availability of each habitat was measured. Preference for the different habitats was analysed by using the data collected during the surveys for wildebeest described in Chapter 4. These surveys provided frequency of occurrence of both types of wildebeest in each habitat over time. Thomas and Taylor (1990) suggested that at least 50 observations on at least 20 animals would be required for adequate hypothesis testing, and this was achieved in the present study by the 1 558 observations that were recorded from January 2004 to August 2005. The distribution of the two types of wildebeest within the habitats was also mapped (Figure 5.2).

The availability of a habitat is the quantity of that habitat that is accessible to a population of wildebeest during the study period (Manly *et al.* 1993). Preference implies that the preferred resource is utilised to a significantly greater proportion than its availability would suggest (Thomas and Taylor 1990). Therefore in order to assess preference for a particular habitat by a particular species the amount of that habitat available must be taken into consideration to ensure that mere presence in a widely available habitat is not inferred to mean that the particular habitat under investigation is selected for.

Habitat herbaceous characteristics

A minimum of four and a maximum of eight vegetation plots were located at random in each of the five habitats to assess herbaceous characteristics. The number of plots analysed depended on the size of each habitat. The surveys were done on these sites during April, August and December 2004, representing the end of each of the three ecological seasons, for those characteristics which were likely to change over the seasons (Dörgeloh 1998).

The following vegetation parameters were measured at each site: grass species composition, grass species density (species/m^2), above-ground standing crop (kg/ha), total grass height (cm), grass tuft height (cm), grass canopy cover (%), and grass basal cover (%). Species density, species diversity, veld condition, degree of utilisation and biomass concentration were calculated from the above variables.

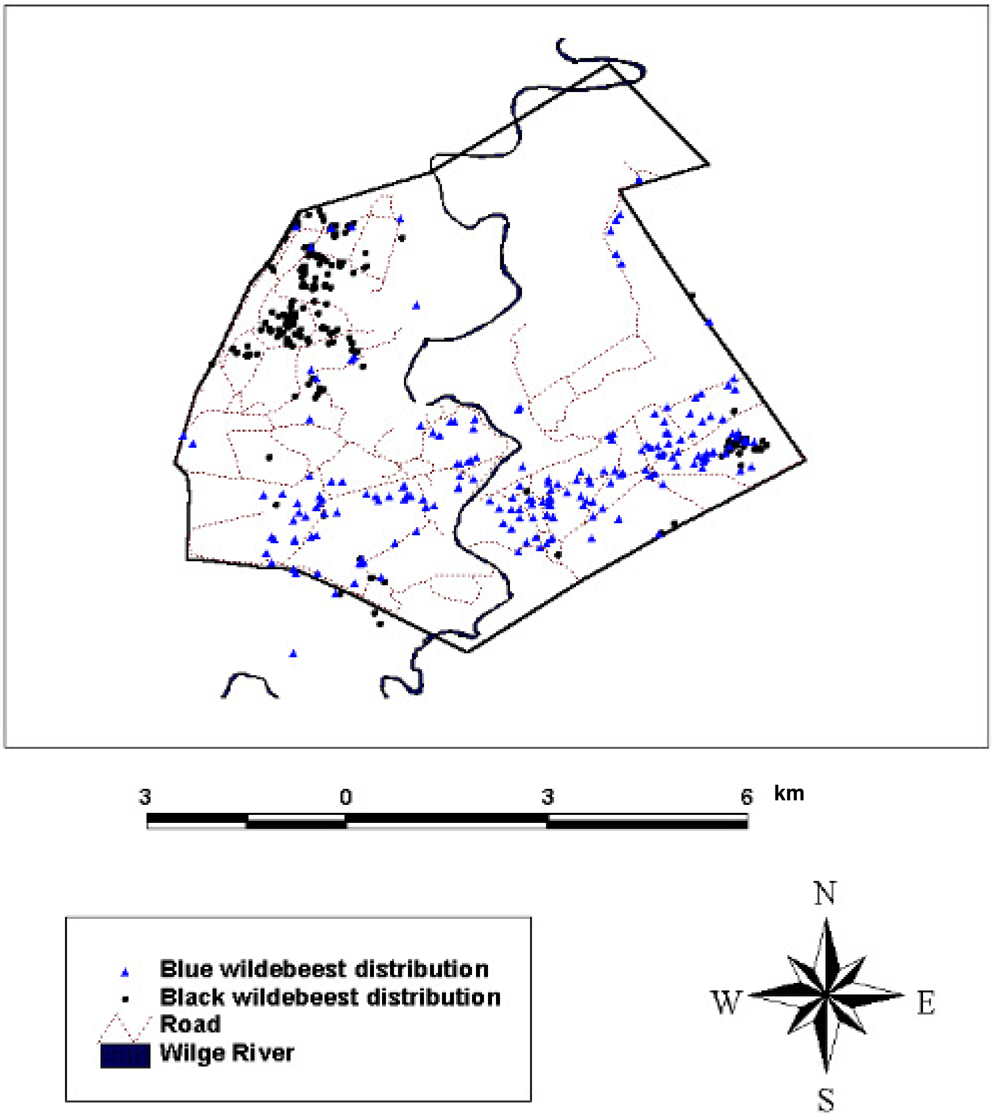

Figure 5.2: The distribution of the black and blue wildebeest at Ezemvelo Nature Reserve, South Africa from January 2004 to August 2005.

Relative grass species composition, diversity, density, degree of utilisation and veld condition

For this part of the study, the sites within each habitat type were surveyed only once for the entire study period. At each site, 20 quadrants of 0.5 x 0.65 m (Barnes *et al.* 1982) were placed 5 m apart along a single north to south transect. Grass species were identified and the percentage cover of each rooted grass species within a quadrant was estimated visually and recorded.

Forbs were treated as a single category. Species density was used as a measure of plant species richness and was calculated from the number of plant species per 6.5 m^2, which is the total area covered by the 20 quadrants for each site. This species density value was converted to species per m^2 for analysis.

The Shannon-Wiener diversity index was calculated from the species frequencies using the following equation (Magurran 1991):

$$H' = -\sum p_i \ln p_i$$

where H' is the Shannon-Wiener diversity index and p_i is the proportion of individuals found in the ith species. The Shannon-Wiener index combines both species richness and evenness in a single value (Magurran 1991). This index measures the degree of uncertainty of predicting the species of an individual that is selected at random from the community. This uncertainty increases as the number of species and equitability increases (Magurran 1991).

The step-point method was used to assess veld condition (Tainton 1999). The recommended sample size for assessing veld condition with this method in grasslands is 200 points per site (Mentis 1981; Hardy and Walker 1991). Each transect consisted of two parallel lines of 200 m long spaced 20 m apart along a north to south direction. At every second pace, the end of a measuring staff was grounded and the grass plant that was hit by it was identified (Dörgeloh 1998). The grass species were grouped into five ecological classes based on their response to grazing, perceived grazing value, phytomass production and palatability (Fourie and Visagie 1985; Trollope *et al.* 1989; Van Oudtshoorn 1999; Bothma *et al.* 2004). These ecological classes were defined as follows (Bothma *et al.* 2004):

Class 1 species

Includes valuable and palatable tufted or stoloniferous grass species with a high productivity and a high grazing value.

Class 2 species

Includes tufted, perennial grass species with an intermediate productivity and moderate grazing value.

Class 3 species

Includes tufted, tall, perennial grass species with a high productivity but a low grazing value.

Class 4 species

Includes generally unpalatable, annual and perennial, tufted or stoloniferous grass species with an intermediate productivity and a low grazing value.

Class 5 species

Includes unpalatable, annual grass and forb species with a low productivity and a low grazing value.

A modification of the ecological index method (Trollope 1990; Tainton 1999) as described by Bothma *et al.* (2004) was used to calculate the veld condition index for each site.

The degree of past utilisation (DOU) to which the herbaceous layer in this study area had been subjected to was established by means of a utilisation index: Class 2, Class 3, Class 4 and Class 5 grass species categories were each allotted values of –1.0, 0.33, 0.67 and 1.0 respectively (Wentzel *et al*. 1991). No value was allocated to the Class 1 grass species as their abundance can decrease under the effect of over- or underutilisation. The frequency value of every grass species category was multiplied by the index values and summed.

Grass cover and grass structure

The step-point method (Holechek *et al.* 1989) was used to assess grass cover and grass structure (Dörgeloh 1998). Each transect consisted of two parallel lines 200 m long and 20 m apart. At every second pace, the end of a measuring staff was grounded and the height above the ground level of the inflorescence (total grass height) and of the leaves (height below which 80% of the leaves occur (Shackleton 1990)) (grass leaf height) was measured with the graduated staff (Voisin 1988). It was also recorded whether the strike was a canopy strike, or if bare ground was hit. This enabled the calculation of the percentage canopy cover and percentage bare ground along the transect.

Above-ground standing crop and biomass concentration

The disc pasture meter was used to measure the above-ground standing crop. (Trollope and Potgieter 1986). At each sample site, 100 readings of the settling height of the disc were taken along two demarcated transects, each 100 m long but 20 m apart) at every 2 m interval (Dörgeloh 1998). The relationship between the disc height readings and the above-ground standing phytomass (kg/ha) was calculated from published regression equations (Trollope and Potgieter 1986). The equation utilsed was as follows:

$$y = -3019+2260x$$

where y = estimated fuel load (kg/ha) and x = mean disc height (cm).

To calculate biomass concentration (BC) (kg/m^3), grass leaf height (cm) and biomass (kg/ha) was used in the equation as an indication of the amount of leaf material present (Dörgeloh 1998): The following equation was used:

$$BC=(BMASS/10\ 000) \times (100/GLH)$$

where BC=Biomass concentration in kg/m^3
BMASS= Biomass in kg/ha
GLH= Grass leaf height in cm.

Statistical analysis

Data from all the sites within each habitat were pooled for statistical analysis. Observations were weighted according to the herd size variable as described in Chapter 4. The Chi-squared goodness of fit test was used to compare the habitat use by the two types of wildebeest and availability of the habitat statistically (Thomas and Taylor 1990; Manly *et al.* 1993). Expected frequencies were calculated from the available proportions of habitats. This was achieved by using the area of each habitat and converting it to a proportion of the total area available. If the Chi-squared test was found to be significant, the null hypothesis that all habitats were used in proportion to their availability on the study area (no selection) was rejected. Subsequently, the cell Chi-squared values for each habitat type were calculated. If these values were significant, then the differences between the observed and expected values were examined. If the observed value was greater than the expected value, a positive selection for that habitat type was indicated. It was here concluded that the type of wildebeest under investigation actively selected the habitat type in question and therefore utilised it in greater proportion than its availability. If the expected value was greater than the observed value, it was concluded that the habitat type involved was utilised to a lesser degree than expected based on its availability by the relevant type of wildebeest. For comparison, the Bonferroni adjusted 100 (1-α)% confidence intervals for habitat use were calculated for each habitat type where α is 5% (Byers *et al*. 1984; Manly *et al.* 1993). A habitat was selected for use by the wildebeest type under investigation if the lower confidence interval for that habitat type was greater than the corresponding wildebeest population proportion within that habitat type. Similarly, a habitat was not preferred when the upper confidence interval for that habitat type excluded the corresponding wildebeest population proportion in that habitat type (Namgail *et al*. 2004). Spatial and temporal differences in vegetation characteristics between habitat types were tested with general linear modelling by using the PROC GLM procedure at 95% confidence intervals (SAS®[7]). This procedure involved an analysis of variance. Where a significant difference was found between all the habitat types, differences between individual habitat types were further investigated by using multiple comparisons.

To detect differences in habitat use across the seasons, the data were divided into three ecological seasons, being the late growing season (January to April), the dormant season (May to August) and the early growing season (September to December) as was described in Chapter 2. To detect differences in habitat use among the three social groups of wildebeest, the social class involved in each observation was classified as a territorial bull, a bachelor herd or a female herd following Von Richter (1971a).

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[7] Integrated system of software providing complete control over data management, analysis and presentation. Version 8.2 on UP mainframe, SAS Institute Inc. SAS Campus Drive, Cary, North Carolina 27513

RESULTS

The percentage frequency of the various observations on black and blue wildebeest appear in Table 5.1. The habitat selection results of the black and blue wildebeest at Ezemvelo Nature Reserve based on using the cell Chi-squared calculations and those based on the Bonferroni-adjusted confidence intervals were almost identical (Tables 5.2, 5.3 and 5.4). Based on these results and the recommendations of Groeneveld 2006 (pers. comm.)[8], it was therefore decided to provide habitat use results for both methods only for the seasonal and total data, and to provide the cell Chi-squared habitat selection results for the more detailed analyses that were also performed.

Overall habitat utilisation by all wildebeest social groups

There was a difference in the extent to which the black and blue wildebeest utilised the five broad habitats (Tables 5.2 and 5.3). Neither type of wildebeest utilised all five habitats in proportion to their availability in the study area (Black wildebeest: $\chi^2 = 194.8$; *df* = 4; $p<0.0001$; Blue wildebeest: $\chi^2 = 549.9$; *df* = 4; $p<0.0001$). Black wildebeest selected the sandy grasslands in 62% of the observations and the moist grasslands in 12% of the observations, showing a positive selection for both these habitats, whereas the *Burkea* woodlands were never used (Table 5.2). The old lands were used in proportion to their availability in the study area, whereas the rocky grasslands were used to a lesser degree than expected. Blue wildebeest selected the old lands in 27% of the observations, showing a positive selection for it and for the *Burkea* woodlands. Blue wildebeest utilised the sandy grasslands in proportion to their availability on the study area, but utilised the rocky and moist grasslands to a lesser degree than expected (Table 5.3).

Seasonal influence

Late growing season

There was a strong association between type of wildebeest and the type of habitat used during the late growing season (Black wildebeest: $\chi^2 = 70.0$; *df* = 4; $p<0.001$; Blue wildebeest: $\chi^2 = 484.9$; *df* = 4; $p<0.0001$).

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[8] Prof. H. Groeneveld. Department of Statistics, University of Pretoria, Pretoria, 0002, South Africa.

Table 5.1: The percentage occurrence of the black and blue wildebeest in the five broad habitat types indicating the utilisation of the various habitat types over three ecological seasons and for the total data at Ezemvelo Nature Reserve from January 2004 to August 2005

Size and season	Type of wildebeest	*Burkea* woodland	Moist grassland	Old land	Rocky grassland	Sandy grassland
Area of habitat type (ha)	-	123	658	744	2540	2933
Early growing season	Black wildebeest	0.0	7.5	24.7	12.9	54.9
	Blue wildebeest	8.2	3.1	33.8	23.6	31.4
Dormant season	Black wildebeest	0.0	11.0	10.7	8.3	70.0
	Blue wildebeest	6.6	3.2	23.7	25.5	41.1
Late growing season	Black wildebeest	0.0	19.0	10.5	8.9	61.7
	Blue wildebeest	10.4	6.8	23.3	20.4	39.2
Total data	Black wildebeest	0.0	12.2	15.5	10.1	62.1
	Blue wildebeest	8.4	4.3	26.9	23.2	37.3

Table 5.2: Chi-squared test results to evaluate the hypothesis that the black wildebeest on Ezemvelo Nature Reserve used the available broad habitats in proportion to their occurrence by surface area. Values in brackets indicate sample sizes of <5 and therefore the Chi-squared test results for these entries may be invalid. + indicates a positive selection, - indicates a negative selection and 0 indicates random selection. N/a indicates that that habitat type was not utilised at all

Social group	Habitat	Ecological season											
		Late growing season			Dormant season			Early growing season			Total data		
		χ^2	*df*	Selection	χ^2	*df*	Selection	χ^2	*df*	Selection	χ^2	*df*	Selection
All groups combined	Sandy grasslands	18.15	1	+	28.39	1	+	9.43	1	+	54.95	1	+
	Rocky grasslands	36.07	1	-	37.01	1	-	35.99	1	-	108.92	1	-
	Old lands	12.73	1	+	0.44	1	0	0.02	1	0	3.10	1	0
	Moist grasslands	0.05	1	0	4.78	1	+	34.82	1	+	18.62	1	+
	Burkea woodlands*	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Bachelor herds	Sandy grasslands	0.02	1	0	1.08	1	0	0.18	1	0	0.12	1	0
	Rocky grasslands	(0.48)	1	0	(4.33)	1	-	(3.20)	1	0	7.42	1	-
	Old lands	(0.43)	1	0	(0.50)	1	0	(0.99)	1	0	(1.84)	1	0
	Moist grasslands	(3.76)	1	0	53.42	1	+	15.57	1	+	63.56	1	+
	Burkea woodlands*	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Territorial bulls	Sandy grasslands	(0.05)	1	0	(2.06)	1	0	(1.79)	1	0	1.76	1	0
	Rocky grasslands	(0.81)	1	0	(1.60)	1	0	(1.86)	1	0	(3.96)	1	-
	Old lands	(6.16)	1	+	(0.05)	1	0	(0.09)	1	0	(1.78)	1	0
	Moist grasslands	(0.04)	1	0	(0.02)	1	0	(0.12)	1	0	(0.0002)	1	0
	Burkea woodlands*	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Female herds	Sandy grasslands	21.21	1	+	34.79	1	+	8.34	1	+	62.29	1	+
	Rocky grasslands	36.30	1	-	31.10	1	-	31.13	1	-	98.32	1	-
	Old lands	11.4	1	+	0.16	1	0	0.43	1	0	4.36	1	+
	Moist grasslands	0.59	1	0	0.12	1	0	23.55	1	+	3.31	1	0
	Burkea woodlands*	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a

* The *Burkea* woodlands were never utilised by the black wildebeest in the study area

Table 5.3: Chi-squared test results to evaluate the hypothesis that the blue wildebeest on Ezemvelo Nature Reserve used the available broad habitats in proportion to their occurrence by surface area (values in brackets indicate sample sizes of <5 and therefore the chi-squared test results for these entries may be invalid). + indicates a positive selection, - indicates a negative selection and 0 indicates random selection

Social group	Habitat	Ecological season											
		Late growing season			Dormant season			Early growing season			Total data		
		χ^2	*df*	Selection	χ^2	*df*	Selection	χ^2	*df*	Selection	χ^2	*df*	Selection
All groups combined	Sandy grasslands	10.91	1	-	1.03	1	0	0.68	1	0	0.81	1	0
	Rocky grasslands	35.10	1	-	13.13	1	-	42.22	1	-	83.07	1	-
	Old lands	397.79	1	+	57.08	1	+	39.33	1	+	389.91	1	+
	Moists grasslands	20.67	1	-	9.62	1	-	0.12	1	0	19.74	1	-
	Burkea woodlands	20.48	1	+	0.02	1	0	84.66	1	+	56.37	1	+
Bachelor herds	Sandy grasslands	1.35	1	0	0.73	1	0	0.35	1	0	2.32	1	0
	Rocky grasslands	0.48	1	0	1.04	1	0	1.38	1	0	0.29	1	0
	Old lands	(1.61)	1	0	(1.52)	1	0	(1.79)	1	0	0.87	1	0
	Moist grasslands	(0.58)	1	0	(0.57)	1	0	(0.48)	1	0	0.17	1	0
	Burkea woodlands	53.50	1	+	(0.67)	1	0	(10.80)	1	+	39.42	1	+
Territorial bulls	Sandy grasslands	1.55	1	0	0.12	1	0	0.61	1	0	1.84	1	0
	Rocky grasslands	0.58	1	0	0.98	1	0	1.68	1	0	3.04	1	0
	Old lands	10.08	1	+	5.00	1	+	7.49	1	+	21.95	1	+
	Moist grasslands	(1.26)	1	0	(2.40)	1	0	(0.73)	1	0	4.24	1	-
	Burkea woodlands	(18.37)	1	+	(17.76)	1	+	24.08	1	+	59.37	1	+
Female herds	Sandy grasslands	8.07	1	-	2.57	1	0	2.06	1	0	0.001	1	0
	Rocky grasslands	43.04	1	-	16.77	1	-	41.17	1	-	95.18	1	-
	Old lands	462.66	1	+	66.38	1	+	30.32	1	+	428.15	1	+
	Moist grasslands	(19.47)	1	-	10.12	1	-	0.29	1	0	18.61	1	-
	Burkea woodlands	1.12	1	0	(3.40)	1	0	53.38	1	+	10.71	1	+

Table 5.4: Bonferroni confidence intervals calculated to determine the seasonal broad habitat selection by black and blue wildebeest on Ezemvelo Nature Reserve, South Africa from January 2004 to August 2005 relative to the total land surface area of the reserve. N/a indicates those habitats where that type of wildebeest was never encountered

Variable	Π_i	Black wildebeest					Blue wildebeest				
		u_i	o_i	B_{lower}	B_{upper}	s_i	u_i	o_i	B_{lower}	B_{upper}	s_i
Late growing season											
Sandy grasslands	0.419	105.79	0.63	0.54	0.73	+	106.10	0.30	0.24	0.37	-
Rocky grasslands	0.363	13.93	0.08	0.03	0.14	-	59.86	0.17	0.12	0.22	-
Old lands	0.106	32.76	0.08	0.12	0.27	+	158.15	0.45	0.39	0.52	+
Moist grasslands	0.094	14.85	0.20	0.03	0.15	0	6.74	0.02	0.00	0.04	-
Burkea woodlands	0.018	0.00	0.00	n/a	n/a	n/a	17.61	0.05	0.02	0.08	+
Total	1.000	167.34	1.00				348.46	1.00			
Dormant season											
Sandy grasslands	0.419	119.92	0.68	0.59	0.77	+	163.85	0.45	0.39	0.52	0
Rocky grasslands	0.363	15.44	0.09	0.03	0.14	-	89.64	0.25	0.19	0.31	-
Old lands	0.106	15.88	0.09	0.03	0.15	0	85.04	0.23	0.18	0.29	+
Moist grasslands	0.094	25.53	0.14	0.08	0.21	0	15.88	0.04	0.02	0.07	-
Burkea woodlands	0.018	0.00	0.00	n/a	n/a	n/a	6.83	0.02	0.00	0.04	0
Total	1.000	176.76	1.00				361.24	1.00			
Early growing season											
Sandy grasslands	0.419	95.56	0.57	0.47	0.67	+	148.48	0.45	0.38	0.52	0
Rocky grasslands	0.363	13.87	0.08	0.03	0.14	-	48.98	0.15	0.10	0.20	-
Old lands	0.106	18.32	0.11	0.05	0.17	0	75.27	0.22	0.16	0.28	+
Moist grasslands	0.094	39.05	0.23	0.15	0.32	+	33.05	0.10	0.06	0.14	0
Burkea woodlands	0.018	0.00	0.00	n/a	n/a	n/a	28.43	0.09	0.05	0.13	+
Total	1.000	166.80	1.00				331.21	1.00			
Total data											
Sandy grasslands	0.419	322.34	0.63	0.58	0.69	+	417.46	0.40	0.36	0.44	0
Rocky grasslands	0.363	43.25	0.08	0.05	0.12	-	200.74	0.19	0.16	0.22	-
Old lands	0.106	67.07	0.13	0.09	0.17	0	317.79	0.31	0.27	0.34	+
Moist grasslands	0.094	77.88	0.15	0.11	0.19	+	53.91	0.05	0.03	0.07	-
Burkea woodlands	0.018	0.00	0.00	n/a	n/a	n/a	51.24	0.05	0.03	0.07	+
Total	1.000	510.54	1.00				1041.14	1.00			

Notes: Π_i, proportion of habitat type available; u_i, number of used resource units in category i (weighted according to herd size); o_i, the proportion of used units in category i; B_{lower}, Lower Bonferroni-adjusted 95% confidence intervals for habitat type use; B_{upper}, Upper Bonferroni-adjusted 95% confidence intervals for habitat type use; s_i, selection of habitat category i.

Of the five broad habitats within the range of the wildebeest found within the study area, the black wildebeest positively selected the sandy grasslands and the old lands during the late growing season (Table 5.2). Black wildebeest used the rocky grasslands and *Burkea* woodlands to a lesser degree than expected, but utilised the moist grasslands in proportion to their occurrence on the study area.

Blue wildebeest significantly selected the old lands and the *Burkea* woodlands, but they showed a negative selection for the sandy grasslands, rocky grasslands and moist grasslands during the late growing season (Table 5.3).

Dormant season

During the dormant season there was a strong overall relationship between the type of wildebeest and the type of habitat (Black wildebeest: $\chi^2 = 73.8$; *df* = 4; $p<0.001$; Blue wildebeest: $\chi^2 = 80.9$; *df* = 4; $p<0.001$). Black wildebeest significantly selected the sandy grasslands and the moist grasslands but utilised the rocky grasslands to a lesser degree than expected (Table 5.2). Black wildebeest utilised the old lands in proportion to their availability in the study area but never occurred in the *Burkea* woodlands. Blue wildebeest significantly selected the old lands during the dormant season and showed a negative selection for the moist grasslands and rocky grasslands (Table 5.3).

Early growing season

During the early growing season there was a strong relationship between the type of wildebeest and the type of habitat (Black wildebeest: $\chi^2 = 83.3$; *df* = 4; $p<0.001$; Blue wildebeest: $\chi^2 = 167.0$; *df* = 4; $p<0.0001$). The black wildebeest showed a significant selection for the sandy grasslands and moist grasslands and utilised the rocky grasslands to a lesser degree than expected (Table 5.2). They were never found in the *Burkea* woodland habitat type but selected the old lands in proportion to their availability on the study area. Blue wildebeest significantly selected the *Burkea* woodlands and old lands but utilised the rocky grasslands to a lesser degree than expected during the early growing season (Table 5.3). The sandy grasslands and moist grasslands were utilised in proportion to their availability on the study area.

Between season comparisons

A comparison of the habitat selection of the black and blue wildebeest for the five broad habitats in the study area over the ecological seasons indicated which habitats were selected and those which were utilised to a lesser degree than expected at the different times of the year (Tables 5.2 and 5.3). Even though the black wildebeest actively selected the sandy grasslands throughout the study period, it was most likely to utilise the sandy grasslands during the dormant season ($\chi^2 = 28.4$; $df = 1$; $p<0.001$; Table 5.2). Blue wildebeest did not actively select the sandy grasslands but utilised them in proportion to their availability in the study area throughout most of the study period, except for the late growing season when they were were utilised to a lesser degree than expected. Blue wildebeest utilised the rocky grasslands to a lesser degree than expected throughout the study period but were most likely to do so during the dormant season. Black wildebeest utilised the rocky grasslands to a lesser degree than expected with an equal intensity year round. Black wildebeest did not actively select the old lands and utilised them in proportion to their availability throughout most of the study period, except for the late growing season when they were selected for. Blue wildebeest actively selected the old lands throughout the study period but were most likely to select the old lands during the late growing season. Black wildebeest did not occur in the *Burkea* woodlands at any time, but blue wildebeest actively selected the *Burkea* woodlands throughout the study period except for during the dormant season when they were used in proportion to their availability in the study area. Blue wildebeest were most likely to select the *Burkea* woodlands during the early growing season. Black wildebeest actively selected the moist grasslands throughout most of the study period except during the late growing season when they were utilised in proportion to their availability in the study area. Black wildebeest were most likely to select the moist grasslands during the early growing season. Blue wildebeest avoided the moist grasslands throughout the study period except during the early growing season.

Social group influence

Bachelor herds

There were a limited number of bachelor herds of both types of wildebeest in the study area. Therefore the data set for this social group was not as robust as the data sets for the other social groups. Black wildebeest bachelor herds showed a significant positive selection for the moist grasslands and tended to utilise the rocky grasslands to a lesser degree than expected (Table 5.2). They utilised the sandy grasslands and old lands in proportion to their availability in the study area. All habitats were utilised in accordance with their availability in the late growing season, while in the dormant season the bachelor herds selected the moist grasslands and showed a negative selection for the rocky grasslands. In the early growing season the black wildebeest bachelor herds selected the moist grasslands but used all the other habitat types in proportion to their availability in the study area.

Blue wildebeest bachelor herds were seldom encountered, but when they were encountered they utilised all the habitats in proportion to their availability in the study area except the *Burkea* woodlands, which they seemed to actively select throughout the study period.

Territorial bulls

Black wildebeest territorial bulls seldom occurred alone and usually formed part of a female herd. Therefore the data set for black wildebeest territorial bulls is small due to the clouding of these data. Black wildebeest territorial bulls therefore had a similar distribution in terms of habitat choice, as did the female herds. However, their frequency of occurrence individually was too low for the Chi-squared tests for broad habitat type selection to be valid (Table 5.2).

Lone blue wildebeest territorial bulls were encountered with a higher frequency than black wildebeest bulls, but the sample sizes were also too small for detailed seasonal analysis. The results did, however, indicate that blue wildebeest bulls tended to show a significant selection for the *Burkea* woodlands and old lands and a negative selection for the moist grasslands. Blue wildebeest territorial bulls utilised the sandy grasslands and rocky grasslands in proportion to their availability in the study area (Table 5.3).

Female herds

An analysis of the total data revealed that black wildebeest female herds never occurred in the *Burkea* woodlands and that the frequency of occurrence in the rocky grasslands was lower than expected. They actively sought out the sandy grasslands and old lands and utilised the moist grasslands in proportion to their availability in the study area. An analysis of the seasonal data indicated that the above pattern of habitat selection occurred during the late growing season but that in the dormant season the old lands were no longer selected but were rather utilised in proportion to their availability in the study area. In the early growing season, black wildebeest female herds showed the same pattern of habitat selection as that of the dormant season except that they tended to select the moist grasslands instead of utilising them in proportion to their availability in the study area.

An analysis of the total data revealed that the blue wildebeest female herds actively selected the old lands and the *Burkea* woodlands but utilised the rocky grasslands and moist grasslands to a lesser degree than expected (Table 5.3). They utilised the sandy grasslands in proportion to their availability in the study area. An analysis of the seasonal data indicated that during the late growing season a similar pattern to that observed in the total data occurred, except that the sandy grasslands were utilised to a lesser degree than expected and the *Burkea* woodlands were used in proportion to their availability in the study area during the late growing season. During the dormant season the habitats were utilised in a similar way to that described for the total data except that the *Burkea* woodlands were used in proportion to their availability in the study area instead of being positively selected. In the early growing season the *Burkea* woodlands were actively selected and the moist grasslands were utilised in proportion to their availability in the study area. The rest of the habitats were utilised in a similar manner to that described for the total data.

Vegetation assessment by broad habitat types

During the study period a total of 51 grass species were recorded in the vegetation surveys at Ezemvelo Nature Reserve in the broad habitats that were utilised by the two types of wildebeest.

Ecological Class 1 grass species at Ezemvelo Nature Reserve in those habitats that were utilised by both types of wildebeest included: *Diheteropogon amplectens, Digitaria eriantha, Monocymbium ceressiforme, Panicum natalense, Setaria sphacelata,* and *Themeda triandra.* Based on the results of the generalised linear model procedures (PROC GLM), there were no significant differences in percentage of Class 1 grass species between the broad habitats that were utilised by the black and blue wildebeest (p = 0.4438) (Figure 5.3).

Ecological Class 2 grass species at Ezemvelo Nature Reserve in the broad habitats that were utilised by both types of wildebeest included: *Trachypogon spicatus, Tristachya rehmannii, Schizachyrium sanguineum, Melinis nerviglumis, Imperata* *cylindrica, Hyparrhenia filipendula, Cymbopogon excavatus, Brachiaria brizantha* and *Andropogon schirensis.* The generalised linear model procedures (PROC GLM) indicated acceptance of the null hypothesis of no difference regarding the abundance of Class 2 grass species in the respective broad habitat types (p = 0.0578) (Figure 5.3).

Ecological Class 3 grass species were generally rare at Ezemvelo Nature Reserve, especially in the broad habitats that were occupied by the two types of wildebeest (Figure 5.3). This indicated that tufted tall perennial grass species with a high productivity but a low grazing value and which tend to increase with light overutilisation are not abundant in the study area.

Ecological Class 4 grass species at Ezemvelo Nature Reserve in those broad habitats that were utilised by both types of wildebeest included: *Eragrostis chloromelas, Eragrostis curvula, Elionurus muticus, Eragrostis racemosa,* and *Sporobolus festivus.* The generalised linear model procedures (PROC GLM) showed no significant difference between the abundance of Class 4 grass species between the broad habitat types (p = 0.1631) (Figure 5.3).

Ecological Class 5 grass species at Ezemvelo Nature Reserve in those habitats that were utilised by both types of wildebeest included: *Sporobolus africanus, Perotis patens, Pogonarthria squarrosa, Melinis repens, Microchloa caffra, Eragrostis plana, Eragrostis inamoena,* and *Eragrostis gummiflua.* The results of the PROC GLM procedures indicated that there was no significant difference in the abundance of Ecological class 5 grass species between the habitats (p = 0.7530) (Figure 5.3).

In general, Ecological Classes 4 and 5 made a larger contribution to the grass composition than Ecological Classes 1 and 2. Only in the rocky grasslands was there an equal distribution of Ecological Classes 1 and 2 compared with Ecological Classes 4 and 5. Old lands and *Burkea* woodlands had a low percentage of Class 2 grass species while the moist grasslands had a low percentage of Class 1 grass species. The old lands and sandy grasslands were dominated by Class 4 grass species, while the moist grasslands were dominated by Class 5 grass species. Class 1 grass species made a large contribution to the grass species in the *Burkea* woodlands (26%), rocky grasslands (18%) and in the old lands (18%).

The degree of past utilisation as calculated from the ecological species composition of each habitat type did not differ significantly between habitat types ($p = 0.1281$). The rocky grasslands had the lowest degree of utilisation (~15%) of all the habitats investigated, while all the other habitat types all were utilised at a frequency of >50% (Figure 5.4).

The generalised linear model procedures (PROC GLM) indicated that there was no significant difference in veld condition between the broad habitats ($p = 0.9417$). The veld condition score at Ezemvelo Nature Reserve is poor (veld condition score: 350-450). This indicated that the veld was generally dominated by an abundance of Ecological Classes 4 and 5 grass species. The *Burkea* woodlands had the highest veld condition score while the moist grasslands had the lowest veld condition score of all the habitats investigated (Figure 5.5).

The Shannon-Wiener index of diversity indicated that the grass species diversity of all the habitat types was relatively low ($D<2.5$), yet there was a significant difference in grass species diversity between the habitats ($p = 0.0133$). The PROC GLM test results also indicated that the grass species diversity index in the rocky grasslands was significantly higher than that of old lands ($p = 0.0025$) and the moist grasslands ($p = 0.0040$) (Figure 5.6).

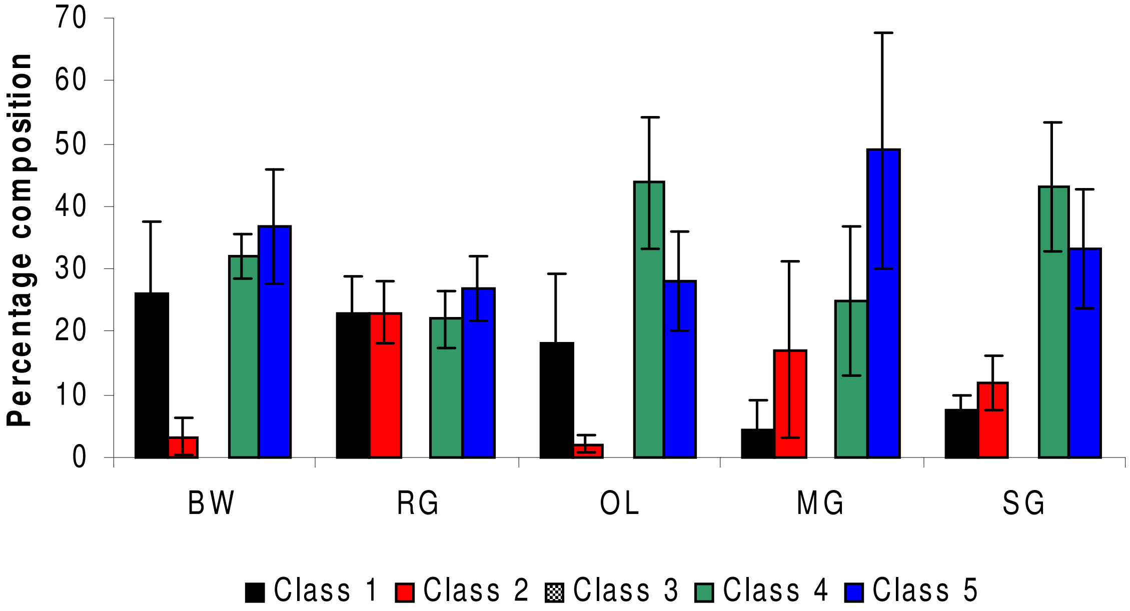

Figure 5.3: Mean percentage composition of the five ecological classes of grass species in the five broad habitats that were utilised by the black and blue wildebeest at Ezemvelo Nature Reserve in 2004. Bars represent the standard error of the percentage composition. No significant differences between habitats were found. BW = *Burkea* woodlands, RG = rocky grasslands, OL = old lands, MG = moist grasslands, SG = sandy grasslands.

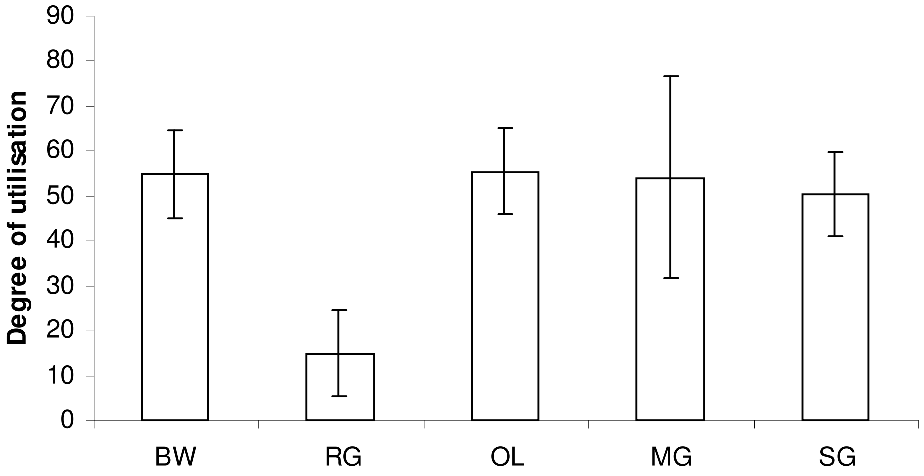

Figure 5.4: Mean (columns) and standard error (bars) of the degree of past utilisation of the five broad habitats utilised by the black and blue wildebeest at Ezemvelo Nature Reserve in 2004 as calculated from the percentage composition of the five ecological classes of grass species present within these habitats. No significant differences between habitats were found. BW = *Burkea* woodlands, RG = rocky grasslands, OL = old lands, MG = moist grasslands, SG = sandy grasslands.

The PROC GLM tests showed a significant difference in grass species density between habitat types (p = 0.0011). According to the PROC GLM tests, the rocky grasslands had a significantly higher grass species density than the *Burkea* woodlands (p = 0.0067), the moist grasslands (p = 0.0007) and the old lands (p = 0.0003) (Figure 5.7). The old lands had a grass species density that was significantly lower than that of the sandy grasslands (p = 0.0255). The moist grasslands also had a significantly lower grass species density than the sandy grasslands (p = 0.0373).

The percentage bare ground present differed significantly between the habitat types (p = 0.0004). The rocky grasslands had a significantly higher percentage of bare ground compared with the *Burkea* woodlands (p = 0.0003), the moist grasslands (p = 0.0009), the old lands (p = 0.0008) and the sandy grasslands (p = 0.0002) (Figure 5.8).

All the habitat types had a grass canopy cover of >60% during all the ecological seasons (Figure 5.9). The percentage canopy cover differed significantly between the habitat types during the late growing season (p = 0.0461). In the late growing season the moist grasslands had a significantly higher canopy cover than the rocky grasslands (p = 0.0067), as did the *Burkea* woodlands (p = 0.0332) and the old lands (p = 0.0234). In the dormant season, the percentage canopy cover also differed significantly between habitat types (p = 0.0046). The moist grasslands then had a significantly higher percentage canopy cover than the old lands (p = 0.0097) and the rocky grasslands (p = 0.0003), while the rocky grasslands also had a significantly lower percentage canopy cover than the sandy grasslands (p = 0.0053). In the early growing season the percentage canopy cover also differed significantly between habitat types (p = 0.0472). The moist grasslands had a significantly higher percentage canopy cover than the old lands (p=0.0206) and the rocky grasslands (p = 0.0261), while the sandy grasslands had a significantly higher percentage canopy cover than the old lands (p=0.0352) and the rocky grasslands (p = 0.0473).

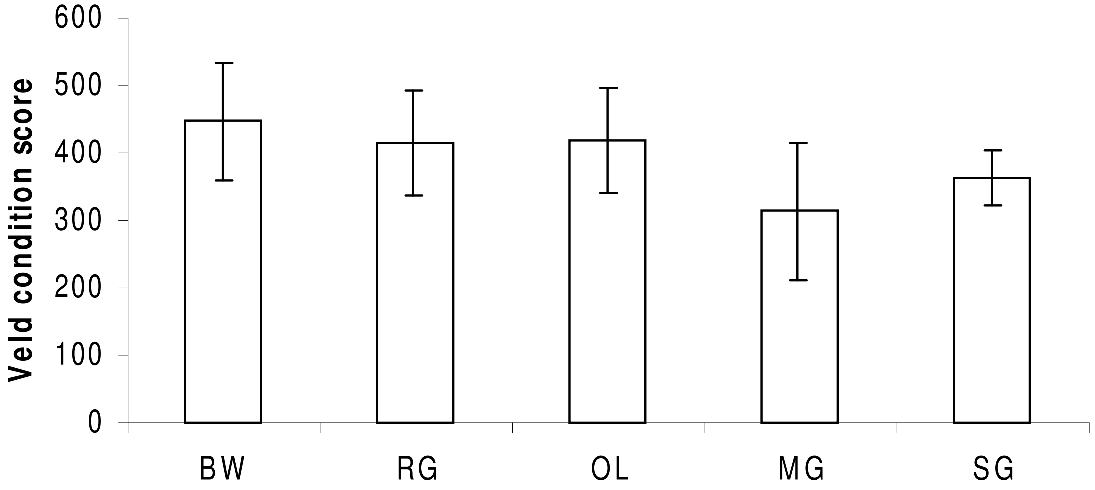

Figure 5.5: Mean (columns) and standard error (bars) of the veld condition score of the five broad habitats utilised by the black and blue wildebeest at Ezemvelo Nature Reserve in 2004 as calculated from the percentage composition of the five ecological classes of grass species present within these habitats. No significant differences between habitats were found. BW = *Burkea* woodlands, RG = rocky grasslands, OL = old lands, MG = moist grasslands, SG = sandy grasslands.

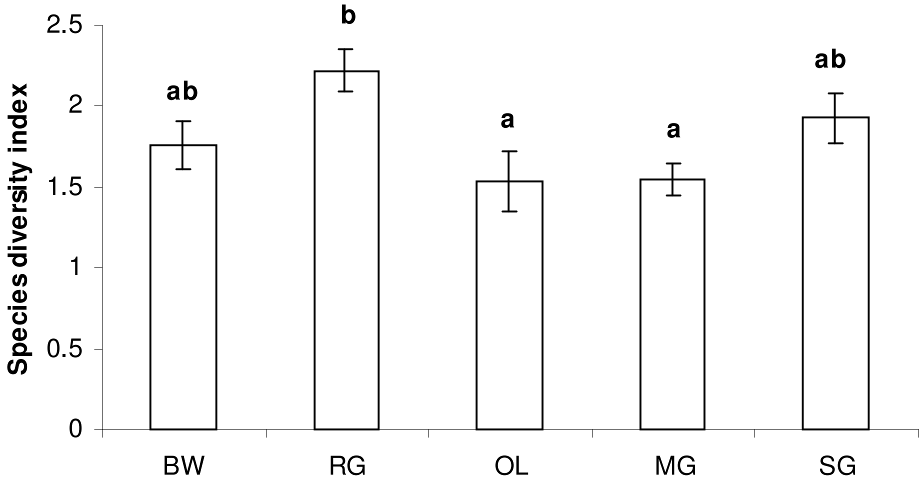

Figure 5.6: Mean (columns) and standard error (bars) of the Shannon-Wiener diversity index of the five broad habitats utilised by the black and blue wildebeest at Ezemvelo Nature Reserve in 2004 as calculated from the percentage composition of grass species present within these habitats. Means with the same superscripts were not significantly different from each other. BW = *Burkea* woodlands, RG = rocky grasslands, OL = old lands, MG = moist grasslands, SG = sandy grasslands.

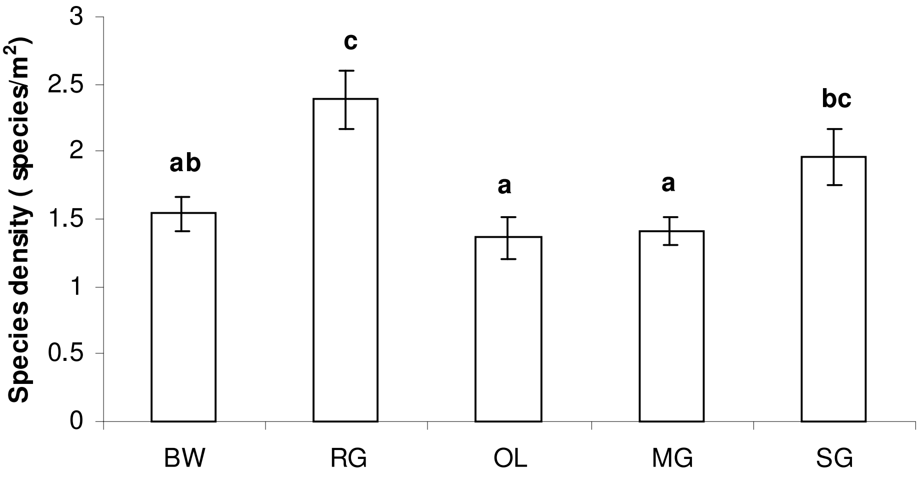

Figure 5.7: Mean (columns) and standard error (bars) of the plant species density of the five broad habitats utilised by the black and blue wildebeest at Ezemvelo Nature Reserve in 2004 as calculated from the percentage composition of the five ecological classes of grass species present within these habitats. Means with the same superscripts were not significantly different from each other. BW = *Burkea* woodlands, RG = rocky grasslands, OL = old lands, MG = moist grasslands, SG = sandy grasslands.

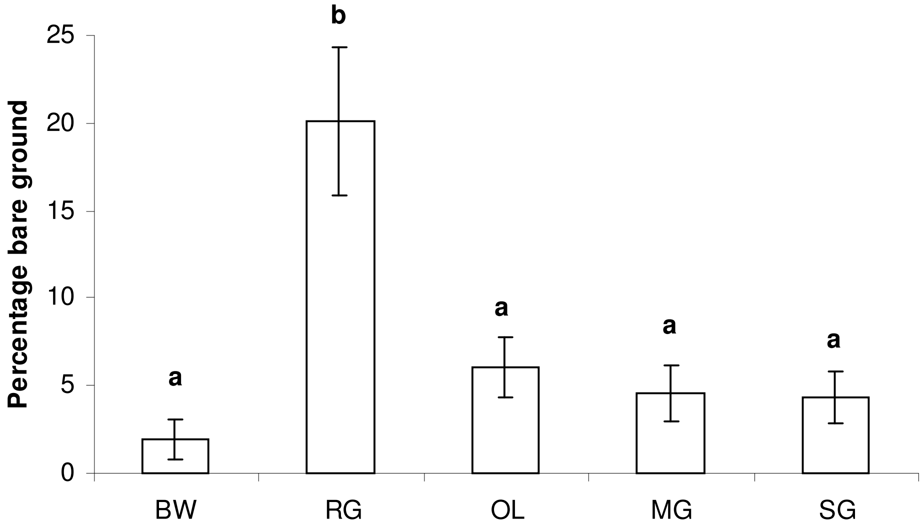

Figure 5.8: Mean (columns) and standard error (bars) of the percentage bare ground of the five broad habitats utilised by the black and blue wildebeest at Ezemvelo Nature Reserve in 2004. Means with the same superscripts were not significantly different from each other. BW = *Burkea* woodlands, RG = rocky grasslands, OL = old lands, MG = moist grasslands, SG = sandy grasslands.

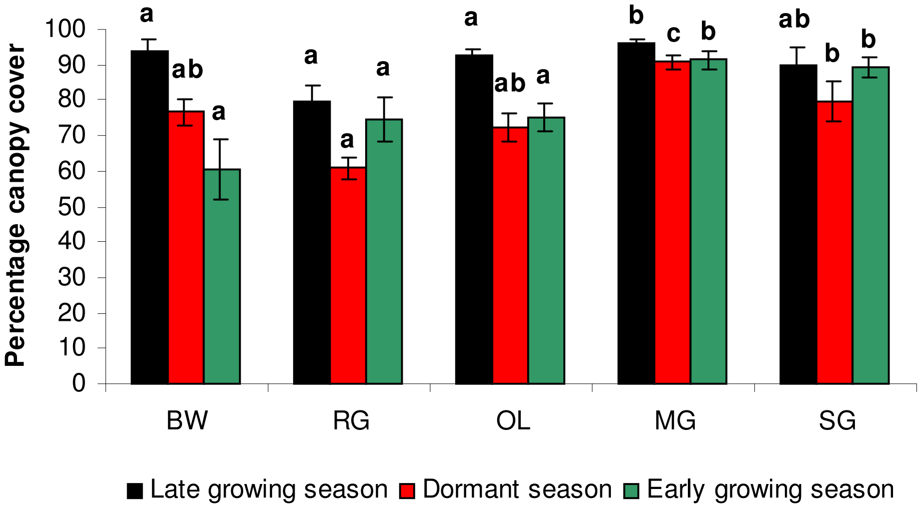

Figure 5.9: Mean (columns) and standard error (bars) of the percentage canopy cover of the herbaceous layer of the five broad habitats utilised by the black and blue wildebeest at Ezemvelo Nature Reserve over the three ecological seasons in 2004. Means with the same superscripts were not significantly different from each other; these are compared across the five habitats within each season. BW = *Burkea* woodlands, RG = rocky grasslands, OL = old lands, MG = moist grasslands, SG = sandy grasslands.

The lowest total grass height was found in the old lands and the highest in the *Burkea* woodlands throughout all seasons (Figure 5.10). The highest grass leaf height was found in the moist grasslands and the lowest grass leaf height was found in the old lands (Figure 5.11). There was no significant difference in total grass height between the habitat types in the late growing season (p = 0.7280). There also was no significant difference in grass leaf height between the broad habitat types in late growing season (p = 0.2354). In the dormant season there was no significant difference between habitat types in total grass height (p = 0.5295). Grass leaf height between habitat types also did not differ significantly (p = 0.0786) during this season. The total grass height (p = 0.9563) and grass leaf height (p = 0.9243) did not differ significantly between the habitat types in the early growing season.

The highest grass biomass was found in the moist grasslands (4 900 kg/ha) and the lowest in the old lands (2 500 kg/ha) throughout all seasons (Figure 5.12). No significant difference was found in biomass between habitat types (p=0.1403) in late growing season. There also was no significant difference in grass biomass between the habitat types in the dormant season (p = 0.3202) or in the early growing season (p = 0.3391).

There was no significant difference in the biomass concentration between habitat types in the late growing season (p=01971), and there was no significant difference in grass biomass concentration between the habitat types in the dormant season (p = 0.4375), but there was a significant difference in grass biomass concentration between habitat types in the early growing season (p = 0.0579) (Figure 5.13). During the early growing season, the moist grasslands had a significantly higher grass biomass concentration than the old lands (p = 0.0073) and rocky grasslands (p = 0.0459). The sandy grasslands had a significantly higher biomass concentration than the old lands in the early growing season (p = 0.0333).

Tables 5.5 and 5.6 summarise all the characteristics of the five broad habitat types that were utilised by the black or blue wildebeest at Ezemvelo Nature Reserve during the study period.

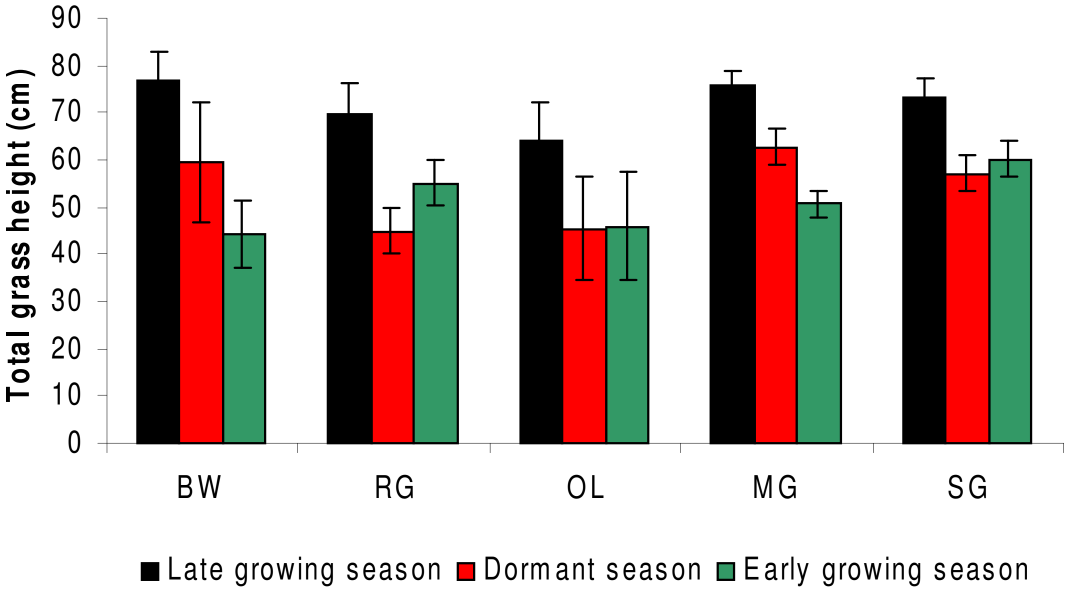

Figure 5.10: Mean (columns) and standard error (bars) of the total grass height of the herbaceous layer in the five broad habitats utilised by the black and blue wildebeest at Ezemvelo Nature Reserve over the three ecological seasons in 2004. No significant differences were found between the means of the different habitat types. BW = *Burkea* woodlands, RG = rocky grasslands, OL = old lands, MG = moist grasslands, SG = sandy grasslands.

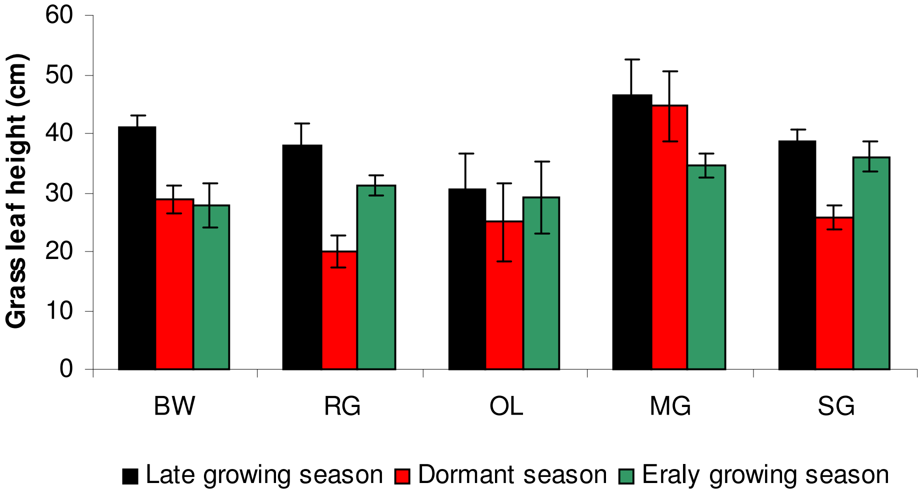

Figure 5.11: Mean (columns) and standard error (bars) of the grass leaf height of the herbaceous layer in the five broad habitats utilised by the black and blue wildebeest at Ezemvelo Nature Reserve over the three ecological seasons in 2004. No significant differences between categories were found. BW = *Burkea* woodlands, RG = rocky grasslands, OL = old lands, MG = moist grasslands, SG = sandy grasslands.

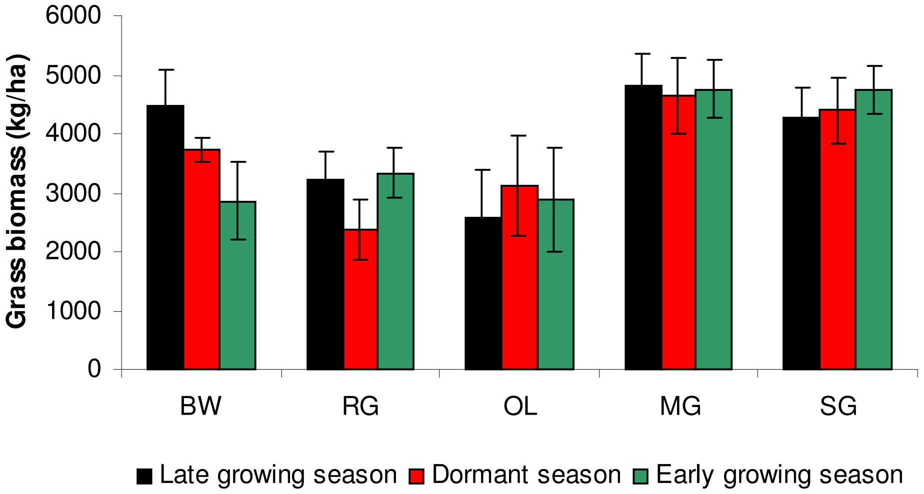

Figure 5.12: Mean (columns) and standard error (bars) of the grass biomass of the herbaceous layer in the five broad habitats utilised by the black and blue wildebeest at Ezemvelo Nature Reserve over the three ecological seasons in 2004. No significant differences between categories were found. BW = *Burkea* woodlands, RG = rocky grasslands, OL = old lands, MG = moist grasslands, SG = sandy grasslands.

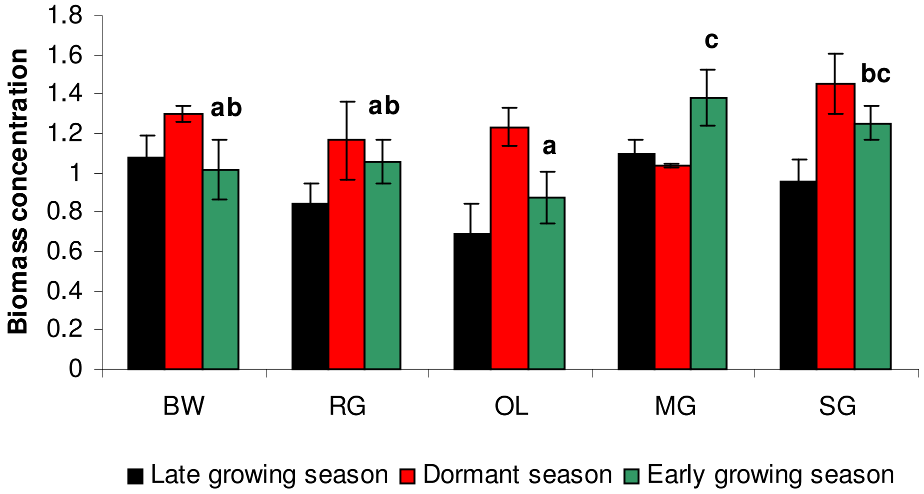

Figure 5.13: Mean (columns) and standard error (bars) of the biomass concentration of the herbaceous layer in the five broad habitats utilised by the black and blue wildebeest at Ezemvelo Nature Reserve over the three ecological seasons in 2004. Superscripts that are the same indicate no significant differences. BW = *Burkea* woodlands, RG = rocky grasslands, OL = old lands, MG = moist grasslands, SG = sandy grasslands.

Table 5.5: Summary of the characteristics of the five broad habitat types utilised by black and blue wildebeest at Ezemvelo Nature Reserve in 2004

Habitat	Surface area in ha	General characteristics	Dominant plant species	Ecological composition	Percentage utilisation	Veld condition score	Grass species diversity	Grass species density
Burkea woodlands	123	Open woodland, no rock cover, deep sandy soils	*Setaria sphacelata* *Burkea africana*	Highest % Class 1, low % Class 2	55	447	1.8	1.5
Rocky grasslands	2540	>30% rock cover, shallow soils, exposed areas	*Xerophyta retinervis* *Loudetia simplex*	Highest % Class 2	15	414	2.2	2.4
Old lands	744	Short stoloniferous grasses, flat areas, no rock cover	*Eragrostis curvula* *Digitaria eriantha*	High % Class 4, second highest Class 1 %, very low % Class 2	55	418	1.5	1.3
Moist grasslands	658	Tall fibrous grasses, drainage areas, valleys, fine clay soils, no rock cover, seasonally waterlogged	*Eragrostis nindensis* *Aristida junciformis* *Eragrostis gummiflua*	High Class 5 %, Moderate Class 2 %, lowest Class 1 %	54	313	1.5	1.4
Sandy grasslands	2933	Rock cover <30%, open high-lying plains, deep sandy soils	*Eragrostis curvula* *Setaria sphacelata* *Eragrostis chloromelas*	High % Class 4 and 5, low % Class 1 and Class 2.	50	363	1.9	2

Table 5.6: Summary of the herbaceous characteristics of the five habitat types utilised by the black and blue wildebeest at Ezemvelo Nature Reserve over the three ecological seasons in 2004. BC = biomass concentration

Habitat	Ecological season														
	Late growing season					Dormant season					Early growing season				
	Canopy cover (%)	Total grass height (cm)	Grass leaf height (cm)	Biomass (kg/ha)	BC	Canopy cover (%)	Total grass height (cm)	Grass leaf height (cm)	Grass biomass (kg/ha)	BC	Canopy cover (%)	Total grass height (cm)	Grass leaf height (cm)	Grass biomass (kg/ha)	BC
Burkea woodlands	83	77	41	4462	1.1	95	59	29	3733	1.3	96	44	28	2858	1.0
Rocky grasslands	80	69	38	3224	0.8	60	45	20	2359	1.2	74	55	31	3330	1.1
Old Lands	82	64	31	2568	0.7	72	45	25	3123	1.2	75	46	29	2870	0.9
Moist grasslands	95	73	43	4562	1.1	90	60	41	4343	1.0	91	52	34	4657	1.4
Sandy grasslands	89	71	39	3857	1.0	80	56	27	3965	1.5	89	61	36	4386	1.3

DISCUSSION

The results of the present study indicated that ecological separation between the black and blue wildebeest does exist to some extent on the basis of broad habitat type selection. Observations of the two types of wildebeest indicated a distinct habitat divergence with the black wildebeest selecting the open and moist bunch grass habitats and blue wildebeest the habitats that provided some form of cover and with extensive grazing sites. This study therefore further supported previous observations that blue wildebeest prefer areas where cover is readily available (Skinner and Chimimba 2005). Previous research also supports the results of this study that black wildebeest prefer open grasslands with little tree cover (Von Richter 1971b; Schmidt 1988). A preference for open grasslands has been attributed to predation risk, as black wildebeest rely more on speed than on camouflage to escape predators (Chapter 3). Moreover, open areas also do not allow for concealment of approaching predators (Schmidt 1988). However, other studies have indicated that territorial defence may play a larger role in the preferences of black wildebeest for open areas (Brink *et al*. 1999). This theory may be more appropriate in a reserve where predation does not play an important role such as at Ezemvelo Nature Reserve.

According to Von Richter (1971a) the black wildebeest prefers short grasslands and avoids areas where tall mature grasses predominate. The same is true for the blue wildebeest (Child 1968; Estes 1969). Both types of wildebeest also tend to condition their grazing sites in such a way that they keep the grass short (Von Richter 1971a). Past land use practices at Ezemvelo Nature Reserve, such as planted pastures and cattle kraals as was described in Chapter 2, have left a large proportion of the reserve as optimal habitat for wildebeest with large areas of short grass. Before being declared a nature reserve, a large portion of Ezemvelo consisted of ploughed lands. These lands were sown with *Eragrostis curvula* and *Digitaria eriantha* to provide a cultivated pasture (Tau 2004 pers. comm.)[9]. The above two grass species are still the most abundant plant species in the old lands, with a mean percentage frequency of 25% and 47% respectively.

It would therefore be expected that both types of wildebeest would preferentially select the old lands. The results of the present study indicated that the blue wildebeest showed a strong preference for the old lands, whereas the black

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wildebeest only showed a preference for this habitat during the late growing season and used it in a random manner throughout the rest of the year. The black wildebeest instead tended to select the sandy grasslands that consisted mainly of tall mature grass stands. Possible conflict between black and blue wildebeest may occur in the late growing season when they both are selecting the old lands as a preferred habitat.

With their habit of remaining in one area for extended periods of time (Von Richter 1971a), the black wildebeest tends to trample and overgraze certain areas. The dominant grasses in the sandy grasslands where the black wildebeest predominated at Ezemvelo Nature Reserve are not stoloniferous but are stemmy grasses replaced through grazing pressure by grasses with a low palatability, such as *Aristida congesta* (Van Oudtshoorn 1999). The basal cover therefore decreases over time, after which the black wildebeest will move off to another grazing area where the grasses have not yet been degraded. Selection of the grazing site tended to depend on the openness of the habitat rather than the quality of the footage available. This high affinity for open areas at the expense of forage and feeding site suitability, suggested that forage was not the only constraint on black wildebeest habitat use. This selection could have been as a result of a trade-off between selecting for open, high-lying areas for territorial defence and areas that provide the most suitable feeding grounds (Namgail *et al*. 2004). The differences in old land habitat use that were found between the black and blue wildebeest may therefore well be attributable to species-specific differences in territorial behaviour as suggested by Brink *et al.* (1999) in his study of fossil evidence.

It appears that both types of wildebeest avoided the rocky grassland habitats throughout all the seasons. This may be due to large portions of the rocky grasslands being in areas far from the nearest water. Therefore only those sections of this habitat type that have water in its vicinity would be utilised. The rocky grasslands had the lowest degree of utilisation by wildebeest (15%), but also the highest proportion of Ecological Class 2 grass species, most of which were highly unpalatable (Van Oudtshoorn 1999). Avoidance of this habitat by both types of wildebeest may therefore be more related to its grass species composition than the physical rockiness of the terrain.

The moist grasslands in the drainage areas that were selected by the black wildebeest and avoided by the blue wildebeest, tended to have the lowest veld condition score, the lowest grass species diversity, the highest percentage canopy and basal cover, and the tallest stands of grasses of all the habitat types studied (Table 5.6). Black wildebeest tended to concentrate in the higher-lying parts of this habitat type. They also tended to show the most preference for this habitat type during the early growing season when it tended to be dominated by nutritious forbs and sedges (Cyperaceae), which appeared in highest abundance after the first rains in the moist grasslands. Observations of black wildebeest utilising these ephemeral plant species have been recorded by Furstenberg (2002a) and data from field studies have shown a higher browse intake by black wildebeest as compared to blue wildebeest (Codron and Brink In press). Where this habitat occurs in higher-lying areas, it may be used by the black wildebeest as a substitute for the old lands to meet their nutritional requirements. This habitat type would have a higher percentage of C_3 monocotyledons such as reeds (*Phragmites* spp.) and sedges (Cyperaceae) which have been shown to contribute to the diets of wildebeest and of making up 40 to 50% of the plant species in the South African central interior (Stock *et al.* 2004).

In total, 62% of the black wildebeest and 40% of the blue wildebeest observations were in the sandy grasslands. This habitat type is extremely important in the study area due to its large surface area. Spatial heterogeneity within this habitat type is higher than the other habitat types investigated due to patches of bunch grass being intermingled with patches of lawn grasses. Spatial heterogeneity within this habitat could allow for use of this habitat type by both the black and blue wildebeest without competition.

Habitat segregation between the three social groups in both the types of wildebeest was not clearly indicated. The results did, however, indicate that the bachelor herds of both types of wildebeest randomly selected most habitat types during all the seasons, indicating that the bachelor herds may be forced to occupy those habitats that were not utilised by the other social groups. This tended to support the observations of Von Richter (1971a). The sample size for bachelor herd sightings may, however, have been too small to demonstrate clear habitat selection, but it is feasible that the bachelor herds would tend to roam widely through the study area without selecting specific areas (Penzhorn 1982). The female herds of both types of wildebeest on the other hand were more sedentary than the bachelor herds.

In order to ensure some measure of separation of the two types of wildebeest on Ezemvelo Nature Reserve, the establishment of *Burkea* woodlands should be encouraged and the loss of these woodlands due to fire and insect infestation must be prevented. The *Burkea* woodlands provide cover for the blue wildebeest, while the black wildebeest completely avoid this habitat. This habitat type may therefore provide one of the main means of providing mutually exclusive habitat for the two types of wildebeest and thus its preservation should be promoted. Other wildlife such as red hartebeest and Burchell's zebra also utilised this habitat to a large degree. The dynamics of why these even age stands of *Burkea* woodland (cohorts) occur in certain areas and not in others are not yet clearly understood (Wilson and Witkowski 2003). Research into these cohorts may provide details on establishment of *Burkea africana* and thus ensure that these stands are actively managed for the continued coexistence of the two types of wildebeest in the study area.

The greater the impact of a particular vegetation pattern on the foraging behaviour of a particular herbivore species, the greater may be the divergence of impact of that species on the areas which have different distributions of the same vegetation types (Bailey *et al.* 1998). The grasslands that were dominated by stoloniferous grazing lawn grass species were characterised by a high overall degree of utilisation by both the black and blue wildebeest, indicating that this habitat may generally offer a better food quality but possibly a lower food availability (standing grass biomass) than the bunch grass communities on the sandy grasslands, rocky grasslands and moist grasslands (Cromsigt 2006). Several studies have shown that grass production in grazing lawns is higher than in other grassland types (Hik and Jeffries 1990).

CONCLUSION

Pianka (1978) indicated that ecologists have long considered that habitat separation can serve to decrease both interference and exploitative competition and could facilitate coexistence of ecologically similar species. Selection by black and blue wildebeest of the various habitat types on Ezemvelo Nature Reserve was found to be mainly due to the physical characteristics of the habitats and a certain degree of ecological separation was evident through this habitat dimension. Therefore habitat separation in terms of degree of openness and elevation may reduce competition and facilitate the coexistence of the black and blue wildebeest at Ezemvelo Nature Reserve as was also shown in New Zealand for Tahr and Camois by Namgail *et al.* (2004).

CHAPTER 6:HABITAT SELECTION AND SEPARATION: MESOHABITAT SCALE

INTRODUCTION

Habitat selection does not only occur at the broad habitat scale as was analysed in Chapter 5. The sites that are utilised by an animal may occur within a particular habitat, but the features of those sites of utilisation may be the actual cause of selection for that site rather than the fact that the site occurs within that particular habitat. This requires analysis of habitat selection and separation at the meso-habitat scale. In determining whether habitat separation occurs between two types of wildlife there is a wide range of possible meso-habitat factors to be considered that could be responsible for its existence. Habitats are defined by certain geomorphological factors such as topography, geological formations and soil types, as well as weather and vegetation (Theron 1991). It is imperative to assess as many meso-habitat factors as possible to determine which factors are most important in differentiating between areas selected by one type of wildlife and perhaps not by the other.

For African ungulates, the main determinants of local movements are forage availability, forage quality in terms of mineral nutrition, water availability (Ben-Shahar and Coe 1992) and certain landscape types and features such as topography, soil type and vegetation composition and structure (Ben-Shahar 1995). Seasonal movements of animals may be attributed to climatic conditions, the seasonal phenological development of forage and the occurrence of fire (Munthali and Banda 1992). For water dependent wildlife like the black and blue wildebeest the availability of water would be most important in habitat preference, but when water is abundant the physical structure of the habitat would become more important. Physical aspects such as topography, slope, geomorphology and rock cover do not change over short periods of time and thus can be regarded as relatively constant. Vegetation structure would then be expected to determine the suitability of a habitat for such factors as available shade and visibility. Within this context the plant species composition would play an important role in determining whether the food source is sufficient for the requirements of the species (Strauss 2003).

Since it was expected that the black and blue wildebeest are too ecologically similar to be kept in the same area, it was hypothesised that there would be no meso-habitat separation between the black and blue wildebeest at Ezemvelo Nature Reserve.
The objectives of this part of the study were therefore to:

- Determine which habitat factors (if any) separate the habitats of the two types of wildebeest and whether the bachelor herds, territorial bulls and female herds of the black and blue wildebeest have different separating mechanisms.
- Determine if the black and blue wildebeest graze in habitats with different meso-habitat characteristics.
- Determine if habitat separation (if found) of the black and blue wildebeest is affected by any seasonal influences, time of day influences, daily temperature fluctuations or daily cloud cover fluctuations

METHODS

All the data for this section of the study were obtained by using the methods described in Chapter 4.

Statistical analysis of the data

In the past, simple qualitative descriptions of the data were used to determine the habitat preferences of a species (Lamprey 1963). Later, quantitative techniques were introduced. In their simplest form, quantitative studies on habitat selection expressed habitat utilisation in terms of the proportion of animals seen in each sub-habitat or habitat (Scogings *et al.* 1990). A comparison of the observed habitat use with the expected habitat use, according to habitat availability, is an extension of these simple quantitative techniques (Hirst 1975).

Multivariate analyses have more recently been used to quantify the relationship between herbivores and their habitat. Studies using multivariate analysis techniques do not require information on the amount of sub-habitat available, as a record of habitat variables at each animal location is sufficient (Strauss 2003). Some of the drawbacks of the traditional multivariate analysis methods, however, include the assumption of normally distributed data, which is seldom justified in ecological data, and the assumption of linear relationships between variables, which is often violated as the relationships between variables is usually more complex in ecological data (Beardell *et al*. 1984).

Among those techniques that are used in multivariate analyses are discriminant function analysis (Ferrar and Walker 1974), multiple regression (Hirst 1975; Ben-Shahar 1986), correspondence analysis (Beardell *et al.* 1984; Engelbrecht 1986) and detrended correspondence analysis (Scogings *et al*. 1990). Even more recently the categorical modelling (CATMOD) of data has been used to determine habitat selection where categorical variables can easily be investigated (Weaver 1995; Von Holdt 1999). This procedure, however, has proven extremely time-consuming for previous researchers as multiple runs and variable recategorisations have to be performed in order to obtain a model with the most significant variables (Van der Linde 2006 pers. comm.)[10]. Logistic regression analysis has also been used by researchers in habitat studies (Morrison *et al*. 1992; Pauley *et al*. 1993).

Since the aim of the present study was to determine the habitat separation between the black and blue wildebeest, a simple analysis of which habitat factors were related to the habitat use of each type of wildebeest, would not be sufficient to separate their habitat choices. Thus, it was decided to use a multivariate approach to determine predictor variables for determining the occurrence of a black wildebeest or a blue wildebeest.

Both data management and statistical analyses were performed by using SAS version 8.01 (SAS Institute, Inc., Cary, NC, USA). In the current study, each observation consisted of 43 variables. The data associated with each of these variables were investigated in groups of categories. The variable coding and explanations can be found in Appendix 2.

The multivariate approach that was used here was that of linear logistic regression. Logistic regression analysis is a combination of multiple discriminant function analysis and multiple regression analysis (Hair *et al.* 1995). It is a robust alternative to simple discriminant analysis (Dattalo 1994; Lottes *et al*. 1996). Logistic regression analysis was performed with the PROC LOGISTIC procedure to determine predictor variables (at the 5% level) that would separate the habitats that were utilised by the black wildebeest from those that were utilised by the blue wildebeest. The PROC LOGISTIC procedure was used to investigate the relationship between discrete or binary responses and a set of explanatory variables by fitting linear logistic regression models through the method of maximum likelihoods. The response variable is the dependent variable. This procedure can handle both continuous or categorical explanatory variables and can analyse large data sets. The aim of maximum likelihood estimation is to find the parameter value(s) that makes the

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observed data most likely. This is because the likelihood of the parameters, given the data, is defined to be equal to the probability of the data, given the parameters.
The basic logistic model as described by Ely *et al*. (1996) was applied:

$$\text{Logit}(p) = \log(p/1-p) = \alpha+\beta'x$$

Where p is the probability of finding a black wildebeest

α = intercept parameter
β' = row vector of slope parameter
x = column vector of explanatory variables

The parameters of the standard logistic model can be interpreted directly or indirectly, after transformation to odds ratios, to a probability or to a difference in probability (McArdle and Hamagami 1996; Groeneveld 2006 pers. comm.[11]). The power value or log odds (Hall and Round 1994) for each observation was calculated based on the mean value of each habitat variable. Probabilities (p) were calculated from the antilog of the power value or odds. Probabilities were used to identify the habitat variables which best described the variation between the black and blue wildebeest habitat types. If the predicted probability was >0.5, then the prediction was taken to relate to a black wildebeest, otherwise it related to a blue wildebeest (Hair *et al.* 1995).

All the variables were categorised before input into the PROC LOGISTIC model (Appendix 2). Before input, the variables were examined for missing values, correlation and singularity. A number of variables were not included in the analysis due to missing values. These were drainage (V42), dominant plant species (V37) and sub-dominant plant species (V38). The association variable (V32) was not included in this analysis but it was used for further analysis in the behavioural interaction section of this study. The vegetation structure (V33) was found to be correlated to a number of other variables and was omitted in this analysis.

The data set submitted to the PROC LOGISTIC procedure included the following explanatory variables: habitat type (V15), aspect (V16), slope analysis (V17), distance to water (V19), woody vegetation cover (V20), grass cover (V21), rock cover (V26), total grass height (V27), grass leaf height (V28), plant utilisation (V29),

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visibility (V30), distance to shade (V31), erosion (V34), altitude (V35), time since last burn (V36), exposure (V39), geomorphology (V40), and forb : grass ratio (V41). The herd size (V13) was used as a weighting factor.

A stepwise selection procedure was then followed to select variables that would be significant in differentiating between habitats that were utilised preferentially by black and blue wildebeest. The probability modelled was for the presence of a black wildebeest. The model was tested for significance by the –2 log-likelihood statistic, explanatory power by the maximum rescaled r^2 value and its capacity to successfully discriminate black or blue wildebeest habitat use by the c value (While and McArthur 2005). The Wald statistic was used to test the significance of effects of each independent variable. Once these variables were selected they were rerun through a PROC LOGISTIC analysis process with no selection and the probabilities associated with each category of each selected variable were calculated. When the significant variables are examined it is possible to identify which categories are preferred by which type of wildebeest when all the other factors are held constant. This was done by examining p-values from 0 to 0.2 indicating preference by blue wildebeest and p-values from 0.8 to 1 indicating preference by black wildebeest. The percentage of the observations with p-values from 0 to 0.2 and from 0.8 to 1 were tabulated to indicate the preferred categories within each variable for each model by each type of wildebeest. Preference for a particular category within a variable by a type of wildebeest was shown by the presence of a high percentage of probabilities indicating the likelihood of finding a certain type of wildebeest within that category. Therefore if 80% of the 0.8-1.0 probabilities (indicating a high probability of finding a black wildebeest) were within the south-facing category of the aspect variable, then this indicates that the black wildebeest preferred (or were most likely) to be found in this category of the aspect variable.

This process was repeated to obtain predictor variables for the three ecological seasons. The same variables were thereafter submitted to PROC LOGISTIC analysis by the type of activity (V14), time of the day (V3), cloud cover (V22), temperature (V23), and finally by social group (V43).

RESULTS

A total of 1 558 wildebeest observations were made. Of these, 24% (371 observations) were of black wildebeest and 76% (1187 observations) were of blue wildebeest. The number of observations reflects the number of herds and individuals of each type of wildebeest that was present on the reserve. There were approximately 256 blue wildebeest in seven main herds, and approximately 98 black wildebeest in five main herds at Ezemvelo Nature Reserve. There were many more single blue wildebeest bulls than there were single black wildebeest bulls, and therefore the blue wildebeest data set has also been increased due to this effect. The observations were evenly spread through the three seasons.

Bachelors comprised 10% of the data, female herds made up 32% of the data and territorial bulls made up 58% of the data. The percentage sightings per season and per social group per type of wildebeest are shown in Table 6.1.

The logistic regression procedure (PROC LOGISTIC) was able to provide models for predictor variables that could separate out the black and blue wildebeest habitat choices at most of the levels analysed (Table 6.2). All the models ran provided good predictive capacity for separating out the black and blue wildebeest habitat choices.

Entire study period analysis

Model 1

The logistic regression correctly classified 93.4% of the habitat samples according to type of wildebeest. The discriminating power of this model was excellent (c = 0.936). Twelve predictor variables were identified to be significant in discriminating between the sites occupied by the two types of wildebeest during the entire study period. The important habitat separating variables were: habitat type (V15), aspect (V16), slope (V17), distance to water (V19), woody vegetation cover (V20), total grass height (V27), plant utilisation (V29), distance to shade (V31), altitude (V35), time since last burn (V36), geomorphology (V40) and forb : grass ratio (V41) (-2 log likelihood = 1 339.99; *df*; = 33; $p<0.0001$) (Table 6.3).

Table 6.1. The percentage observations of black and blue wildebeest social groups over the three ecological seasons at Ezemvelo Nature Reserve obtained by using the methods described in Chapter 4 from January 2004 to August 2005

Type of wildebeest	Social group	Late growing season	Dormant season	Early growing season	Overall
Black wildebeest	Bachelor herds	11.02	19.69	17.95	16.17
	Territorial bulls	39.37	25.20	35.90	33.42
	Female herds	49.61	55.12	46.15	50.40
Blue wildebeest	Bachelor herds	6.33	9.00	8.40	7.92
	Territorial bulls	69.22	64.72	64.04	66.13
	Female herds	24.05	26.28	27.56	25.95

Table 6.2: Predictor variables for the various combinations of season, social structure, activity, time of day and weather conditions used in the PROC LOGISTIC procedure (SAS 8.01) to determine those variables that separate the habitats used by the black and blue wildebeest on Ezemvelo Nature Reserve. This analysis was based on 1 558 wildebeest observations that were collected from January 2004 to August 2005

Activity	Time of the day	Season	Model	Predictor variables	c-value
Not specified	Not specified	Not specified	1	V15, V16, V17, V19, V20, V27, V29, V31, V35, V36, V40, V41.	0.94
Not specified	Not specified	Late growing	2	V26, V31	0.83
Not specified	Not specified	Dormant	3	V17, V26, V28, V29, V31, V35, V36	0.95
Not specified	Not specified	Early growing	4	V15, V16, V31, V35, V36	0.91
Grazing	Not specified	Not specified	5	V15, V16, V17, V21, V27, V31, V35, V36	0.91
Grazing	Not specified	Late growing	6	V16, V26, V31	0.75
Grazing	Not specified	Dormant	7	V17, V21, V26, V28, V31, V35, V36	0.95
Grazing	Not specified	Early growing	8	V15, V16, V31, V35, V36	0.92
Not specified	Before 10:00	Not specified	9	V15, V16, V17, V20, V31, V35, V36, V40	0.93
Not specified	10:00-14:00	Not specified	10	V15, V26, V31, V36	0.92
Not specified	After 14:00	Not specified	11	V15, V16, V31	0.84

Temperature	Cloud cover	Season	Social group	Model	Predictor variables	c-value
<15℃	Not specified	Not specified	Not specified	12	None	
15 – 25℃	Not specified	Not specified	Not specified	13	V15, V16, V17, V18, V20, V21, V27, V31, V35, V36	0.91
>25℃	Not specified	Not specified	Not specified	14	V15, V16, V27, V31, V35, V36, V40, V41	0.94
Not specified	0%	Not specified	Not specified	15	V16, V17, V26, V27, V29, V30, V31, V35, V36, V40	0.93
Not specified	>0-50%	Not specified	Not specified	16	V15, V16, V18, V21, V27, V31, V35, V36, V40, V41	0.93
Not specified	>50%	Not specified	Not specified	17	V15, V31, V35, V36	0.92
Not specified	Not specified	Not specified	Female herds	18	V15, V16, V17, V19, V26, V31, V36, V40	0.98
Not specified	Not specified	Not specified	Territorial bulls	19	V16, V20, V31, V34, V35, V36, V40, V41	0.91
Not specified	Not specified	Not specified	Bachelor herds	20	V31, V41	0.83

Note: The c-value indicates the discriminatory power of the model. Appendix 2 provides an explanation of the variable codes listed in the above table

Table 6.3: The percentage of the probabilities (indicating the presence of either a black ($0.8 \leq P \leq 1.0$) or a blue ($0 \leq P \leq 0.2$) wildebeest) associated with each category of the variables selected by Model 1 in the logistic regression analysis to separate between the habitat of the black and blue wildebeest. Percentages in bold indicate those categories that were significantly selected by the one type of wildebeest over the other ($p<0.05$). Data collected on Ezemvelo Nature Reserve from January 2004 to August 2005

Variables selected by the model	Category	Black wildebeest	Blue wildebeest
Habitat type	*Burkea* woodland	0.00	**10.13**
	Moist grassland	**14.88**	3.83
	Old land	13.64	**28.61**
	Rocky grassland	6.20	**24.98**
	Sandy grassland	**65.29**	32.45
Aspect	North-facing	32.64	**72.96**
	South-facing	**67.36**	27.04
Slope	Flat	**19.83**	2.75
	Gentle	26.45	**46.61**
	Moderate	53.72	50.64
Distance to water (m)	0-50	12.40	12.68
	>50-300	21.49	**37.27**
	>300-500	**33.88**	20.16
	>500	32.23	29.89
Woody vegetation cover	None	**100.00**	53.00
	Sparse	0.00	**33.04**
	Open	0.00	**13.96**
Total grass height (mm)	0-50	5.37	**16.03**
	>50-500	45.45	35.99
	>500-800	**42.98**	25.37
	>800	6.20	**22.62**
Plant utilisation	Low	2.89	8.55
	Moderate	28.10	23.80
	High	21.07	20.55
	Excessive	47.93	47.10
Distance to shade (m)	0-5	0.00	**16.91**
	>5-100	7.02	**60.37**
	>100-600	18.60	21.24
	>600	**74.38**	1.47
Altitude (m.a.s.l.)	≤1340	18.60	**37.36**
	>1340-1360	**34.30**	23.80
	>1360-1380	17.77	18.68
	>1380	29.34	20.16
Time since last burn	2001 or earlier	**98.76**	66.37
	2002	0.00	1.77
	2003	0.00	2.36
	2004	1.24	**28.71**
	2005	0.00	0.79
Geomorphology	Concave	**45.04**	19.96
	Convex	30.17	**77.38**
	Flat	**24.79**	2.65
Forb : grass ratio	0:100	23.55	17.99
	10:90	49.17	38.35
	30:70	25.21	39.04
	50:50	2.07	4.62

The variables that contributed the most to the separation of the habitat of the two types of wildebeest were distance to shade (Wald χ^2 = 156.4764; *df* = 3; p<0.0001), habitat type (Wald χ^2 = 68.5961; *df* = 4; p<0.0001) and time since last burn (Wald χ^2 = 65.0; *df* = 4; p<0.0001). Woody vegetation cover contributed the least to the analysis (Wald χ^2 = 9.9045; *df* = 2; p = 0.0071).

The results indicated that black wildebeest were more likely to be found in sandy grasslands than any other habitat type while blue wildebeest were equally likely to be found in old lands and sandy grasslands. Black wildebeest were more likely to be found in south facing aspects while blue wildebeest were more likely to be found on north-facing aspects. The blue wildebeest was most likely to be found on gentle or moderate slopes with a northerly aspect. Black wildebeest, however, were more likely to occur on moderate slopes with a southerly aspect. Blue wildebeest favoured distances of >50 to 300 m from the nearest water, whereas black wildebeest preferred distances >300 m from the nearest water. Blue wildebeest showed a preference for total grass height ranging from >50 to 500 mm, while black wildebeest showed a clear preference for sites where the total grass height was >50 to 800 mm. Both types of wildebeest were more likely to occur on sites where the herbaceous layer had been heavily utilised. The blue wildebeest strongly preferred habitats where the distance to the nearest shade was much less than what the black wildebeest preferred (>5 to 100 m as opposed to >600 m). The blue wildebeest also tended to be more likely to occur at lower altitudes than the black wildebeest (≤1340 m as opposed to 1341 to 1360 m). The blue wildebeest preferred recently burnt areas, whereas the black wildebeest were more likely to occur at sites that had not been burnt in a while.

The blue wildebeest most frequently utilised sites with a convex geomorphology, whereas the black wildebeest tended to utilise all types of geomorphology equally, although it tended to favour a concave geomorphology to a certain degree. The blue wildebeest was more likely to utilise habitats where the forb : grass ratio was higher than that used by the black wildebeest.

Seasonal analyses

Model 2: Late growing season

The logistic regression correctly classified 78.0 % of the habitat samples according to type of wildebeest. The discriminating power of this model was good (c = 0.832).

Only two predictor variables were identified to be significant in discriminating between the sites occupied by the two types of wildebeest during the late growing season. The important habitat separating variables were: rock cover (V26) and distance to shade (V31) (-2 log likelihood = 305.8227; *df* = 5; p<0.0001) (Table 6.4). Distance to shade contributed the most to the analysis (Wald χ^2 = 105.9141; *df* = 3; p<0.0001).

The late growing season is when resources are abundant and animals are in a peak physical condition. Therefore few mechanisms separating the habitat of the black and blue wildebeest would be expected. The only separation found was that the blue wildebeest were most likely to occur in habitats with no rock cover while black wildebeest were more likely to utilise areas where the rock cover was <30%. Black wildebeest showed a strong preference for areas that were >600 m away from the nearest shade, while blue wildebeest preferred areas where the shade was ≤100 m away.

Model 3: Dormant season

The logistic regression correctly classified 94.6% of the habitat samples according to type of wildebeest. The discriminating power of this model was excellent (c = 0.947). Seven predictor variables were identified to be most significant in discriminating between the sites occupied by the two types of wildebeest during the dormant season. The important habitat separating variables were: slope (V17), rock cover (V26), grass leaf height (V28), plant utilisation (V29), distance to shade (V31), altitude (V35) and time since last burn (V36) (-2 log likelihood = 484.74367; *df* = 23; p<0.0001) (Table 6.5).

Distance to shade contributed the most to separating the habitat choices of the two types of wildebeest during the dormant season (Wald χ^2 = 83.6146; *df* = 3; p<0.0001). Plant utilisation contributed the least to the analysis (Wald χ^2 = 14.2395; *df* = 3; p = 0.0026).

Table 6.4: The percentage of the probabilities (indicating the presence of either a black ($0.8 \leq P \leq 1.0$) or a blue ($0 \leq P \leq 0.2$) wildebeest) associated with each category of the variables selected by Model 2 in the logistic regression analysis to separate between the habitat of the black and blue wildebeest. Percentages in bold indicate those categories that were significantly selected by the one type of wildebeest over the other ($p<0.05$). Data collected on Ezemvelo Nature Reserve from January 2004 to August 2005

Variables selected by the model	**Category**	**Black wildebeest**	**Blue wildebeest**
Rock cover (%)	None	62.16	**73.93**
	1-30	**37.84**	3.72
	>30	0.00	**22.35**
Distance to shade (m)	0-5	0.00	**18.62**
	>5-100	0.00	59.03
	>100-600	0.00	22.35
	>600	**100.00**	0.00

Table 6.5: The percentage of the probabilities (indicating the presence of either a black ($0.8 \leq P \leq 1.0$) or a blue ($0 \leq P \leq 0.2$) wildebeest) associated with each category of the variables selected by Model 3 in the logistic regression analysis to separate between the habitat of the black and blue wildebeest. Percentages in bold indicate those categories that were significantly selected by the one type of wildebeest over the other ($p < 0.05$). Data collected on Ezemvelo Nature Reserve from January 2004 to August 2005

Variables selected by the model	Category	Black wildebeest	Blue wildebeest
Slope	Flat	**13.68**	2.13
	Gentle	18.95	45.74
	Moderate	67.37	52.13
Rock cover (%)	None	27.37	53.99
	1-30	**69.47**	21.54
	>30	3.16	**24.47**
Grass leaf height (mm)	0-50	22.11	35.90
	>50-100	17.89	9.04
	>100-400	**47.37**	30.59
	>400	**12.63**	24.47
Plant utilisation	Low	12.63	25.53
	Moderate	2.11	5.85
	High	22.11	31.65
	Excessive	**63.16**	36.97
Distance to shade (m)	0-5	0.00	**12.77**
	>5-100	13.68	**61.17**
	>100-600	26.32	24.73
	>600	**60.00**	1.33
Altitude (m.a.s.l.)	≤1340	12.63	34.84
	>1340-1360	**35.79**	23.14
	>1360-1380	23.16	17.82
	>1380	28.42	24.2
Time since last burn	2001 or earlier	**95.79**	70.48
	2002	0.00	2.39
	2003	0.00	1.33
	2004	2.11	**23.67**
	2005	2.11	2.13

The dormant season is when resources become limiting and it was therefore expected that there would be more factors that would participate in separating the habitats utilised by black and blue wildebeest to minimise competition. Blue wildebeest preferred gentle and moderate slopes with equal frequency, but black wildebeest were more likely to select moderate slopes than any other slope category. Blue wildebeest were most likely to utilise areas with no rock cover while black wildebeest most frequently selected areas with a rock cover of 1 to 30%. Blue wildebeest were most likely to utilise areas with grass leaf heights of <50 mm or those >100 to 400 mm. Black wildebeest, however, were most likely to select sites where the grass leaf height was >100 to 400 mm. Black wildebeest also were more likely to select heavily utilised areas while blue wildebeest were more likely to select areas where the use pressure ranged from moderate to excessive. Blue wildebeest preferred habitats where the nearest shade was >5 to 100 m away, whereas black wildebeest favoured areas where the nearest shade was >600 m away, as they did in the late growing season.

Blue wildebeest showed no clear preference for any altitudinal range, whereas black wildebeest were most likely to utilise habitats at altitudes >1340 m above sea level. Blue wildebeest were ten times more likely to utilise recently burnt areas than black wildebeest.

Model 4: Early growing season

The logistic regression correctly classified 90.2% of the habitat samples according to type of wildebeest. The discriminating power of this model was excellent (c = 0.911). Five predictor variables were identified to be significant in discriminating between the sites occupied by the two types of wildebeest during the early growing season. The important habitat separating variables were: habitat type (V15), aspect (V16), distance to shade (V31), altitude (V35) and time since last burn (V36). (-2 log likelihood = 426.0372; *df* = 14; p<0.0001) (Table 6.6).

Distance to shade contributed the most to separating the habitats of the black and blue wildebeest (Wald χ^2 = 77.9892; *df* = 3; p<0.0001) followed by the time since last burn variable (Wald χ^2 = 46.5893; *df* = 4; p<0.0001). Aspect contributed the least to the analysis (Wald χ^2 = 28.6237; *df* = 1; p<0.0001).

Table 6.6: The percentage of the probabilities (indicating the presence of either a black (0.8≤P≤1.0) or a blue (0≤P≤0.2) wildebeest) associated with each category of the variables selected by Model 4 in the logistic regression analysis to separate between the habitat of the black and blue wildebeest. Percentages in bold indicate those categories that were significantly selected by the one type of wildebeest over the other (p<0.05). Data collected on Ezemvelo Nature Reserve from January 2004 to August 2005

Variables selected by the model	Category	Black wildebeest	Blue wildebeest
Habitat type	*Burkea* woodland	0.00	**13.31**
	Moist grassland	**23.75**	8.12
	Old land	7.50	26.30
	Rocky grassland	8.75	14.61
	Sandy grassland	**60.00**	37.66
Aspect	North-facing	36.25	**80.52**
	South-facing	**63.75**	19.48
Distance to shade (m)	0-5	0.00	**21.10**
	>5-100	0.00	**54.87**
	>100-600	10.00	21.43
	>600	**90.00**	2.60
Altitude (m.a.s.l.)	≤1340	25.00	**44.81**
	>1340-1360	33.75	24.35
	>1360-1380	21.25	14.94
	>1380	20.00	15.91
Time since last burn	2001 or earlier	**97.50**	59.09
	2002	0.00	0.97
	2003	0.00	0.97
	2004	2.5	**38.96**
	2005	0.00	0.00

In the early growing season there was a separation in aspect choice between the black and blue wildebeest, with the blue wildebeest being more likely to select northerly slopes while the black wildebeest was more likely to select southerly slopes. Blue wildebeest were also more likely to occur in areas with shade within 100 m while black wildebeest were most likely to utilise areas with shade at >600 m away. Blue wildebeest tended to favour low-lying areas while black wildebeest were more likely to occur at higher altitudes. Blue wildebeest were more likely to utilise recently burnt areas, whereas black wildebeest tended to prefer areas that had not been burnt recently.

Analyses of data where wildebeest were grazing

Model 5: Overall

When only those observations where the wildebeest were grazing were taken into account, the logistic regression was able to discriminate between black and blue habitat variables (c = 0.914) and correctly classified 91.2% of the habitat samples according to type of wildebeest. Eight predictor variables were identified which were significant in discriminating between the sites occupied by the two types of wildebeest while they were grazing. The important habitat separating variables were: habitat type (V15), aspect (V16), slope (V17), grass cover (V21), total grass height (V27), distance to shade (V31), altitude (V35) and time since last burn (V36) (-2 log likelihood = 595.9007; *df* = 22; p<0.0001) (Table 6.7). The variables that contributed most to the separation in the habitat choices of the two types of wildebeest were distance to shade (Wald χ^2 = 122.2178; *df* = 3; p<0.0001) and time since last burn (Wald χ^2 = 51.5282; *df* = 4; p<0.0001). Slope contributed the least to the analysis (Wald χ^2 = 9.7449; *df* = 2; p = 0.0077).

When grazing the black wildebeest were most likely to occur in sandy grasslands and moist grasslands, while the blue wildebeest preferred old lands and rocky grasslands. Grazing activities for the blue wildebeest were most likely to occur on northerly slopes, whereas the black wildebeest showed an equal preference for both northerly and southerly slopes.

Table 6.7: The percentage of the probabilities (indicating the presence of either a black ($0.8 \leq P \leq 1.0$) or a blue ($0 \leq P \leq 0.2$) wildebeest) associated with each category of the variables selected by Model 5 in the logistic regression analysis to separate between the habitat of the black and blue wildebeest. Percentages in bold indicate those categories that were significantly selected by the one type of wildebeest over the other ($p<0.05$). Data collected on Ezemvelo Nature Reserve from January 2004 to August 2005

Variables selected by the model	Category	Black wildebeest	Blue wildebeest
Habitat type	*Burkea* woodland	0.00	2.94
	Moist grassland	**22.12**	5.28
	Old land	8.85	**27.59**
	Rocky grassland	7.96	**29.75**
	Sandy grassland	**61.06**	34.44
Aspect	North-facing	43.36	72.41
	South-facing	**56.64**	27.59
Slope	Flat	**15.04**	2.35
	Gentle	33.63	43.84
	Moderate	51.33	53.82
Grass cover	Sparse	13.27	19.37
	Medium	50.44	46.77
	Dense	36.28	33.86
Total grass height (mm)	0-50	7.08	14.29
	>50-500	40.71	34.05
	>500-800	**47.79**	27.01
	>800	4.42	**24.66**
Distance to shade (m)	0-5	0.00	4.31
	>5-100	0.00	**72.21**
	>100-600	13.27	22.50
	>600	**86.73**	0.98
Altitude (m.a.s.l.)	≤1340	17.70	**35.03**
	>1340-1360	**45.13**	25.24
	>1360-1380	21.24	17.42
	>1380	15.93	22.31
Time since last burn	2001 or earlier	**93.81**	66.93
	2002	0.00	1.57
	2003	0.00	2.74
	2004	5.31	**27.79**
	2005	0.88	0.89

Both black and blue wildebeest were most likely to occur on moderate slopes. The blue wildebeest was least likely to occur on flat areas. Black and blue wildebeest preferred areas where the grass cover was medium, but the blue wildebeest were more likely than the black wildebeest, to occur where the grass cover was sparse. Blue wildebeest preferred areas where the grass sward was >500 to 800 mm tall and avoided grass swards of <50 mm and >800 mm tall. Blue wildebeest were more likely to occur across the full range of grass sward heights, but they were most likely to graze in grass sward heights of >50 to 500 mm tall. Black wildebeest showed a strong preference for areas where the nearest shade was >600 m away and avoided grazing in areas where they were <100 m away from shade.

Blue wildebeest were most likely to graze in habitats where the nearest shade was >5 to 100 m away. Black wildebeest were most likely to graze at altitudes of >1341 to 1360 m, while blue wildebeest tended to prefer to graze at lower altitudes, thus being more likely to graze at altitudes of <1340 m above sea level.

Model 6: Early growing season

The logistic regression correctly classified 72.8% of the habitat samples according to type of wildebeest. The discriminating power of this model was medium (c = 0.761). Three predictor variables were identified to be significant in discriminating between the sites occupied by the two types of wildebeest while they were grazing during the early growing season. The important habitat separating variables were: aspect (V16), rock cover (V26) and distance to shade (V31) (-2 log likelihood = 135.4589; *df* = 6; p<0.0001) (Table 6.8). Distance to shade contributed most to this analysis (Wald χ^2 = 49.9599; *df* = 3; p<0.0001) while rock cover contributed the least (Wald χ^2 = 10.8034; *df* = 2; p = 0.0045).

When grazing, blue wildebeest preferred northerly slopes while black wildebeest showed no preference in their grazing patterns in respect of aspect chosen during the early growing season. Blue wildebeest were most likely to graze in areas where there was no rock cover, whereas black wildebeest preferred to graze in areas where the rock cover was 1 to 30%. Blue wildebeest were most likely to graze where the distance to shade was >5 to 100 m, while black wildebeest were most likely to graze in areas where the nearest shade was >600 m away.

Table 6.8: The percentage of the probabilities (indicating the presence of either a black ($0.8 \leq P \leq 1.0$) or a blue ($0 \leq P \leq 0.2$) wildebeest) associated with each category of the variables selected by Model 6 in the logistic regression analysis to separate between the habitat of the black and blue wildebeest. Percentages in bold indicate those categories that were significantly selected by the one type of wildebeest over the other ($p<0.05$). Data collected on Ezemvelo Nature Reserve from January 2004 to August 2005

Variables selected by the model	Category	Black wildebeest	Blue wildebeest
Aspect	North-facing	45.45	69.46
	South-facing	54.55	30.54
Rock cover (%)	None	54.55	65.87
	1-30	42.42	16.77
	>30	3.03	17.37
Distance to shade (m)	0-5	0.00	5.39
	>5-100	0.00	**77.25**
	>100-600	15.15	17.37
	>600	**84.85**	0.00

Model 7: Dormant season

The logistic regression correctly classified 93.8% of the habitat samples according to type of wildebeest. The discriminating power of this model was excellent (c = 0.939). Seven predictor variables were identified to be significant in discriminating between the sites occupied by the two types of wildebeest while they were grazing during the dormant season. The important habitat separating variables were: slope (V17), grass cover (V21), rock cover (V26), grass leaf height (V28), distance to shade (V31), altitude (V35) and time since last burn (V36) (-2 log likelihood = 242.3448; *df* = 19; p<0.0001) (Table 6.9). Distance to shade contributed the most to separating the habitats of the black and blue wildebeest while grazing during the dormant season (Wald χ^2 = 37.5790; *df* = 3; p<0.0001), while grass cover (Wald χ^2 = 12.0868; *df* = 2; p = 0.0024) and altitude (Wald χ^2 = 13.0609; *df* = 3; p = 0.0045) contributed the least.

During the dormant season black wildebeest preferred moderate slopes while blue wildebeest were most likely to occupy gentle and moderate slopes. Blue wildebeest preferred to graze where there was no rock cover or where the rock cover was >30%, whereas black wildebeest were most likely to graze in habitats where the rock cover was 1 to 30%. Blue wildebeest showed an equal preference for areas with all grass leaf height classes, but preferred not to graze in areas with grass leaf heights of >50 to 100 mm. Black wildebeest showed a clear preference for grass leaf heights of >100 to 400 mm when grazing. When grazing, blue wildebeest preferred distances of >5 to 100 m away from the nearest shade, while black wildebeest were most likely to utilise habitats >600 m from the nearest shade although they showed some tendency to graze in habitats that were >100 to 600 m from the nearest shade during the dormant season. Blue and black wildebeest showed no specific preference for a specific altitudinal range when grazing in the dormant season. Blue wildebeest were more likely than black wildebeest to graze in recently burnt areas.

Model 8: Early growing season

The logistic regression correctly classified 91.0% of the habitat samples according to type of wildebeest. The discriminating power of this model was excellent (c = 0.917). Five predictor variables were identified to be significant in discriminating between the sites occupied by the two types of wildebeest while they were grazing during the late growing season. The important habitat separating variables were: habitat type (V15), aspect (V16), distance to shade (V31), altitude (V35) and time since last burn (V36) (-2 log likelihood = 245.3268; *df* = 14; p<0.0001) (Table 6.10).

Table 6.9: The percentage of the probabilities (indicating the presence of either a black ($0.8 \leq P \leq 1.0$) or a blue ($0 \leq P \leq 0.2$) wildebeest) associated with each category of the variables selected by Model 7 in the logistic regression analysis to separate between the habitat of the black and blue wildebeest. Percentages in bold indicate those categories that were significantly selected by the one type of wildebeest over the other ($p<0.05$). Data collected on Ezemvelo Nature Reserve from January 2004 to August 2005

Variables selected by the model	Category	Black wildebeest	Blue wildebeest
Slope	Flat	**10.87**	3.63
	Gentle	17.39	44.04
	Moderate	71.74	52.33
Grass cover	Sparse	30.43	22.28
	Medium	50.00	56.48
	Dense	19.57	21.24
Rock cover (%)	None	32.61	45.08
	1-30	**65.22**	22.80
	>30	2.17	**32.12**
Grass leaf height (mm)	0-50	17.39	29.53
	>50-100	21.74	9.33
	>100-400	47.83	34.20
	>400	13.04	26.94
Distance to shade (m)	0-5	0.00	3.63
	>5-100	10.87	**70.98**
	>100-600	32.61	24.35
	>600	**56.52**	1.04
Altitude (m.a.s.l.)	≤1340	13.04	31.09
	>1340-1360	34.78	25.39
	>1360-1380	23.91	18.13
	>1380	28.26	25.39
Time since last burn	2001 or earlier	95.65	70.98
	2002	0.00	1.04
	2003	0.00	1.04
	2004	0.00	**24.87**
	2005	4.35	2.07

Table 6.10: The percentage of the probabilities (indicating the presence of either a black (0.8≤P≤1.0) or a blue (0≤P≤0.2) wildebeest) associated with each category of the variables selected by Model 8 in the logistic regression analysis to separate between the habitat of the black and blue wildebeest. Percentages in bold indicate those categories that were significantly selected by the one type of wildebeest over the other (p<0.05). Data collected on Ezemvelo Nature Reserve from January 2004 to August 2005

Variables selected by the model	**Category**	**Black wildebeest**	**Blue wildebeest**
Habitat type	*Burkea* woodland	0.00	4.57
	Moist grassland	**34.09**	11.43
	Old land	4.55	22.29
	Rocky grassland	11.36	21.14
	Sandy grassland	50.00	40.57
Aspect	North-facing	47.73	79.43
	South-facing	**52.27**	20.57
Distance to shade (m)	0-5	0.00	5.14
	>5-100	0.00	**70.29**
	>100-600	6.82	21.71
	>600	**93.18**	2.86
Altitude (m.a.s.l.)	≤1340	25.00	41.14
	>1340-1360	**43.18**	23.43
	>1360-1380	25.00	12.57
	>1380	6.82	22.86
Time since last burn	2001 or earlier	90.91	64.57
	2002	0.00	1.14
	2003	0.00	1.14
	2004	9.09	33.14
	2005	0.00	0.00

Distance to shade contributed the most to separating out the black and blue wildebeest in this analysis (Wald χ^2 = 38.7172; *df* = 3; p<0.0001) while habitat type contributed the least (Wald χ^2 = 12.7942; *df* = 4; p = 0.0123).

Blue wildebeest preferred to graze on northerly slopes and were more likely to do so than black wildebeest. Black wildebeest grazed on all aspects without preference. During the early growing season blue wildebeest were most likely to be found grazing at distances >5 to 100 m from the nearest shade but on occasion they showed a tendency to graze >100 m away from the nearest shade. Black wildebeest showed a strong preference for grazing >600 m from the nearest shade. Blue wildebeest tended to graze with the most likelihood at low altitudes during the early growing season, while black wildebeest preferred to graze at altitudes >1340 to 1360 m. Blue wildebeest were more likely to graze at the high altitudes than the black wildebeest. Blue wildebeest were also more likely to utilise recently burnt areas than black wildebeest.

Time of the day analyses

Model 9: >05:00 – 10:00

The logistic regression correctly classified 92.3% of the habitat samples according to type of wildebeest based on the time of the day. The discriminating power of this model was excellent (c = 0.928). Eight predictor variables were identified to be significant in discriminating between the sites occupied by the two types of wildebeest during this time of the day. The important habitat separating variables were: habitat type (V15), aspect (V16), slope (V17), woody vegetation cover (V20), distance to shade (V31), altitude (V35), time since last burn (V36) and geomorphology (V40) (-2 log likelihood = 504.2736; *df* = 21; p<0.0001) (Table 6.11). Distance to shade contributed the most to separating the black from the blue wildebeest in this analysis (Wald χ^2 = 63.0404; *df* = 3; p<0.0001) followed by the time since last burn (Wald χ^2 = 40.4576; *df* = 4; p<0.0001). Woody vegetation cover contributed the least (Wald χ^2 = 9.3081; *df* = 2; p = 0.0095).

Table 6.11: The percentage of the probabilities (indicating the presence of either a black (0.8≤P≤1.0) or a blue (0≤P≤0.2) wildebeest) associated with each category of the variables selected by Model 9 in the logistic regression analysis to separate between the habitat of the black and blue wildebeest. Percentages in bold indicate those categories that were significantly selected by the one type of wildebeest over the other (p<0.05). Data collected on Ezemvelo Nature Reserve from January 2004 to August 2005

Variables selected by the model	Category	Black wildebeest	Blue wildebeest
Habitat type	*Burkea* woodland	0.00	8.70
	Moist grassland	9.41	3.82
	Old land	9.41	28.03
	Rocky grassland	9.41	28.03
	Sandy grassland	**71.76**	31.42
Aspect	North-facing	38.82	72.40
	South-facing	**61.18**	27.60
Slope	Flat	**11.76**	3.82
	Gentle	34.12	48.20
	Moderate	54.12	47.98
Woody vegetation cover	None	**100.00**	52.23
	Sparse	0.00	**32.91**
	Open	0.00	**14.86**
Distance to shade (m)	0-5	0.00	13.80
	>5-100	9.41	**64.76**
	>100-600	27.06	20.59
	>600	**63.53**	0.85
Altitude (m.a.s.l.)	≤1340	9.41	**40.98**
	>1340-1360	27.06	23.14
	>1360-1380	25.88	16.99
	>1380	**37.65**	18.90
Time since last burn	2001 or earlier	**98.82**	65.61
	2002	0.00	1.49
	2003	0.00	2.12
	2004	1.18	**29.72**
	2005	0.00	1.06
Geomorphology	Concave	**44.71**	20.59
	Convex	41.18	75.58
	Flat	**14.12**	3.82

The sandy grassland habitat type was favoured by black wildebeest in the morning (>05:00 to 10:00), while blue wildebeest were equally likely to occur on old lands, on rocky grasslands and in sandy grasslands during this time. Blue wildebeest were most likely to utilise northerly slopes while black wildebeest were most likely to utilise southerly slopes. Blue wildebeest were most likely to occur in habitats with no woody vegetation. Black wildebeest showed a strong preference for habitats where there was no woody vegetation cover. Blue wildebeest preferred areas of >5 to 100 m from the nearest shade, but were almost as likely to utilise areas >100 m away from the nearest shade. Black wildebeest were most likely to occur where the nearest shade was >600 m away, but also were as likely to utilise habitats where the nearest shade was >100 to 600 m away. Blue wildebeest were more likely to utilise lower altitudes than black wildebeest, and also most likely to occur in habitats with a convex geomorphology, while black wildebeest showed an equal preference for both convex and concave areas.

Model 10: >10:00 – 14:00

The logistic regression correctly classified 90.9% of the habitat samples according to type of wildebeest. The discriminating power of this model was excellent (c = 0.918). Four predictor variables were identified to be significant in discriminating between the sites occupied by the two types of wildebeest during this time of the day. The important habitat separating variables were: habitat type (V15), rock cover (V26), distance to shade (V31) and time since last burn (V36) (-2 log likelihood = 491.8874; *df* = 13; $p<0.0001$) (Table 6.12). Distance to shade contributed the most to the analysis (Wald $\chi^2 = 89.0344$; *df* = 3; $p<0.0001$) while habitat type contributed the least (Wald $\chi^2 = 21.7419$; *df* = 4; $p = 0.0002$).

Blue wildebeest were equally likely to occur on old lands, rocky grasslands and sandy grasslands, while black wildebeest preferred sandy grasslands and were more likely than blue wildebeest to occur in moist grasslands. During midday (>10:00 to 14:00), the hottest part of the day, blue wildebeest were more likely to frequent habitats where there was no rock cover. Black wildebeest were least likely to use areas where the rock cover was >30%, but showed an equal preference for habitats where there was no rock cover and where it was ≤30%.

Table 6.12: The percentage of the probabilities (indicating the presence of either a black (0.8≤P≤1.0) or a blue (0≤P≤0.2) wildebeest) associated with each category of the variables selected by Model 10 in the logistic regression analysis to separate between the habitat of the black and blue wildebeest. Percentages in bold indicate those categories that were significantly selected by the one type of wildebeest over the other (p<0.05). Data collected on Ezemvelo Nature Reserve from January 2004 to August 2005

Variables selected by the model	Category	Black wildebeest	Blue wildebeest
Habitat type	*Burkea* woodland	0.00	**11.99**
	Moist grassland	**21.09**	5.24
	Old land	17.01	**27.72**
	Rocky grassland	2.72	**26.59**
	Sandy grassland	**59.18**	28.46
Rock cover (%)	None	49.66	58.43
	1-30	**49.66**	15.36
	>30	0.68	**26.22**
Distance to shade (m)	0-5	0.00	**22.47**
	>5-100	0.00	**54.31**
	>100-600	12.93	21.72
	>600	**87.07**	1.50
Time since last burn	2001 or earlier	**99.32**	53.18
	2002	0.00	**3.37**
	2003	0.00	2.25
	2004	0.00	**40.45**
	2005	0.68	0.75

Blue wildebeest were most likely to occur at distances >5 to 100 m away from the nearest shade. Black wildebeest consistently favoured habitats where the shade was >600 m away.

Model 11: >14:00 – 19:00

The logistic regression correctly classified 80.8% of the habitat samples according to type of wildebeest. The discriminating power of this model was good (c = 0.829). Three predictor variables were identified to be significant in discriminating between the sites occupied by the two types of wildebeest during this time of the day. The important habitat separating variables were: habitat type (V15), aspect (V16) and distance to shade (V31) (-2 log likelihood = 195.5085; *df* = 8; $p<0.0001$) (Table 6.13). Distance to shade contributed the most to separating the black from the blue wildebeest in this analysis (Wald χ^2 = 50.8243; *df* = 3; $p<0.0001$) while habitat type contributed the least (Wald χ^2 = 28.4887; *df* = 4; $p<0.0001$).

After 14:00 black wildebeest were more likely to utilise old lands than other times of the day but they were still most likely to be found on sandy grasslands. Blue wildebeest were most likely to be found on old lands and sandy grasslands during this time. Blue wildebeest preferred northerly slopes, while black wildebeest showed a strong preference for southerly slopes. Blue wildebeest preferred habitats >5 to 100 m from the nearest shade, while black wildebeest showed a strong preference for distances >600 m from the nearest shade.

Temperature analyses

Model 12: Temperatures <15 °C

There were not enough observations in this temperature range to discriminate between sites at this level.

Model 13: Temperatures ≥15-25 °C

The logistic regression correctly classified 90.9% of the habitat samples according to type of wildebeest. The discriminating power of this model was excellent (c = 0.913). Ten predictor variables were identified to be significant in discriminating between the sites occupied by the two types of wildebeest when the temperatures were ≥*15-25 °C*

Table 6.13: The percentage of the probabilities (indicating the presence of either a black ($0.8 \leq P \leq 1.0$) or a blue ($0 \leq P \leq 0.2$) wildebeest) associated with each category of the variables selected by Model 11 in the logistic regression analysis to separate between the habitat of the black and blue wildebeest. Percentages in bold indicate those categories that were significantly selected by the one type of wildebeest over the other ($p<0.05$). Data collected on Ezemvelo Nature Reserve from January 2004 to August 2005

Variables selected by the model	Category	Black wildebeest	Blue wildebeest
Habitat type	*Burkea* woodland	0.00	11.99
	Moist grassland	**17.39**	0.37
	Old land	26.09	34.83
	Rocky grassland	4.35	21.72
	Sandy grassland	52.17	31.09
Aspect	North-facing	0.00	**85.02**
	South-facing	**100.00**	14.98
Distance to shade (m)	0-5	0.00	19.48
	>5-100	0.00	57.68
	>100-600	0.00	22.85
	>600	**100.00**	0.00

The important habitat separating variables were: habitat type (V15), aspect (V16), slope (V17), landscape position (V18), woody vegetation cover (V20), grass cover (V21), total grass height (V27), distance to shade (V31), altitude (V35), and time since last burn (V36) (-2 log likelihood = 453.8716; *df* = 27; $p<0.0001$) (Table 6.14). Distance to shade contributed the most to the analysis (Wald χ^2 = 66.2119; *df* = 3; $p<0.0001$), while slope (Wald χ^2 = 6.8763; *df* = 2; p = 0.0321) and woody vegetation cover (Wald χ^2 = 8.1849; *df* = 2; p = 0.0167) contributed the least.

When the temperature was from 15 to 25°C, blue wildebeest showed an equal likelihood to utilise old lands and rocky grasslands, but were most likely to utilise sandy grasslands. Black wildebeest were most likely to be found in the sandy grasslands. Blue wildebeest were twice as likely to occur on northerly slopes than black wildebeest, as the black wildebeest showed a strong preference for southerly slopes. Blue wildebeest were most likely to occur on plains and also with an equal likelihood on gently sloping landscapes, while black wildebeest preferred the plains and to some extent the plateaus. Black wildebeest showed a strong preference for habitats where there was no woody vegetation, while blue wildebeest were equally likely to occur in habitats without woody vegetation and in habitats where the woody vegetation cover was sparse or open. Blue wildebeest were equally likely to spend their time in areas containing all grass height categories, while black wildebeest preferred only habitats where the total grass height was >50 to 800 mm. Blue wildebeest were most likely to occur at distances of >5-100 m from the nearest shade, while black wildebeest preferred distance of >600 m from the nearest shade. Blue wildebeest were most likely to occur at altitudes of <1340 m, while black wildebeest tended to utilise with equal likelihood altitudes >1340 to 1360 m.a.s.l. and >1380 m.a.s.l. Both types of wildebeest were most likely to be found in habitats that had not been recently burnt but blue wildebeest were much more likely to utilise recently burnt habitats than black wildebeest.

Table 6.14: The percentage of the probabilities (indicating the presence of either a black ($0.8 \leq P \leq 1.0$) or a blue ($0 \leq P \leq 0.2$) wildebeest) associated with each category of the variables selected by Model 13 in the logistic regression analysis to separate between the habitat of the black and blue wildebeest. Percentages in bold indicate those categories that were significantly selected by the one type of wildebeest over the other ($p<0.05$). Data collected on Ezemvelo Nature Reserve from January 2004 to August 2005

Variables selected by the model	Category	Black wildebeest	Blue wildebeest
Habitat type	*Burkea* woodland	0.00	7.98
	Moist grassland	**14.29**	4.49
	Old land	4.76	**25.69**
	Rocky grassland	11.90	25.69
	Sandy grassland	**69.05**	36.16
Aspect	North-facing	39.29	70.57
	South-facing	**60.71**	29.43
Slope	Flat	**14.29**	2.74
	Gentle	30.95	44.14
	Moderate	54.76	53.12
Landscape position	Gentle slopes	2.38	**29.18**
	Plains	64.29	55.36
	Plateau	**14.29**	2.74
	Valley	19.05	12.72
Woody vegetation cover	None	**100.00**	54.61
	Sparse	0.00	**32.67**
	Open	0.00	**12.72**
Grass cover	Sparse	19.05	21.20
	Medium	46.43	48.63
	Dense	34.52	30.17
Total grass height (mm)	0-50	4.76	18.95
	>50-500	40.48	29.43
	>500-800	**51.19**	25.19
	>800	3.57	**26.43**
Distance to shade (m)	0-5	0.00	**12.97**
	>5-100	4.76	**64.34**
	>100-600	28.57	20.20
	>600	**66.67**	2.49
Altitude (m)	>1340	17.86	**36.16**
	>1340-1360	30.95	20.45
	>1360-1380	16.67	18.70
	>1380	34.52	24.69
Time since last burn	2001 or earlier	**98.81**	**62.34**
	2002	0.00	3.24
	2003	0.00	2.00
	2004	**0.00**	**31.17**
	2005	1.19	1.25

Model 14: Temperatures >25 °C

The logistic regression correctly classified 93% of the habitat samples according to type of wildebeest. The discriminating power of this model was excellent (c = 0.935). Eight predictor variables were identified to be significant in discriminating between the sites occupied by the two types of wildebeest when the temperatures were *>25°C*. The important habitat separating variables were: habitat type (V15), aspect (V16), total grass height (V27), distance to shade (V31), altitude (V35), and time since last burn (V36), geomorphology (V40) and forb : grass ratio (V41) (-2 log likelihood = 823.2523; *df* = 23; p<0.0001) (Table 6.15). Distance to shade contributed the most to separating black from blue wildebeest in this analysis (Wald χ^2 = 90.9291; *df* = 3; p<0.0001) while aspect contributed the least (Wald χ^2 = 10.0159; *df* = 1; p = 0.0016).

At temperatures >25 *°C*, blue wildebeest were most likely to occur on the old lands, while black wildebeest preferred sandy grasslands. Blue wildebeest were most likely to occur on northerly aspects while black wildebeest preferred southerly aspects. Blue wildebeest were most likely to utilise habitats where the total grass height was >50 to 500 mm, while black wildebeest were most likely to utilise habitats where the total grass height was >50 to 800 mm. Blue wildebeest preferred distances >5 to 100 m away from the nearest shade, whereas black wildebeest preferred distances >600 m away from the nearest shade and were least likely to occur at distances <100 m away from the nearest shade. Blue wildebeest preferred areas with a convex geomorphology and were least likely to utilise flat areas, while black wildebeest were most likely to occur in areas with a concave geomorphology, but also utilised areas with convex and flat geomorphologies with an equal likelihood to each other but less than that for concave areas. Blue wildebeest were more likely to occur in habitats with a greater percentage of forbs making up the herbaceous layer than did black wildebeest.

Table 6.15: The percentage of the probabilities (indicating the presence of either a black ($0.8 \leq P \leq 1.0$) or a blue ($0 \leq P \leq 0.2$) wildebeest) associated with each category of the variables selected by Model 14 in the logistic regression analysis to separate between the habitat of the black and blue wildebeest. Percentages in bold indicate those categories that were significantly selected by the one type of wildebeest over the other ($p<0.05$). Data collected on Ezemvelo Nature Reserve from January 2004 to August 2005

Variables selected by the model	**Category**	**Black wildebeest**	**Blue wildebeest**
Habitat type	*Burkea* woodland	0.00	**13.08**
	Moist grassland	**18.23**	3.22
	Old land	17.68	**34.00**
	Rocky grassland	5.52	**22.33**
	Sandy grassland	**58.56**	27.36
Aspect	North-facing	38.12	**76.46**
	South-facing	**61.88**	23.54
Total grass height (mm)	0-50	4.97	**15.29**
	>50-500	46.96	42.05
	>500-800	**40.33**	23.94
	>800	7.73	18.71
Distance to shade (m)	0-5	0.00	**22.94**
	>5-100	5.52	**54.73**
	>100-600	15.47	20.93
	>600	**79.01**	1.41
Altitude (m.a.s.l)	≤1340	20.44	**36.62**
	>1340-1360	38.12	27.77
	>1360-1380	19.34	19.32
	>1380	22.10	16.30
Time since last burn	2001 or earlier	**96.13**	67.00
	2002	0.00	0.60
	2003	0.00	3.02
	2004	3.31	**29.18**
	2005	0.55	0.20
Geomorphology	Concave	**46.96**	17.51
	Convex	28.18	**79.28**
	Flat	**24.86**	3.22
Forb : grass ratio	0:100	**25.97**	11.07
	10:90	47.51	36.42
	30:70	25.41	**46.48**
	50:50	1.10	6.04

Cloud cover analyses

Model 15: No cloud cover (Clear skies)

The logistic regression correctly classified 93.1% of the habitat samples according to type of wildebeest. The discriminating power of this model was excellent (c = 0.927). Ten predictor variables were identified to be significant in discriminating between the sites occupied by the two types of wildebeest when there was no cloud cover. The important habitat separating variables were: aspect (V16), slope (V17), rock cover (V26), total grass height (V27), plant utilisation (V29), visibility (V30), distance to shade (V31), altitude (V35), time since last burn (V36), and geomorphology (V40) (-2 log likelihood = 496.8198; *df* = 26; $p<0.0001$) (Table 6.16). Distance to shade contributed the most to separating the black from the blue wildebeest in this analysis (Wald χ^2 = 71.1455; *df* = 3; $p<0.0001$), while visibility (Wald χ^2 = 7.3556; *df* = 3; p = 0.0614) and plant utilisation (Wald χ^2 = 7.9505; *df* = 3; p = 0.0470) contributed the least.

During days with clear skies, blue wildebeest were most likely to occur on northern slopes while black wildebeest preferred southern slopes. Blue wildebeest were also most likely to occur on moderate and gentle slopes and were least likely to utilise areas that had no slope, while black wildebeest preferred moderate slopes and were less likely to utilise gentle slopes and flat areas. Blue wildebeest preferred habitats free of rock cover and were less likely to utilise areas with a rock cover of >30%. Black wildebeest, however, were most likely to occur in habitats with a rock cover of <30% and least likely to utilise areas where it was >30%. Blue wildebeest were equally likely to occur at all classes of total grass height, while black wildebeest were least likely to occur in habitats where the total grass height was <50 mm or >800 mm. Blue wildebeest preferred habitats where the visibility was relatively low, while black wildebeest were most likely to occupy habitats with a high degree of visibility. Blue wildebeest preferred habitats where the distance to shade was >5 to 100 m, with the highest likelihood of occurrence in the 0 - 5 m shade class.

Table 6.16: The percentage of the probabilities (indicating the presence of either a black ($0.8 \leq P \leq 1.0$) or a blue ($0 \leq P \leq 0.2$) wildebeest) associated with each category of the variables selected by Model 15 in the logistic regression analysis to separate between the habitat of the black and blue wildebeest. Percentages in bold indicate those categories that were significantly selected by the one type of wildebeest over the other ($p<0.05$). Data collected on Ezemvelo Nature Reserve from January 2004 to August 2005

Variables selected by the model	Category	Black wildebeest	Blue wildebeest
Aspect	North-facing	35.96	72.80
	South-facing	**64.04**	27.20
Slope	Flat	**16.85**	1.76
	Gentle	21.35	**48.61**
	Moderate	61.80	49.62
Rock cover (%)	None	33.71	56.17
	1-30	**60.67**	20.65
	>30	5.62	**23.17**
Total grass height (mm)	0-50	3.37	**20.40**
	>50-500	48.31	36.52
	>500-800	**43.82**	20.65
	>800	4.49	**22.42**
Plant utilisation	Low	3.37	6.55
	Moderate	30.34	26.20
	High	21.35	23.68
	Excessive	44.94	43.58
Visibility (m)	0-50	0.00	7.30
	>50-100	12.36	34.01
	>100-200	44.94	31.49
	>200	**42.70**	27.20
Distance to shade (m)	0-5	0.00	**16.62**
	>5-100	5.62	**57.93**
	>100-600	21.35	23.17
	>600	**73.03**	2.27
Altitude (m.a.s.l.)	≤1340	16.85	35.52
	>1340-1360	**41.57**	21.91
	>1360-1380	15.73	20.91
	>1380	25.84	21.66
Time since last burn	2001 or earlier	**100.00**	61.21
	2002	0.00	2.77
	2003	0.00	0.76
	2004	0.00	**33.75**
	2005	0.00	1.51
Geomorphology	Concave	**50.56**	21.91
	Convex	29.21	**76.07**
	Flat	**20.22**	2.02

Black wildebeest were most likely to occur at distances of >600 m from the nearest shade. Blue wildebeest preferred low altitudes of <1340 m above sea level, while black wildebeest preferred areas that had an altitude >1340 to 1360 m above sea level. Blue wildebeest were most likely to occur in areas with a convex geomorphology, while black wildebeest preferred areas with a concave geomorphology, but they were also found in convex and flat areas with equal likelihood if slightly less than the likelihood for concave areas.

Model 16: >0 – 50% cloud cover (Partly cloudy)

The logistic regression correctly classified 92.4% of the habitat samples according to type of wildebeest. The discriminating power of this model was excellent (c = 0.927). Ten predictor variables were identified to be significant in discriminating between the sites occupied by the two types of wildebeest when there was >0 to 50% cloud cover. The important habitat separating variables were: habitat type (V15), aspect (V16), landscape position (V18), grass cover (V21), total grass height (V27), distance to shade (V31), altitude (V35), time since last burn (V36), geomorphology (V40) and forb : grass ratio (V41) (-2 log likelihood = 520.8920; *df* = 28; p<0.0001) (Table 6.17). Distance to shade (Wald χ^2 = 57.7461; *df* = 3; p<0.0001) and habitat type (Wald χ^2 = 38.7367; *df* = 4; p<0.0001) contributed the most to separating black from blue wildebeest in this analysis, while grass cover (Wald χ^2 = 6.490; *df* =2; p = 0.0389), landscape position (Wald χ^2 = 9.110; *df* =4; p = 0.0279) and forb : grass ratio (Wald χ^2 = 9.2272; *df* = 3; p = 0.0264) contributed the least.

With partly cloudy skies, blue wildebeest were most likely to occur on old lands and sandy grasslands, while black wildebeest preferred sandy grasslands but also showed some preference for moist grasslands. Blue wildebeest were most likely to occur on northern slopes while black wildebeest preferred southern slopes. Blue wildebeest were least likely to occur on plateaus, while black wildebeest were least likely to utilise gentle slope landscapes. Blue wildebeest were most likely to occur in habitats where the total grass height >50 to 500 mm and also with some likelihood in areas where the grass was >500 mm tall. Black wildebeest preferred areas where the total grass height was >50 to 800 mm and were least likely to occur where it was >800 mm tall. Blue wildebeest occurred with the highest likelihood at distances of >5 to 100 m away from the nearest shade, but were also likely to occur at distances <5 m away and >100 to 600 m away with an equal likelihood. Black wildebeest preferred distances >600 m from the nearest shade and were least likely to occur at distances <5 m away.

Table 6.17: The percentage of the probabilities (indicating the presence of either a black ($0.8 \le P \le 1.0$) or a blue ($0 \le P \le 0.2$) wildebeest) associated with each category of the variables selected by Model 16 in the logistic regression analysis to separate between the habitat of the black and blue wildebeest. Percentages in bold indicate those categories that were significantly selected by the one type of wildebeest over the other ($p < 0.05$). Data collected on Ezemvelo Nature Reserve from January 2004 to August 2005

Variables selected by the model	Category	Black wildebeest	Blue wildebeest
Habitat type	*Burkea* woodland	0.00	11.17
	Moist grassland	**20.51**	2.73
	Old land	17.95	31.76
	Rocky grassland	8.97	24.81
	Sandy grassland	**52.56**	29.53
Aspect	North-facing	38.46	76.92
	South-facing	**61.54**	23.08
Landscape position	Gentle slopes	6.41	30.77
	Plains	58.97	56.33
	Plateau	**19.23**	1.49
	Valley	15.38	11.41
Grass cover	Sparse	16.67	24.81
	Medium	46.15	45.91
	Dense	37.18	29.28
Total grass height (mm)	0-50	10.26	12.90
	>50-500	44.87	40.45
	>500-800	37.18	25.81
	>800	7.69	20.84
Distance to shade (m)	0-5	0.00	**19.11**
	>5-100	12.82	**59.80**
	>100-600	10.26	20.10
	>600	**76.92**	0.99
Altitude (m.a.s.l.)	≤1340	20.51	36.97
	>1340-1360	32.05	24.57
	>1360-1380	17.95	17.62
	>1380	29.49	20.84
Time since last burn	2001 or earlier	**98.72**	70.97
	2002	0.00	0.50
	2003	0.00	3.97
	2004	1.28	**24.32**
	2005	0.00	0.25
Geomorphology	Concave	**50.00**	17.12
	Convex	19.23	**79.90**
	Flat	**30.77**	2.98
Forb : grass ratio	0:100	**23.08**	12.66
	10:90	51.28	35.98
	30:70	24.36	45.66
	50:50	1.28	5.71

Blue wildebeest were most likely to occur in areas with a convex geomorphology and least likely in flat areas. Black wildebeest preferred areas with a concave geomorphology but were just as likely to spend time on flat areas. Black wildebeest were more likely than blue wildebeest to occur in habitats with a low forb : grass ratio.

Model 17: >50% cloud cover (Overcast)

The logistic regression correctly classified 91.2% of the habitat samples according to type of wildebeest. The discriminating power of this model was excellent (c = 0.918). Four predictor variables were identified to be significant in discriminating between the sites occupied by the two types of wildebeest when there was >50% cloud cover. The important habitat separating variables were: habitat type (V15), distance to shade (V31), altitude (V35) and time since last burn (V36) (-2 log likelihood = 325.9301; *df* = 14; $p<0.0001$) (Table 6.18). Distance to shade contributed the most to separating out the black and blue wildebeest in this analysis (Wald χ^2 = 59.3605; *df* = 3; $p<0.0001$) and altitude contributed the least (Wald χ^2 = 23.7720; *df* = 3; $p<0.0001$).

During overcast conditions, blue wildebeest were most likely to occur on old lands, rocky grasslands and sandy grasslands but least likely to occur on moist grasslands. Black wildebeest were most likely to occur on sandy grasslands and least likely to occur in *Burkea* woodlands or rocky grasslands. Blue wildebeest were most likely to utilise distances of >5 to 100 m away from the nearest shade, while black wildebeest preferred distances >600m away from the nearest shade. Blue wildebeest preferred the low altitudes of <1340 m, while black wildebeest were most likely to be found at altitudes of >1340 to 1360 m above sea level.

Social group analyses

Model 18: Female herds

The logistic regression correctly classified 98.3% of the habitat samples according to type of wildebeest. The discriminating power of this model was excellent (c = 0.982).

Table 6.18: The percentage of the probabilities (indicating the presence of either a black (0.8≤P≤1.0) or a blue (0≤P≤0.2) wildebeest) associated with each category of the variables selected by Model 17 in the logistic regression analysis to separate between the habitat of the black and blue wildebeest. Percentages in bold indicate those categories that were significantly selected by the one type of wildebeest over the other (p<0.05). Data collected on Ezemvelo Nature Reserve from January 2004 to August 2005

Variables selected by the model	**Category**	**Black wildebeest**	**Blue wildebeest**
Habitat type	*Burkea* woodland	0.00	6.73
	Moist grassland	**16.25**	1.44
	Old land	16.25	28.85
	Rocky grassland	2.50	**26.44**
	Sandy grassland	**65.00**	36.54
Distance to shade (m)	0-5	0.00	**12.98**
	>5-100	0.00	**70.19**
	>100-600	25.00	15.87
	>600	**75.00**	0.96
Altitude (m.a.s.l.)	≤1340	16.25	38.94
	>1340-1360	**40.00**	25.96
	>1360-1380	18.75	14.42
	>1380	25.00	20.67
Time since last burn	2001 or earlier	**98.75**	64.42
	2002	0.00	2.88
	2003	0.00	2.40
	2004	0.00	**29.81**
	2005	1.25	0.48

Eight predictor variables were identified to be significant in discriminating between the sites occupied by the female herds of the two types of wildebeest. The important habitat separating variables were: habitat type (V15), aspect (V16), slope (V17), distance to water (V19), rock cover (V26), distance to shade (V31), time since last burn (V36) and geomorphology (V40) (-2 log likelihood = 496.9715; *df* = 21; p<0.0001) (Table 6.19). Distance to shade contributed the most to separating the black from the blue wildebeest female herds in this analysis (Wald χ^2 = 33.8164; *df* = 3; p<0.0001), followed by habitat type (Wald χ^2 = 18.2259; *df* = 4; p<0.0001). Rock cover (Wald χ^2 = 6.9409; *df* = 2; p = 0.0311) contributed the least.

Female herds of blue wildebeest were most likely to occur on northerly slopes while black wildebeest females preferred southerly slopes. Blue wildebeest female herds were most likely to utilise moderate slopes and least likely to utilise flat areas, while black wildebeest female herds preferred moderate slopes, but they were also likely to utilise flat areas and gentle slope. Blue wildebeest female herds were most likely to occur >50 to 300 m away from the nearest water, whilst black wildebeest female herds preferred distances away from water of >300 m. Blue wildebeest female herds were most likely to be found in habitats with no rock cover while black wildebeest female herds were most likely to utilise areas where the rock cover was <30%. Blue wildebeest female herds preferred distances of >5 to 100 m away from the nearest shade, whereas the female herds of black wildebeest preferred distances >600 m away from the nearest shade and were least likely to use areas where the nearest shade was <100 m away. Blue wildebeest female herds were most likely to utilise areas with a convex geomorphology, while black wildebeest preferred areas with a concave geomorphology. Whereas blue wildebeest were least likely to utilise flat areas, black wildebeest were most likely to utilise areas with both a flat and a convex geomorphology.

Model 19: Territorial bulls

The logistic regression correctly classified 91.2% of the habitat samples according to type of wildebeest. The discriminating power of this model was excellent (c=0.909). Eight predictor variables were identified to be significant in discriminating between the sites occupied by the territorial bulls of the two types of wildebeest. The important habitat separating variables were: aspect (V16), woody vegetation cover (V20), distance to shade (V31), erosion (V34), altitude (V35), time since last burn (V36), geomorphology (V40) and forb : grass ratio (V41) (-2 log likelihood = 298.4180, *df* = 20, p<0.0001) (Table 6.20).

Table 6.19: The percentage of the probabilities (indicating the presence of either a black (0.8≤P≤1.0) or a blue (0≤P≤0.2) wildebeest) associated with each category of the variables selected by Model 18 in the logistic regression analysis to separate between the habitat of the black and blue wildebeest. Percentages in bold indicate those categories that were significantly selected by the one type of wildebeest over the other (p<0.05). Data collected on Ezemvelo Nature Reserve from January 2004 to August 2005

Variables selected by the model	Category	Black wildebeest	Blue wildebeest
Habitat type	*Burkea* woodland	0.00	3.93
	Moist grassland	**11.92**	3.93
	Old land	16.56	**36.79**
	Rocky grassland	7.28	16.07
	Sandy grassland	**64.24**	39.29
Aspect	North-facing	28.48	**70.71**
	South-facing	**71.52**	29.29
Slope	Flat	**22.52**	2.50
	Gentle	23.18	**37.50**
	Moderate	54.30	60.00
Distance to water (m)	0-50	12.58	12.50
	>50-300	18.54	**42.86**
	>300-500	33.11	26.07
	>500	**35.76**	18.57
Rock cover (%)	None	33.11	**69.64**
	1-30	**60.93**	15.71
	>30	5.96	14.64
Distance to shade (m)	0-5	0.00	**10.36**
	>5-100	9.27	**60.00**
	>100-600	17.22	27.14
	>600	**73.51**	2.50
Time since last burn	2001 or earlier	**98.01**	50.71
	2002	0.00	2.86
	2003	0.00	2.86
	2004	1.32	**41.79**
	2005	0.66	1.79
Geomorphology	Concave	**43.71**	20.71
	Convex	29.14	**76.79**
	Flat	**27.15**	2.50

Table 6.20: The percentage of the probabilities (indicating the presence of either a black ($0.8 \leq P \leq 1.0$) or a blue ($0 \leq P \leq 0.2$) wildebeest) associated with each category of the variables selected by Model 19 in the logistic regression analysis to separate between the habitat of the black and blue wildebeest. Percentages in bold indicate those categories that were significantly selected by the one type of wildebeest over the other ($p<0.05$). Data collected on Ezemvelo Nature Reserve from January 2004 to August 2005

Variables selected by the model	Category	Black wildebeest	Blue wildebeest
Aspect	North-facing	15.00	72.85
	South-facing	**85.00**	27.15
Woody vegetation cover	None	**100.00**	47.74
	Sparse	0.00	**36.35**
	Open	0.00	**15.91**
Distance to shade (m)	0-5	0.00	**19.81**
	>5-100	0.00	**60.69**
	>100-600	15.00	17.78
	>600	**85.00**	1.72
Erosion	Low	10.00	15.29
	Moderate	60.00	70.67
	High	30.00	14.04
Altitude (m.a.s.l.)	≤1340	0.00	**41.34**
	>1340-1360	**50.00**	17.78
	>1360-1380	15.00	19.34
	>1380	35.00	21.53
Time since last burn	2001 or earlier	100.00	70.98
	2002	0.00	1.72
	2003	0.00	2.65
	2004	0.00	**24.18**
	2005	0.00	0.47
Geomorphology	Concave	**60.00**	16.07
	Convex	20.00	**80.03**
	Flat	**20.00**	3.90
Forb : grass ratio	0:100	20.00	14.66
	10:90	65.00	36.51
	30:70	15.00	43.06
	50:50	0.00	5.77

Distance to shade contributed the most to the separation of black and blue wildebeest in this analysis (Wald $\chi^2 = 46.9783$; *df* = 3; $p<0.0001$) followed closely by altitude (Wald $\chi^2 = 40.1248$; *df* = 3; $p<0.0001$), while aspect contributed the least (Wald $\chi^2 = 5.7413$; *df* = 1; $p = 0.0166$).

Blue wildebeest territorial bulls were most likely to occur on northerly aspects while those of the black wildebeest preferred on southerly aspects. Blue wildebeest territorial bulls were equally likely to occur in habitats with no woody vegetation and those with sparse woody vegetation. Black wildebeest territorial bulls showed a strong preference for areas where there was no woody vegetation. Blue wildebeest territorial bulls were most likely to utilise areas at distances of >5 to 100 m away from the nearest shade, and least likely to utilise areas at distances >600 m, while black wildebeest territorial bulls were most likely to occur at distances >600 m away from the nearest shade. Blue wildebeest territorial bulls were more likely to occur where the erosion was moderate, whereas black wildebeest were more likely to occur where the degree of erosion was high. Blue wildebeest territorial bulls preferred altitudes of <1340 m, while black wildebeest territorial bulls were most likely to occur at altitudes >1340 to 1360 m above sea level. Blue wildebeest territorial bulls were to some extent likely to make use of recently burnt areas but those of black wildebeest were least likely to utilise recently burnt areas. Blue wildebeest territorial bulls preferred areas with a convex geomorphology and were least likely to occur in flat areas, while those of black wildebeest preferred areas with a concave geomorphology but were also likely to utilise areas with a convex and flat geomorphology to some degree. Blue wildebeest territorial bulls were more likely than those of black wildebeest to utilise areas where the forb : grass ratio was 10:90.

Model 20: Bachelor herds

The logistic regression correctly classified 81.2% of the habitat samples according to type of wildebeest. The discriminating power of this model was good (c = 0.838). Two predictor variables were identified to be significant in discriminating between the sites occupied by the bachelor herds of the two types of wildebeest. The important habitat separating variables were: distance to shade (V31) and forb : grass ratio (V41) (-2 log likelihood = 73.4035; *df* = 6; $p<0.0001$) (Table 6.21). Distance to shade contributed the most to differentiating black from blue wildebeest habitat in this analysis (Wald $\chi^2 = 22.958$; *df* = 3; $p<0.0001$), while the forb : grass ratio contributed the least (Wald $\chi^2 = 14.5510$; *df* = 3; $p = 0.0022$).

Table 6.21: The percentage of the probabilities (indicating the presence of either a black (0.8≤P≤1.0) or a blue (0≤P≤0.2) wildebeest) associated with each category of the variables selected by Model 20 in the logistic regression analysis to separate between the habitat of the black and blue wildebeest. Percentages in bold indicate those categories that were significantly selected by the one type of wildebeest over the other (p<0.05). Data collected on Ezemvelo Nature Reserve from January 2004 to August 2005

Variables selected by the model	Category	Black wildebeest	Blue wildebeest
Distance to shade (m)	0-5	0.00	**24.29**
	>5-100	0.00	**55.71**
	>100-600	0.00	20.00
	>600 m	**100.00**	0.00
Forb : grass ratio	0:100	0.00	**38.57**
	10:90	**65.38**	8.57
	30:70	34.62	42.86
	50:50	0.00	10.00

Blue wildebeest bachelor herds tended to favour distances of >5 to 100 m away from the nearest shade, while those of black wildebeest were least likely to venture <600 m away from the nearest shade. Bachelor herds of the blue wildebeest were more likely to utilise areas with a forb : grass ratio of 30:70 than those of black wildebeest.

DISCUSSION

Habitat separation has been demonstrated to be one of the most common forms of resource partitioning in sympatric species (Cody 1978; Werner and Hall 1979; Reinert 1984; Wei *et al*. 2000). The present study has demonstrated that habitat separation at least at the meso-habitat scale could aid the co-existence of black and blue wildebeest at Ezemvelo Nature Reserve.

The present study showed that the habitats selected by the black and blue wildebeest could be separated in terms of a number of mainly physical habitat factors. Therefore, black and blue wildebeest used the habitat available differentially, and thus accomplished resource partitioning. This pattern of resource separation varied across the different ecological seasons, times of the day and weather conditions, indicating that behavioural adjustments were being made depending on the circumstances encountered and differences between the two types of wildebeest were not merely inherent. The selection of different habitat features by different types of wildlife has been related to antipredator strategies, protection against adverse climatic conditions, reduction of interspecific competition, and establishment of routes to reproductive and feeding sites (Alvarez-Cardenas *et al*. 2001). It is, however, based on the results of the present study, expected that the pattern of resource partitioning observed could possibly be explained by means of specific differences in territoriality, body size, and temperature tolerance between the two types of wildebeest (Brink *et al*. 1999; Skinner and Chimimba 2005; Codron and Brink In press).

All the analyses showed that the distance to shade was an extremely important variable separating the habitat use of the black and blue wildebeest at Ezemvelo Nature Reserve. Distance to shade is affected by the vegetation structure. Blue wildebeest were shown to be much more dependent on nearby shade than black wildebeest and actively sought out shade during the hot parts of the day especially during the hot months in the late growing season and the early growing season in the study area (Pers. obs.). Blue wildebeest prefer open savanna habitats but readily make use of other habitats under certain conditions (Hirst 1975). Therefore it is possible to find the blue wildebeest in open habitats during certain times of the year when weather conditions permit it. They, however, tend to remain in habitats with cover nearby unless certain factors such as lack of suitable habitat, or overpopulation forcing bachelors into sub-optimal areas, prevent it. It would be these bachelors, which could be the cause of hybridisation between the two types of wildebeest (Vrahimis 2003b). Due to their body conformation, black wildebeest are able to withstand direct sunlight at all irradiances and thus shade-seeking behaviour does not normally form part of their behavioural repertoire at any time of the year (Skinner and Chimimba 2005). For black wildebeest an open habitat is a necessity, while for blue wildebeest a habitat with cover is optimal but not a necessity for survival. Therefore, in areas where there is no cover, this separating mechanism between the black and blue wildebeest would no longer be operative.

Distance to shade is related to visibility, exposure and woody vegetation structure. Visibility only separated the habitat use of black from blue wildebeest when the skies were clear, with black wildebeest preferring habitats with a higher visibility than blue wildebeest. The results, therefore indicate that both the black and blue wildebeest require habitats with a high visibility, which has been suggested to be related to antipredator behaviour (Hirst 1975).

Exposure never featured as a separating mechanism as all wildebeest were mostly found in full sun. Woody vegetation cover proved to be an important habitat separating mechanism throughout the entire study period (Model 1). It was also important for the data representing the territorial bulls (Model 19), early in the morning (Model 9) and at moderate temperatures (Model 13). Black wildebeest territorial bulls only utilised habitats where there was no woody vegetation, while blue wildebeest territorial bulls were more inclined to utilise habitats with sparse woody vegetation.

The above findings can be related to the fossil record which suggests that morphological aspects which are associated with the distinct territorial social behaviour of the black wildebeest were the first to change after the geographical separation of the common wildebeest ancestor 1 million years ago, indicating that a shift in breeding behaviour (especially territoriality) accompanied the appearance of the first ancestral black wildebeest (Brink *et al.* 1999). This shift to a more territorial behaviour is linked to the evolution of treeless grasslands in the central interior of southern Africa over a million years ago. This is borne out by the present results which indicated that black wildebeest, but most notably the territorial bulls, selected treeless habitats while blue wildebeest tended to be less selective for woody vegetation cover.

Territorial bulls of the two types of wildebeest were also separated in terms of aspect utilisation, erosion levels, altitude and forb : grass ratio (Model 19). In contrast, the habitats of the female herds of the two types of wildebeest (Model 18) were not separated in terms of any of these factors. This may possibly indicate that these differentiating factors are solely the result of differences in the territorial behaviour of the black and blue wildebeest.

Black wildebeest territorial bulls mainly utilised the southerly aspects while blue wildebeest utilised the northerly aspects. Southerly aspects on the study area are usually cooler and wetter than the northerly aspects. In contrast, northerly aspects tended to be hot and dry (Tainton 1999). Since black wildebeest mainly occupied treeless habitats with no shade at distances <600 m, another technique for cooling may be needed. This could be achieved by the utilisation of the cooler southerly aspects as opposed to the hotter northerly aspects. Blue wildebeest occurred close to shade and in sparse woody vegetation and would therefore not need to compensate by selecting the southerly aspects that would maximise cooling. The orientation of slopes may afford protection against adverse weather conditions as it determines temperature and wind differences during the day or among seasons (Alvarez-Cardenas *et al.* 2001).

Territories occupied by black wildebeest territorial bulls were often more heavily eroded than those occupied by blue wildebeest bulls. Due to increased territoriality, black wildebeest spent more time in their territory and hence more time displaying than blue wildebeest bulls, thus increasing the erosion levels locally. The black wildebeest tends to overgraze and trample the areas where they stay for prolonged periods (Von Richter 1971b). As water is easily available throughout the year there is no incentive to move within the reserve. The size of the reserve makes seasonal movements impossible. The behaviour of territorial bulls pawing and horning the ground aggravates the condition by removing the soil cover in the favoured areas in the reserve as was described in other areas by Von Richter (1971b).

Black wildebeest bulls never occurred in the low-lying areas of the reserve, and tended to occur mostly at high-lying locations, while blue wildebeest bulls favoured low-lying areas and were much less likely to utilise high-lying areas. The higher the altitude, the more exposed the landscape, the lower the temperatures and the higher the visibility (Tainton 1999). Fabricius (1984) found that black wildebeest chose northern gentle slopes and at higher altitudes. This was related to increased visibility for territorial defense of territories. Altitude was found to be an important habitat separating mechanism between the black and blue wildebeest during the dormant season and the early growing season but not during the late growing season. This result is due to the blue wildebeest utilising a wider range of altitudes during the late growing season. The late growing season is when the rut takes place and the normally relaxed breeding behaviour of the blue wildebeest becomes more rigid and territoriality becomes more important.

When grazing, black and blue wildebeest were no longer separated by distance to water, woody vegetation cover, plant utilisation, geomorphology and forb : grass ratio as they were when all the activities combined were analysed. However, when grazing the grass cover became an additional separating mechanism. With their remarkably wide dental pad and incisor row, it has been suggested that wildebeest obtain a high intake of forage on short and leafy grass swards (Owen-Smith 1985). They are also most efficient at harvesting grass swards with a high biomass of green leaf (Murray and Brown 1993).

Seasonal differences were found in the resource separation patterns between the two types of wildebeest. During the late growing season, which by definition has a high forage quantity (Chapter 2), only rock cover and distance to shade separated the habitats utilised by the two types of wildebeest. This indicated that both types of wildebeest were utilising a broad range of habitats during the late growing season. Due to the abundance of resources during the late growing season, there may be no incentive for one type of wildebeest to choose habitats where the other type of wildebeest does not occur. Therefore during the period when resources are abundant, it may become profitable to utilise resources other than the ones for which the phenotype has been specifically selected (Gordon and Illius 1989). Niche breadth and overlap measures will be analysed in Chapter 9 to study this aspect further. However, the quality of the grass layer during the late growing season would probably already be low (Tainton 1999). Therefore wildlife able to utilise a higher quantity of forage per time period would be better able to maintain their condition during this season.

It has been suggested that during periods of low resource abundance, selection resulting from interspecific competition is likely to result in adaptations most suited for resources that are used exclusively by a species (Schoener 1986). This will result in both types of wildebeest concentrating in areas that would provide the most efficient use of their time. However, if these areas are the same as those preferred by the other type of wildebeest it would be expected that greater competition would result from this greater selectivity. Therefore behavioural adjustments would have to be made by one or both type of wildebeest to ensure greater separation in resource use so that food and space are used optimally during the critical season when it is cold and dry and the vegetation is dormant (dormant season). The rut takes place during the dormant season too. Slope, grass height, plant utilisation, and altitude are the additional factors which separate the habitats of the two types of wildebeest during the dormant season which do not appear to separate their habitat use during the late growing season. Slope and altitude are related to increased territoriality of the black wildebeest as discussed above during the rut.

Black wildebeest concentrated on heavily utilised short grass areas during the dormant season (critical season), while blue wildebeest tended to occur in areas with taller grass and where the grass sward was less intensively utilised. According to a model proposed by Illius and Gordon (1987), short grass swards impose greater limitations on the food intake of larger herbivores than on smaller ones. Quite small differences in body size are expected to cause exclusion of larger herbivore species from swards that are able to sustain the smaller species, suggesting that this mechanism may be important in the common phenomenon of ecological separation in grazing species (Clutton-Brock and Harvey 1983; Gordon and Illius 1989). Therefore the utilisation of short grass areas by the black wildebeest would enable it to sustain itself through the dormant season (critical season), and in addition reduce possible competition with the blue wildebeest during this critical period. Competition could be reduced or minimised because the blue wildebeest with its larger body size may find it difficult to sustain itself in these heavily utilised areas with short grass during the critical period.

An analysis of data available for grazing wildebeest from the present study indicated that grass cover was also an important habitat-separating variable between the two types of wildebeest during the dormant season. The grazing sites that were occupied by the black wildebeest during the dormant season tended to have a lower grass cover than the areas occupied by the blue wildebeest. This may be due to the higher impact of the black wildebeest on such areas during this time.

Limited separation between the habitats selected by the black and blue wildebeest was observed during the early growing season (Model 4). This was the season when calves were dropped by both types of wildebeest in the study area (Pers. obs.) and resources are abundant.

Black and blue wildebeest showed a greater separation in habitat use early in the morning, and this degree of separation decreases as the day progressed. From sunrise until 10:00, slope, woody vegetation cover, altitude and geomorphology separated the habitats used by the black and blue wildebeest. None of these factors separated the two types of wildebeest later in the day. Temperatures were generally lower, moisture levels were higher, the sun was in an easterly position and animals are usually more active at periods of the day before 10:00 as compared to periods after 10:00.

At moderate temperatures, black and blue wildebeest habitats were separated by slope, landscape position, woody vegetation cover, and grass cover which did not separate the two types of wildebeest at temperatures >25℃. Geomorphology and forb : grass ratio were additional variables that separated the habitats of the two types of wildebeest at high temperatures but not at moderate temperatures.

When the skies are clear, black and blue wildebeest habitat use was separated based on slope, rock cover, plant utilisation, and visibility, none of which separated the habitat use of the two types when cloud cover was >0%. During overcast conditions (cloud cover >50%) fewer factors separated the habitat use of the two types of wildebeest than when cloud cover was low or absent.

Black wildebeest did not utilize areas that were recently burnt if such areas did not occur on the open plains. Blue wildebeest in contrast would totally change their distribution patterns to make use of recently burnt areas and were usually the first type of wildlife to be found on burnt areas (Melton 1978). High quality grass in the post-burn areas and its attraction to herbivores has been repeatedly shown (Tomor and Owen-Smith 2002). The observation that blue wildebeest would utilise recently burnt areas no matter where their occurrence and black wildebeest would not, just reaffirms the extreme form of area selection practiced by the black wildebeest (Von Richter 1971b).

CONCLUSION

The question asked here was whether separation in terms of habitat utilisation occurred between the black and blue wildebeest. The data presented here have concluded that separation in terms of meso-habitat does occur between the black and blue wildebeest. The present study clearly showed that there was always some habitat factor causing resource partitioning between the two types of wildebeest and that subtle differences in the way in which the two types reacted to the challenges posed by the different ecological seasons, times of the day and weather conditions may be sufficient to reduce competition between the two types of wildebeest in the study area at the current population levels. Selection for specific environmental parameters contributes to the ecological separation of the black and blue wildebeest at Ezemvelo Nature Reserve.

CHAPTER 7: HABITAT SELECTION AND SEPARATION: MICRO-HABITAT SCALE

INTRODUCTION

Analysis of the five broad habitats at Ezemvelo Nature Reserve revealed some evidence for habitat separation between the black and blue wildebeest. Habitat separation was also demonstrated at the mesohabitat scale. It was found that blue wildebeest preferred habitats where cover was in the near vicinity and would select areas where the grasses were short and in an immature state such as the old lands. Black wildebeest tended to trade-off forage quality for an open habitat and therefore selected the sandy grasslands where visibility was high. Grass cover, grass height, plant utilisation, woody vegetation cover, forb : grass ratio, time since last burn, distance to shade, visibility, and habitat type are all directly related to the vegetation. Factors such as aspect, rockiness, and altitude probably show a correlation to the vegetation type.

In habitats that may seem structurally and compositionally homogeneous, herbivores may select some parts of these habitats over others in a non-random patchy way (Novellie 1990). Due to the broad nature of the five identified habitats, it was expected that there would be abundant small-scale variations in physical factors, plant species composition, grass height and grass cover within these habitats. High spatial heterogeneity within grassland habitats might be essential for maintaining high wildlife species richness and abundance in relatively small nature reserves (Owen-Smith 2004). Therefore, as well as making habitat use decisions at higher scales, such as macro and mesohabitat scales, wild animals must also make decisions at the finer microhabitat scale (While and McArthur 2005). These fine-scale decisions would most frequently be influenced by either predation or foraging requirements.

In a natural situation, a trade-off between high quality food patches and predation is frequently made (While and McArthur 2005). Anecdotal evidence (Von Richter 1971b) suggests that black and blue wildebeest employ different strategies to deal with the threat of predation. Black wildebeest prefer to outrun the predators and blue wildebeest rely more on escape cover. However, with the low predation risk at Ezemvelo Nature Reserve where the present study was done, the selection of feeding sites was expected to be based on factors other than predation. In the absence of predators, or when vulnerability to predation is low, grazers are expected to choose feeding sites that offer the highest net energy gain per unit time spent (Edwards 1983; While and McArthur 2005).

When food resources occur as discrete items such as fruits or seeds, resource partitioning can be accommodated by selecting different food size classes. For large grazers such as the black and blue wildebeest, the grass layer does not consist of easily distinguishable discrete items such as seeds or fruits. However, the grass sward has several characteristics that are related to quantity, such as grass biomass and grass height, and quality such as grass species composition (Voeten and Prins 1999) that can form the basis for selection. These characteristics can be evaluated and any differences found between feeding sites may indicate mechanisms for resource partitioning at the microhabitat scale.

The major variables affecting food intake rate, and hence energy maximisation by grazing herbivores, are the structural characteristics of the vegetation such as height, density and the vertical distribution of biomass (Burlison *et al.* 1991; Illius *et al.* 1992). Past research on assemblages of African grazing herbivores have indicated that the grass sward structure, forage production, plant species composition, grass leaf height and plant biomass, amongst others, are important factors determining resource partitioning between the different grazing species (Bell 1971; Grobler 1983; McNaughton 1985; Novellie and Strydom 1987; Novellie 1990; Wentzel *et al.* 1991; Heitkönig and Owen-Smith 1998).

Both types of wildebeest at Ezemvelo Nature Reserve tended to concentrate their grazing activities on certain patches (feeding sites) within their range. In order to determine why such selection was taking place, a detailed study of the herbaceous characteristics of these feeding sites (microhabitat patch scale) was conducted. It was hoped that such a study would differentiate between the feeding sites selected by black wildebeest and those selected by blue wildebeest at the habitat patch scale.

Through their grazing activity, trampling, defaecation and urination in these feeding sites, wildebeest may affect the nutrient flow, vegetation community dynamics as well as related fauna (Hester *et al.* 1999). Comparing sites that were utilised by wildebeest and sites which were apparently structurally and compositionally similar, but which were not utilised by wildebeest, could provide information which could be used to indicate whether the wildebeest have a negative impact on their preferred grazing sites or not.

Since both black and blue wildebeest have a similar mouth morphology, body size and digestive system (Skinner and Chimimba 2005), it was expected that they would graze at the same height and trophic level and thus little difference was expected to exist between the feeding sites selected by each type of wildebeest at the habitat patch scale. The present study will test this hypothesis.

The following key questions were therefore examined:

1. What herbaceous characteristics can be used to discriminate between a feeding site selected by a black wildebeest and one being selected by a blue wildebeest?
2. What similarities and differences exist between feeding sites selected by black and blue wildebeest and sites that seemed to be suitable but which were consistently not utilised?

METHODS

Seven black wildebeest and 11 blue wildebeest feeding sites were selected to study their resource partitioning at the feeding site scale. A preferred feeding site was defined as an area where most of the members of a female herd of a specific type of wildebeest were found to be feeding actively at the same locality during at least three of five consecutive transect investigations (Wentzel *et al.* 1991) which were conducted during the habitat survey phase of the present study (Chapter 4). Vegetation sampling of these sites was done by using the centre of the herd as the centre of the sampling point. These centres were selected solely on the basis of high animal densities with no consideration for vegetation composition as suggested by Novellie (1990).

The following vegetation parameters were measured at each site by using the same methodology as was applied for the measurement of the herbaceous characteristics of the different habitat types (Chapter 5): Grass species composition, above-ground standing crop (kg/ha), grass height (cm), grass leaf height (cm) and grass canopy cover (%). Plant species density and diversity, veld condition, degree of utilisation and grass biomass concentration were calculated from the above variables using the same equations and methodology as was applied in Chapter 5.

In addition, 17 sites were surveyed where wildebeest, either black or blue, were never recorded but where they were expected to occur. These non-utilisation sites were selected by using a non-random, stratified sampling approach (Novellie 1990). For this part of the study, and due to the time-consuming nature of this type of analysis and the logistical constraints, it was decided to conduct an analysis of the feeding sites on one occasion only and not to repeat the analysis over the three ecological seasons. Surveys were therefore only done in the late growing season. The ideal season for analysis of the vegetation characteristics would have been the dormant season as this would have been when the food resources would have been most limiting. However, the grass species in these feeding sites would have been very difficult to identify and thus severely restricting the number of variables that would have been possible to measure during the dormant season.

Statistical analysis

An ANOVA test was done (PROC GLM) to determine whether there were statistical differences in vegetation characteristics between the sites that were utilised by black wildebeest, blue wildebeest or not at all by either type of wildebeest. These tests were done for each of the herbaceous characteristic variables listed above.

The herbaceous layer variables listed above were submitted to a step-wise discriminant analysis (STEP DISCRIM) with site type (either blue wildebeest utilised, black wildebeest utilised or not utilised) as a class variable, to determine any significant variables that could separate the three site types. Discriminant analysis was used since all the variables measured were continuous and the fact that it has the ability to identify predictor variables from potentially useful environmental factors (Marnell 1998). Discriminant function analysis therefore is a multivariate technique that is particularly useful in habitat use separation studies (Ferrar and Walker 1974). The step-wise approach enters variables into the discriminant function analysis individually, and the variable that minimises the overall Wilks' lambda for the function is selected for entry at each step. The process is repeated until no additional increase in the accuracy of the discriminant function was achieved.

It was also decided to analyse the data for black and blue wildebeest separately, and then to conduct a separate analysis comparing black wildebeest with not utilised sites, blue wildebeest with not utilised sites and both types of wildebeest combined with not utilised sites.

Standardised canonical discriminant function coefficients and correlations between discriminating variables and canonical discriminant functions can be used to estimate the relative contribution of each selected variable to the power of the discriminant function (Wei *et al.* 2000). Larger absolute values of correlations or coefficients indicate stronger contributions to the power of the function for the relevant variables (Cooley and Lohnes 1971). For example, a value of –2.4 for the standardised canonical discriminant function coefficient would indicate that that variable had a stronger contribution to the power of the function than a value of 1.1.

RESULTS

In the present study, the mean and standard error of the 17 herbaceous layer characteristics for the black and blue wildebeest feeding sites and the not utilised sites are shown in Table 7.1. The ANOVA tests revealed no significant differences between the feeding sites utilised by the black and blue wildebeest (Table 7.1). Differences were found between sites that were not utilised by either type of wildebeest and those that were utilised by both types of wildebeest (Table 7.1). One-way analysis of variance detected four variables that differed significantly between the three types of site ($p \leq 0.05$). The grass height and grass leaf height variables were tallest in the not utilised areas, indicating that the feeding sites of both types of wildebeest tended to be under some grazing pressure that decreased the grass height to a more preferred grazing level.

The mean grass biomass in the not utilised sites was significantly higher than in the black wildebeest feeding sites, but not significantly different to the blue wildebeest feeding sites. Grass biomass concentration followed the same trend as grass biomass, being significantly higher in the not utilised sites than in black wildebeest feeding sites, but not significantly different from the sites that were utilised by the blue wildebeest.

Table 7.1: Mean and standard errors of the characteristics of the herbaceous layer of the feeding sites of the black and blue wildebeest, and sites that were not utilised by either of them, that were analysed to indicate differences in the feeding sites of the black and blue wildebeest at Ezemvelo Nature Reserve in April 2004. Bold values indicate a significant difference and different superscripts denote significant differences between sites

Variable	Black wildebeest	Blue wildebeest	Not utilised	P-value
Species diversity	1.8 ± 0.11	1.7 ± 0.14	1.9 ± 0.11	0.37
Species density	1.7 ± 0.17	1.5 ± 0.15	2.0 ± 0.15	0.08
Class 1 (%)	8.8 ± 5.01	18.4 ± 8.58	12.7 ± 3.5	0.57
Class 2 (%)	10.2 ± 4.06	3.2 ± 1.57	16.6 ± 4.63	0.09
Class 3 (%)	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00	-
Class 4 (%)	22.2 ± 6.85	31.5 ± 8.12	36.1 ± 6.06	0.44
Class 5 (%)	44.6 ± 10.83	36.6 ± 8.71	22.1 ± 3.98	0.07
Invaders (%)	2.8 ± 2.79	0.3 ± 0.29	7.1 ± 4.48	0.44
Bare ground (%)	11.4 ± 4.26	10.0 ± 3.46	5.3 ± 1.71	0.26
Veld condition score	310.9 ± 75.71	369.4 ± 71.29	417.1 ± 33.65	0.42
Degree of utilisation	49.2 ± 12.71	54.5 ± 7.82	29.8 ± 8.99	0.15
Total grass height (cm)	**59.5 ± 6.21**^{a}	**66.0 ± 5.85**^{a}	**78.9 ± 1.87**^{b}	**0.007**
Grass leaf height (cm)	**31.0 ± 3.71**^{a}	**33.6 ± 4.39**^{a}	**43.3 ± 1.61**^{b}	**0.01**
Canopy cover (%)	88.5 ± 4.22	89.1 ± 3.2	85.1 ± 4.71	0.77
Biomass (kg/ha)	**2193.1 ± 518.33**^{a}	**3469.2 ± 541.17**^{ab}	**4605.2 ± 278.75**^{b}	**0.002**
Biomass concentration (kg/m^{3})	**0.7 ± 0.14**^{a}	**0.9 ± 0.11**^{ab}	**1.1 ± 0.06**^{b}	**0.04**

The feeding sites of the black and blue wildebeest could be discriminated by using the step-wise disciminant analysis function, based on the percentage of Class 2 plant species, mean grass biomass (kg/ha), mean grass leaf height and the mean percentage of invaders present (Table 7.2). This discriminant function analysis of the two types of wildebeest was significant (Eigenvalue = 1.873, Likelihood ratio = 0.348, *df* = 4, p = 0.0138) which suggested that the two types of wildebeest exhibited different patterns in habitat use in terms of these identified variables. Absolute standardised coefficients of the selected variables ranged from 0.649 to 1.977, with the mean grass biomass contributing the most to the power of the discriminant function and the percentage of invaders contributing the least (Table 7.2).

The sites that were utilised by the black wildebeest and those that were not utilised by either the black or blue wildebeest were discriminated based on the grass leaf height and the percentage of Class 4 grasses present (Table 7.2). The discriminant function analysis of the sites that were utilised by the black wildebeest and those that were not utilised by either type of wildebeest was significant (Eigenvalue = 5.975, Likelihood ratio = 0.143, *df* = 3, p<0.0001) suggesting that there were certain environmental factors that made a feeding site more suitable for a black wildebeest. Absolute standardised coefficients of the selected variables ranged from 1.194 to 2.673 (Table 7.2) with the grass leaf height contributing the most to the power of the discriminant function and the percentage of Class 4 grasses contributing the least.

Sites that were utilised by the blue wildebeest and those that were not utilised by either type of wildebeest were discriminated based on grass leaf height only (Table 7.2). The discriminant function analysis of the sites that were utilised by the blue wildebeest and those that were not utilised by either type of wildebeest was significant (Eigenvalue = 0.224, Likelihood ratio = 0.817, *df* = 1, p = 0.023).

Since the ANOVA test revealed no statistical differences between the feeding sites of the black and blue wildebeest (Table 7.1), it was decided to combine all of the sites utilised by any type of wildebeest by combining the data for black and blue wildebeest feeding sites, and then to compare them with the not utilised sites. The sites that were utilised by wildebeest and those that were not utilised by either type of wildebeest were discriminated based on grass species density, percentage Class 5 grasses and grass biomass (Table 7.2).

Table 7.2: Results of the discriminant function analysis performed to compare the feeding sites of the black with those of the blue wildebeest, and to compare these sites with sites that were not utilised by either type of wildebeest at Ezemvelo Nature Reserve in April 2004

Black wildebeest sites compared with blue wildebeest sites		**Black wildebeest sites compared with not utilised sites**		**Blue wildebeest sites compared with not utilised sites**		**Black and blue wildebeest sites combined compared with not utilised sites**	
Variable	Standardised canonical discriminant function coefficient	Variable	Standardised canonical discriminant function coefficient	Variable	Standardised canonical discriminant function coefficient	Variable	Standardised canonical discriminant function coefficient
Class 2 (%)	0.806	Grass leaf height (cm)	2.673	Grass leaf height (cm)	1.086	Species density	0.508
Biomass (kg/ha)	-1.977	Class 4 (%)	1.194			Class 5 (%)	-0.514
Grass leaf height (cm)	1.556					Biomass (kg/ha)	0.893
Invaders (%)	0.649						

The discriminant function analysis of the two types of site was significant (Eigenvalue = 0.7090, Likelihood ratio = 0.585, *df* = 3, p = 0.0013). Absolute standardised coefficients of the selected variables ranged from 0.508 to 0.893 with grass biomass contributing the most to the power of the discriminant function and grass species density contributing the least (Table 7.2).

Black wildebeest occurred at sites with a lower grass biomass, a higher percentage of Class 2 grass species, a lower grass leaf height and grass height, with more invader species, and a lower biomass concentration than the blue wildebeest. Sites that were selected by both types of wildebeest showed a lower grass biomass, a higher percentage of Class 5 grass species and a lower grass species density than sites that were not utilised by either type of wildebeest. Black wildebeest tended to have a higher impact on their feeding sites, decreasing the grass leaf height and percentage Class 4 grass species, and increasing the percentage basal cover, while the blue wildebeest decreased the grass leaf height in their feeding sites compared to the sites that were not utilised by either type of wildebeest.

DISCUSSION

Black and blue wildebeest showed some discrimination in their feeding site selection based on the grass biomass and the grass height of the herbaceous layer. Further feeding site differentiation between the black and blue wildebeest was obtained through differences in grass species composition. The other variables were not selected in any of the discriminant analyses as they were either correlated with a variable that had been selected already or they could not explain additional variation.

Both types of wildebeest in the present study tended to select feeding sites with a higher percentage of Class 5 grass species than what was found in sites that were not utilised by either type of wildebeest. Class 5 grass species increase with heavy over-utilisation (Bothma *et al.* 2004) and in the study area may indicate that in the feeding sites of the wildebeest, ecologically better plant species were being replaced with those that increase with over-utilisation. The grass species density of the feeding sites that were utilised by wildebeest as feeding sites was also less than that found in the sites that were not utilised by either type of wildebeest, indicating that wildebeest may have been selecting some grass species in their feeding sites, hence decreasing the overall grass diversity. As some areas are being overutilised, such as in the feeding sites of the wildebeest in the present study, grass species richness will decrease with an accompanying increase in the dominance of a few more unpalatable species (Morrison *et al*. 1992). All these factors indicate that the wildebeest on the study area were overutilising the grass in the areas in which they were feeding, or that they were modifying these areas to make them more suitable for their grazing habits which require short grass areas. In order to confirm this observation, before and after studies of these sites should be conducted.

Black wildebeest feeding sites tended to have a higher percentage of Class 2 grass species than those of blue wildebeest. Class 2 grass species increase with under-utilisation. Black wildebeest feeding sites also had a higher percentage of invader plant species than those of blue wildebeest. The feeding sites that were utilised by the black wildebeest had a herbaceous composition made up mainly of 44% Class 5 grass species and a few Class 1 (8%) and Class 2 (10%) grass species. Blue wildebeest feeding sites had a herbaceous composition consisting of 36% Class 5 grass species, 32% Class 4 grass species and 18% Class 1 grass species.

The removal of the above-ground grass biomass stimulates regrowth that produces young plant material that is more digestable and nutritious than older plant material. Repeated grazing during the growing season therefore increases the quality of the forage (Ydenberg and Prins 1981). The creation and maintenance of grazing sites by black wildebeest in particular, improves the quality and digestability of such areas (Augustine *et al*. 2003). These grazing areas are expanses of short grass in an immature state, have grasses with higher stem:leaf ratios, and a higher bulk density than that of tall stands (Cromsigt 2006). The higher bulk density means a potentially higher food yield per bite (McNaughton 1984). The results of the present study, however, indicated that the grazing sites that were utilised by the black wildebeest at Ezemvelo Nature Reserve had a lower bulk density than the taller stands that were not utilised. This may indicate that the grasses that were utilised by the black wildebeest were not the type of grasses that would react to grazing to produce a traditional grazing lawn, but would instead decline until the patch became denuded and the wildebeest were forced onto another area.

The percentage canopy cover has been used to provide a rough indication of the quantity of forage available in a given area (Novellie and Strydom 1987). The phytomass available is important in determining the feeding habits and habitat utilisation of herbivores (Kinyamario and Macharia 1992). Annual consumption of plant material by large herbivores may be limited by the amount of herbage available.

A grass height of less than 30 mm would be the minimum grazing height for most grazing ungulates (Dörgeloh 1998). Grass heights <30 mm would not provide sufficient herbage for the maintenance of a healthy body weight. Some large herbivore species select grass swards that are dominated by Class 1 grasses (with a consequent high veld condition score) while other species favour a grass sward structure that is dominated by Classes 2 to 5 grasses, with a consequent low veld condition score (Novellie 1990).

On the scale of a feeding site, studies have shown that variation in the size, spatial detail and quality of these food patches influence the selectivity of grazer species differentially and could potentially determine large herbivore coexistence and diversity at such a small scale (Hester *et al.* 1999). However, the majority of herbaceous layer characteristics at the feeding sites did not differ between the two types of wildebeest or between those sites utilised by wildebeest species and those not utilised by them. The overall pattern at Ezemvelo Nature Reserve indicated that some degree of species-specific difference did exist between the black and blue wildebeest with regards to the grass phytomass levels, grass sward structure and grass species composition of the feeding sites. These differences were, however, not considered to be large enough to allow for the coexistence of the black and blue wildebeest at this fine scale. Therefore, it is suspected that the black and blue wildebeest in the study area did not partition the food resources at the feeding site scale, and if confined to areas with no habitat variation, they may compete for feeding sites. However, without a detailed floristic analysis to the species level, these results remain inconclusive.

CONCLUSION

The results of the present study indicated that the feeding sites of the black and blue wildebeest were only discriminated based on differences in grass quantity and grass species composition. These differences did not prove to be significantly different when classical hypothesis testing was applied. A greater difference was however detected between the black wildebeest feeding sites and those sites not utilised by either type of wildebeest. These differences were based on grass structure and grass quantity.

CHAPTER 8: ACTIVITY BUDGETS

INTRODUCTION

The daily activity patterns of ungulates are affected by environmental factors such as temperature, cloud cover, wind velocity, moon cycle, as well as the presence of other animals (Berry *et al.* 1984; Theron 1991; Vrahimis and Kok 1992; Vrahimis and Kok 1993). Activity patterns also tend to vary between species experiencing the same environmental factors in the same area, indicating a compromise to a number of factors that act concurrently on the animals (Leuthold 1977). Disparity in the activity patterns occurring between species inhabiting the same area may therefore, mirror their individual physiological adaptations to the prevailing environmental conditions (Ben-Shahar and Fairall 1987).

Animals may also make behavioural adjustments to their natural activity patterns in response to competition from other species in the near vicinity (Pianka 1973). Differences detected between two species in terms of their relative activity patterns may allow for the exploitation of different resources at different times. Such temporal separation of activities may reduce the extent of competition between these two species. Therefore, subtle temporal differences in daily and seasonal activity patterns may allow for coexistence (Pianka 1973).

By quantifying and comparing the activity patterns of the black and blue wildebeest at Ezemvelo Nature Reserve, differences in the requirements of the two types of wildebeest may be evaluated (Ben-Shahar and Fairall 1987). This comparison and quantification would also provide information on the behavioural adjustments made by each type of wildebeest, which may be in response to competition or due to the suitability of their environment.

It has been suggested that the thermal tolerance of the black wildebeest is high due to their body conformation, dark pelage and thick coat adapting them to an open habitat with no shade where they are exposed to the sun throughout the day (Vrahimis and Kok 1992; Skinner and Chimimba 2005). In contrast, other studies have shown that the thermal tolerance of the blue wildebeest is lower than that of the black wildebeest due to their paler pelage and thinner coat (Hofmeyer 1981; Ben-Shahar and Fairall 1987) resulting in shade-seeking behaviour and a concentration of active periods in the early and later parts of the day when temperatures are low (Ben-Shahar and Fairall 1987).

The two types of wildebeest at Ezemvelo Nature Reserve occupy an area outside their historical distribution range, which has sub-optimal habitat for wildebeest, with a long history of human activity and an absence of large natural predators (Chapter 2). These factors may all require some compensatory behaviour by both types of wildebeest in order to survive and reproduce effectively. Combined with the influence that competition may have on activity patterns, it is expected that the black and blue wildebeest activity patterns will be dissimilar. This hypothesis was tested here by the following key questions:

- What are the daytime activity patterns of the two types of wildebeest over the entire study period and over the three ecological seasons?
- What are the different activity patterns adopted by the various social groups of each type of wildebeest?

METHODS

Field collection of data

Observations on the daily activity patterns of the black and blue wildebeest at Ezemvelo Nature Reserve were made from March 2004 to August 2005. Direct field observations were conducted on a monthly basis from a parked vehicle or other vantage point by using a pair of 16 x 50 binoculars during daylight hours. Most of the observations were done at distances of 100 – 500 m. During each observation period, the dominant activity of each individual visible from the observation point was recorded at 5-minute intervals (Grimsdell and Field 1976) by using the scan-sampling method (Altmann 1973). Activities observed were classified into five categories, namely grazing, standing, walking, lying down and other activities (Ben-Shahar and Fairall 1987). The latter included all activities that did not feature strongly in the general activity pattern, such as grooming, running, defaecating and urinating.

Following Von Richter (1971a) and Berry (1980) three basic social groups were recognized for both types of wildebeest, namely breeding herds consisting of females and their calves, bachelor herds consisting of non-breeding males and territorial males. During most sampling sessions it was attempted to keep a female herd with a territorial bull under continuous observation. It was considered that the female herd would be the most representative group to indicate patterns in daily activity of the two types of wildebeest and it also provided for more activity records (Winterbach 1999). Black wildebeest territorial bulls were closely associated with the female herds but blue wildebeest territorial bulls tended to occur around the edges of breeding herds. Thus for the blue wildebeest, a number of nearby territorial bulls could be observed concurrently with the herd. For comparative purposes, activity records for calves, female adults and territorial bulls were recorded separately.

If the presence of the observer caused the herd at any time to appear uneasy for more than 15 minutes, or it ran off for more than 100 m, observations on that herd were discontinued on the assumption that normal activities were interfered with (Vrahimis and Kok 1993; Winterbach 1999). As the number of individuals per observation varied, even between consecutive observations, all the observations were standardised to percentages before analysis to remove the effect of group size (Winterbach 1999).

In addition, the cloud cover, wind speed and wind direction were estimated every two hours. Temperature was recorded in the shade outside the car every 15 minutes.

Statistical analysis of the data

Observations were distributed as equally as possible over the different age and sex classes, thus minimising bias towards observation of the more conspicuous individuals. Imbalances within the data set and potential serial correlations between observations would have severely restricted the options for testing the influence of biological and physical factors on activity patterns (Groeneveld 2006 pers. comm.)[12]. Nonparametric tests were therefore applied to some subsets of the data, but use of the complete data set in a multivariate analysis was not feasible. Frequencies of each activity were calculated by dividing the number of observations by the total observations in each hour. For analysis these percentages were log transformed.

The Kruskal-Wallis test (Zar 1984) was used to test the hypothesis that there was no difference between the times spent per activity between black and blue wildebeest. Analyses were performed on various subsets and groupings of the overall data set. Each of the five activities for the black and blue wildebeest was compared. Four of

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the five activities were further grouped into two categories namely active (feeding and walking) and inactive (standing and lying down) and compared between the two types of wildebeest (the "other" category was left out as it included both active and inactive activities). Seasonal data were analysed separately, as were social groups, while the day was divided into three time periods (<10:00; ≥10:00-14:00; and >14:00) and each time period was analysed separately. Due to the nature of the data, statistical analysis of the daily activity pattern was not feasible.

The generalised linear model procedure (PROC GLM) utilising a number of ANOVA tests was performed to test the null hypothesis that no differences occurred among the seasons for each type of activity, followed by calculation of the Least Square Means to determine categories which were significantly different or not (Zar 1984).

RESULTS

A total of 405 activity hours were recorded for black and blue wildebeest at Ezemvelo Nature Reserve. In total, 198 activity hours were recorded for the black wildebeest, 92 hours during the late growing season, 44 hours during the dormant season and 62 hours during the early growing season. A total of 207 activity hours were recorded for the blue wildebeest, with 65, 62 and 80 hours during the late growing season, the dormant season and the early growing season respectively.

Entire study period daily time budget (all data)

The relative proportion of daily activities as shown by the black and blue wildebeest over the entire study period, combining all age classes and social groups is summarized in Figure 8.1.

The largest part of the day for black wildebeest was spent grazing (35.4%) followed closely by lying down (32.6%). Standing, often not considered a dominant activity (Vrahimis and Kok 1993), formed a substantial portion (26.9%) of the daily time budget. Walking and other activities combined only formed 5.1% of the daily time budget.

Blue wildebeest spent most of their daily time budget by grazing (44.5%). Equal time was spent standing (23.3%) and lying down (23.1%) during the day. Walking, which

Figure 8.1: Daily time budgets for the black and blue wildebeest for the entire study period at Ezemvelo Nature Reserve when combining all the social groups and age classes.

is often not considered a dominant activity formed 7.0% of the daily time budget and other activities represented a minor proportion (2.1%).

According to the Kruskall Wallis test, blue wildebeest spent a significantly greater percentage of their time grazing than did black wildebeest (χ^2 = 7.6464; *df* = 1; p = 0.0057). Blue wildebeest also spent a significantly greater percentage of their time walking than did black wildebeest (χ^2 = 12.8569; *df* = 1; p = 0.0003).

Figure 8.2 shows the relative proportion of the daily time spent on the various activities by territorial bulls, adult females and calves throughout the study period for black and blue wildebeest. Blue wildebeest adult females spent a significantly higher proportion of their time grazing (46.3%) than did black wildebeest adult females (37.2%) (χ^2 = 7.6863; *df* = 1; p = 0.0058). However, black wildebeest adult females spent significantly more time lying down (31.1%) and standing (27.3%) than did blue wildebeest adult females (22.3% and 22.6% respectively) (χ^2 = 4.4625; *df* = 1; p = 0.0346 and χ^2 = 5.4913; *df* = 1; p = 0.0191). Blue wildebeest adult females in turn spent significantly more time walking (7.3%) than did black wildebeest adult females (3.1%) (χ^2 = 4.4625; *df* = 1; p = 0.0346).

Black wildebeest calves spent most of their daily time budgets by lying down (46.0%) while blue wildebeest calves spent most of their time in grazing (40.4%). Blue wildebeest calves spent more of their daily time walking than did black wildebeest calves (7.4% vs 3.2%) (χ^2 = 7.3237, *df* = 1; p = 0.0068), but this was the only significant difference that could be detected between the activities of the calves of the two types of wildebeest.

Black wildebeest territorial bulls spent most of their time standing (42.3%) while blue wildebeest territorial bulls spent most of their time grazing (43.5%). The only significant difference between the activities of the territorial bulls was that blue wildebeest bulls spent more time grazing (43.5%) than did the black wildebeest bulls (28.3%) (χ^2 = 4.0585; *df* = 1; p = 0.0439).

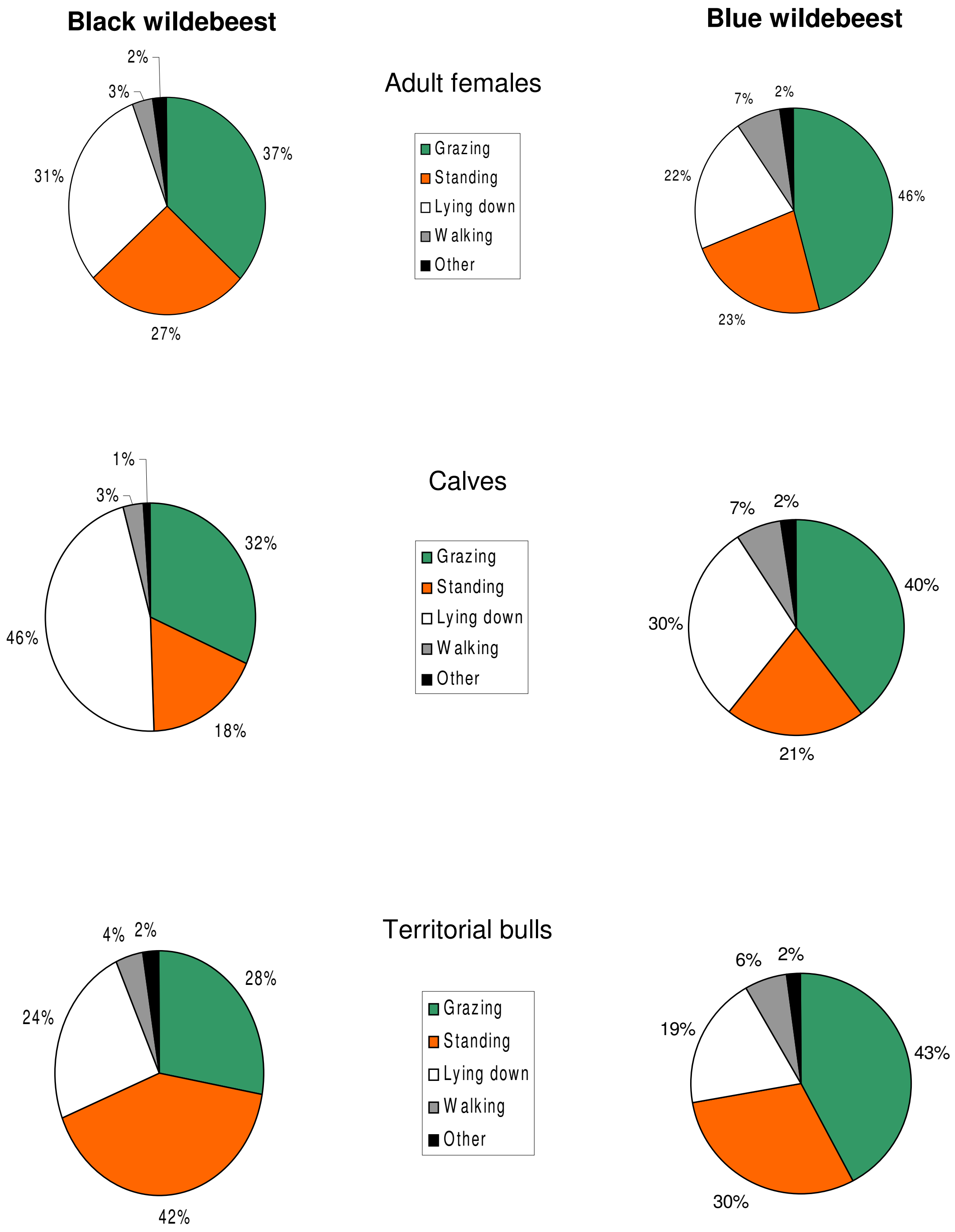


Figure 8.2: Daily time budgets (percentage of time spent) for adult females, calves and territorial bulls of the black and blue wildebeest for the entire study period at Ezemvelo Nature Reserve.

Seasonal daily time budgets

There were not sufficient replicates for an adequate seasonal analysis. Most of the tests conducted indicated non-significant differences between the black and blue wildebeest. This could probably be attributed to the low number of replicates per season. Therefore the results for the seasonal analysis had to be interpreted with caution. Age or sex comparisons were not considered in this section due to the low number of samples available for analysis. Figure 8.3 shows the percentage of time spent in conducting each type of activity in each of the three ecological seasons.

Late growing season

Blue wildebeest spent significantly more time in grazing (40.3%) than black wildebeest (29.9%) during the late growing season ($\chi^2 = 4.8348$; $df = 1$; $p = 0.0279$) and they also spent significantly more time in walking (6.5%) than the black wildebeest (2.5%) ($\chi^2 = 6.4821$; $df = 1$; $p = 0.0109$). Black wildebeest, however, spent significantly more time lying down (39.1%) during this season than the blue wildebeest (24.1%) ($\chi^2 = 4.8348$; $df = 1$; $p = 0.0279$).

Dormant season

During the dormant season the proportional allocation of time to different activities did not differ significantly between the black and blue wildebeest (Figure 8.3).

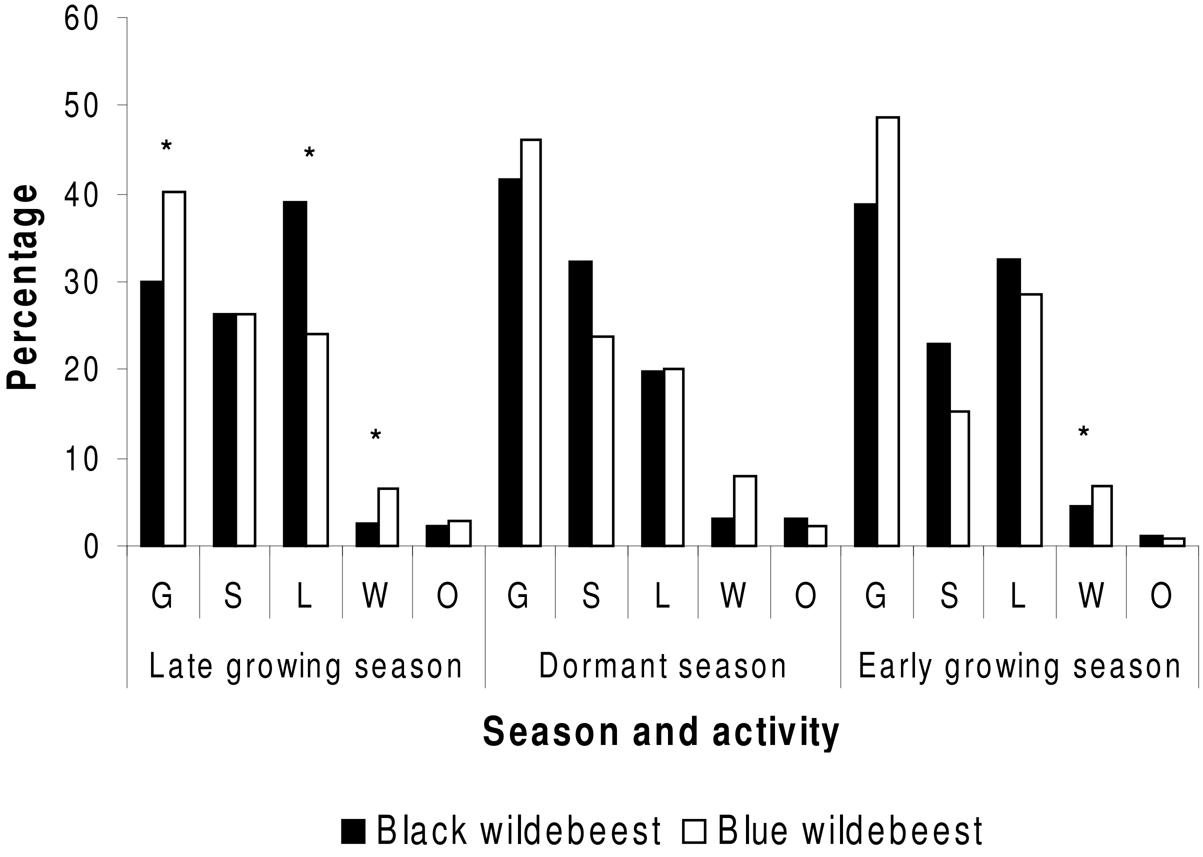


Figure 8.3: Seasonal daily time budgets (percentage time spent) for black and blue wildebeest at Ezemvelo Nature Reserve from January 2004 to August 2005. G=grazing, S=standing, L= Lying down, W=walking, O=other. * indicates a significant difference between the black and blue wildebeest within that season for that activity.

Early growing season

The blue wildebeest spent significantly more time in walking (6.77%) than the black wildebeest (4.6%) during the early growing season (χ^2 = 3.6923; *df* = 1; p = 0.0547). There was no difference in the time allocation patterns of the other activities between the black and blue wildebeest.

Between season comparisons

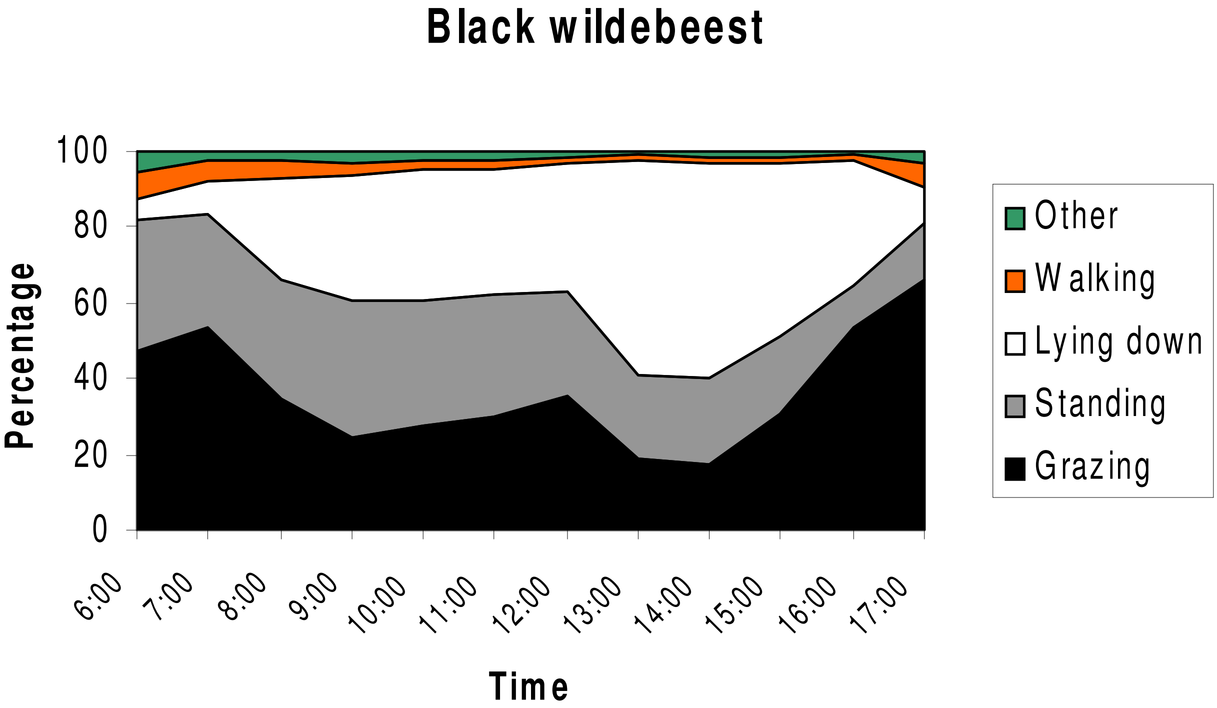
The general linear model procedure (PROC GLM) indicated that black wildebeest spent significantly less time in grazing during the late growing season than during the dormant season (p = 0.0010) and the early growing season (p = 0.0014). There were no seasonal differences in terms of the percentage time spent standing for the black wildebeest. Black wildebeest spent significantly more time lying down during the late growing season than during the dormant season (p = 0.0194) and they also spent less time walking during the late growing season than during the early growing season (p = 0.0214). No seasonal differences were found in terms of percentage time spent conducting other activities by the black wildebeest.

The PROC GLM procedure that was done indicated that there were no seasonal differences in terms of the percentage of time spent in grazing by the blue wildebeest. Blue wildebeest spent significantly more time standing during the late growing season than during the early growing season (p = 0.0179) and also more time standing during the dormant season than during the early growing season (p = 0.0184).

No significant seasonal differences were found in terms of the percentage of time spent lying down and walking in the blue wildebeest. However, the blue wildebeest spent more time conducting "other" activities during the late growing season than during the early growing season (p = 0.0012) and also more time in conducting "other" activities during the dormant season than during the early growing season (p = 0.0050).

Entire study period: diurnal behavioural patterns (all data)

Figure 8.4 illustrates the overall diurnal activity budget for the black and blue wildebeest throughout the study period. Most of the lying down by the black wildebeest occurred just after midday and continued until approximately 15:30 in the afternoon.



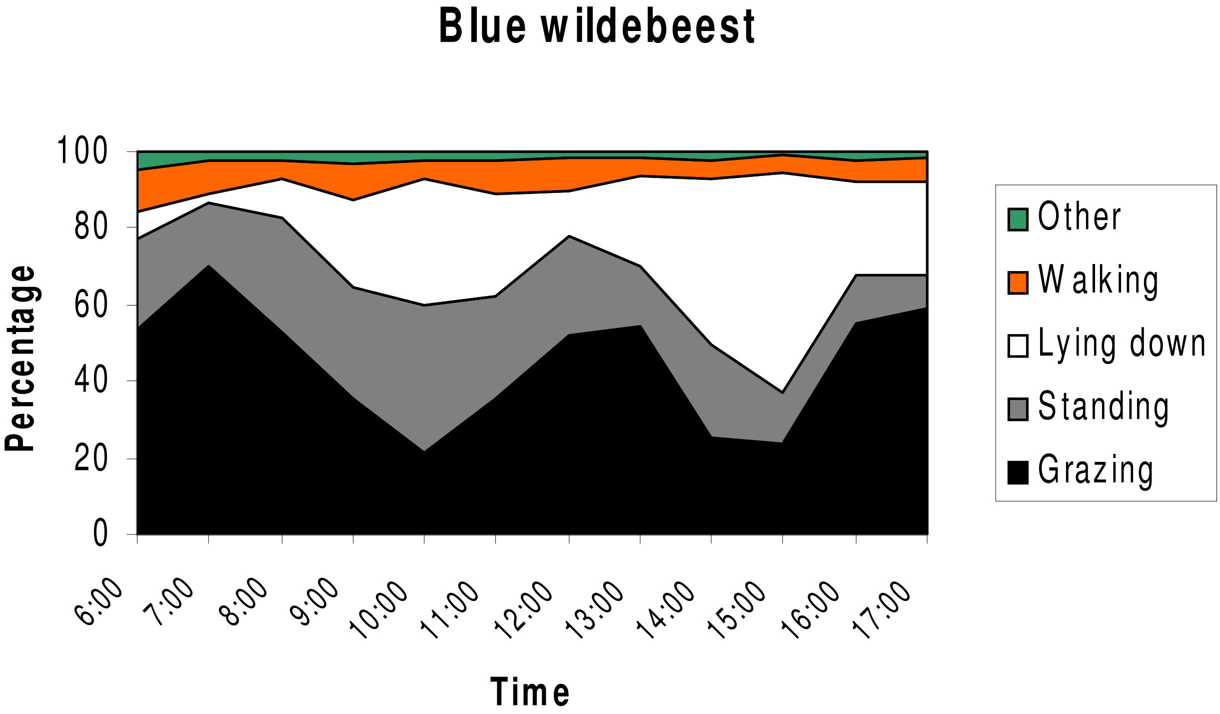


Figure 8.4: Diurnal activity patterns (percentage of time spent) by the black and blue wildebeest for the entire study period at Ezemvelo Nature Reserve.

The main grazing periods when more than 40% of a herd was found grazing were in the morning from sunrise until about 07:30 and again in the afternoon from approximately 15:30 until shortly after sunset.

Another smaller peak in grazing occurred at midday, but was not as marked as the other two peaks. The lowest incidence of grazing occurred from 13:00 to 14:00, as it was the main diurnal resting period. Most walking occurred in the early morning, with a general movement to the daytime resting place and in the late afternoon with a general movement to the night-time resting place. No movement to water was observed during the day. The highest incidence of standing was associated with the period before the daytime resting period (09:00 to 12:00).

Most lying down in blue wildebeest occurred from 14:00 to 16:00 in the afternoon and a smaller peak in lying down from 10:00 to 12:00. Three main peaks in grazing were observed. The highest peak in grazing occurred in the morning from 06:00 to 09:00. Another peak of grazing occurred from 12:00 to 14:00 and the third peak from 16:00 till sunset. Wildebeest tended to stand more than lie down from 09:00 to 12:00. Walking activity was relatively evenly distributed throughout the day with a slight drop off towards the afternoon. Most walking activity in the morning was associated with a movement to water fro drinking.

Figure 8.5 illustrates the results of dividing the daytime into three equal periods <10:00, 10:00 to 14:00, >14:00. The Kruskal Wallis Test indicated that blue wildebeest spent significantly more time grazing in the mornings (<10:00) than did black wildebeest (χ^2 = 5.0370; *df* = 1; p = 0.0248). Black wildebeest spent significantly more time standing in the mornings than did blue wildebeest. Blue wildebeest spent significantly more time walking during midday (10:00 to 14:00) and the afternoon (>14:00) than the black wildebeest (χ^2 = 3.8991; *df* = 1; p = 0.0483 and χ^2 = 6.2267; *df* = 1; p = 0.0126 respectively). No other significant activity differences between the black and blue wildebeest were found.

Seasonal analysis of diurnal behavioural patterns

The diurnal activity patterns that were recorded for the black and blue wildebeest at Ezemvelo Nature Reserve during the three ecological seasons are illustrated in Figures 8.6 to 8.8.

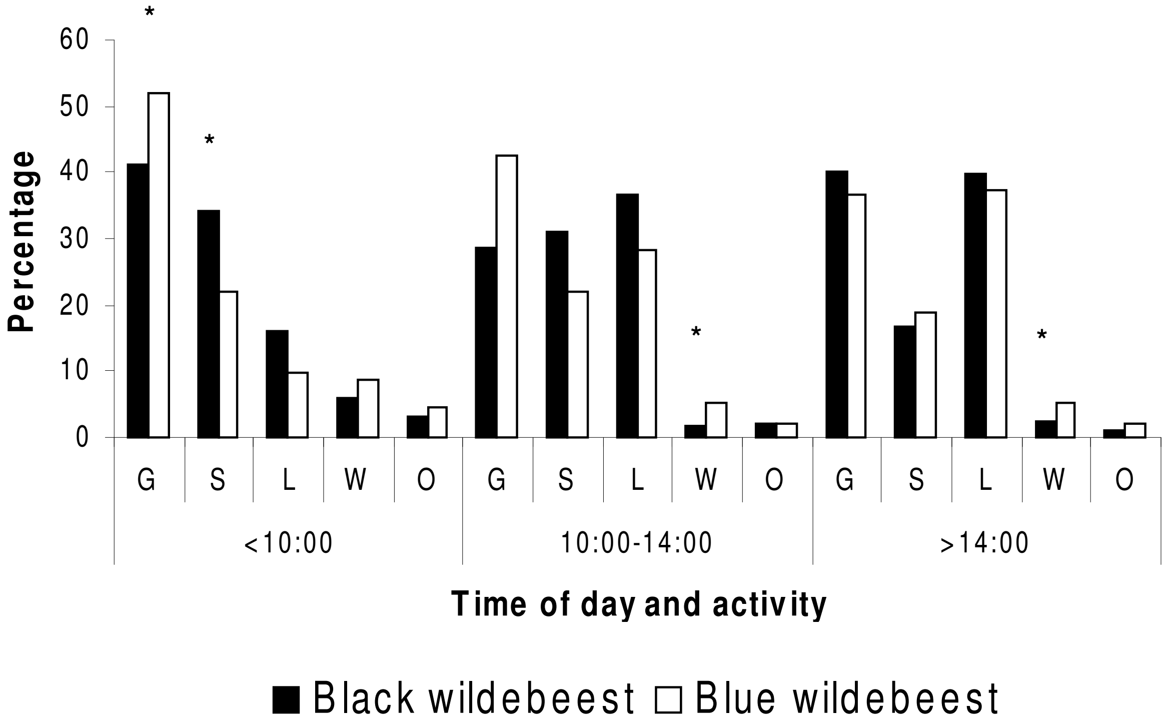
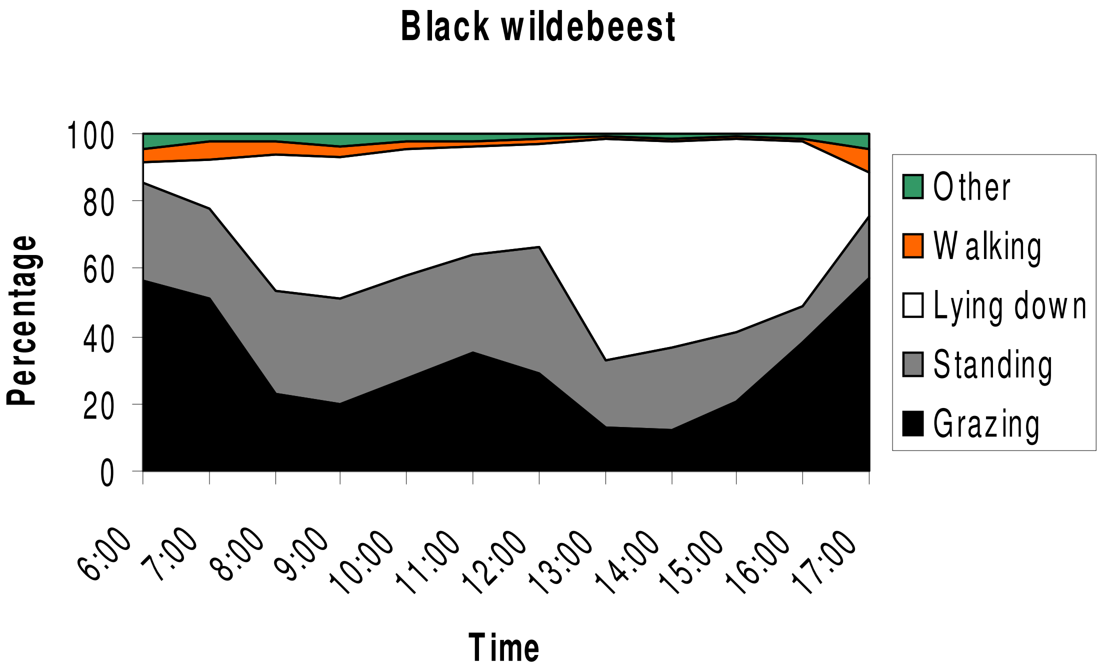


Figure 8.5: Comparison of the diurnal behavioural patterns of the black and blue wildebeest expressed as a percentage of the time spent for the three time periods in the daytime for the entire study period at Ezemvelo Nature Reserve. * indicates a significant difference between the black and blue wildebeest for that activity and time of day with α = 0.05. G = Grazing; S = Standing; L = Lying down; W = Walking; O = Other.



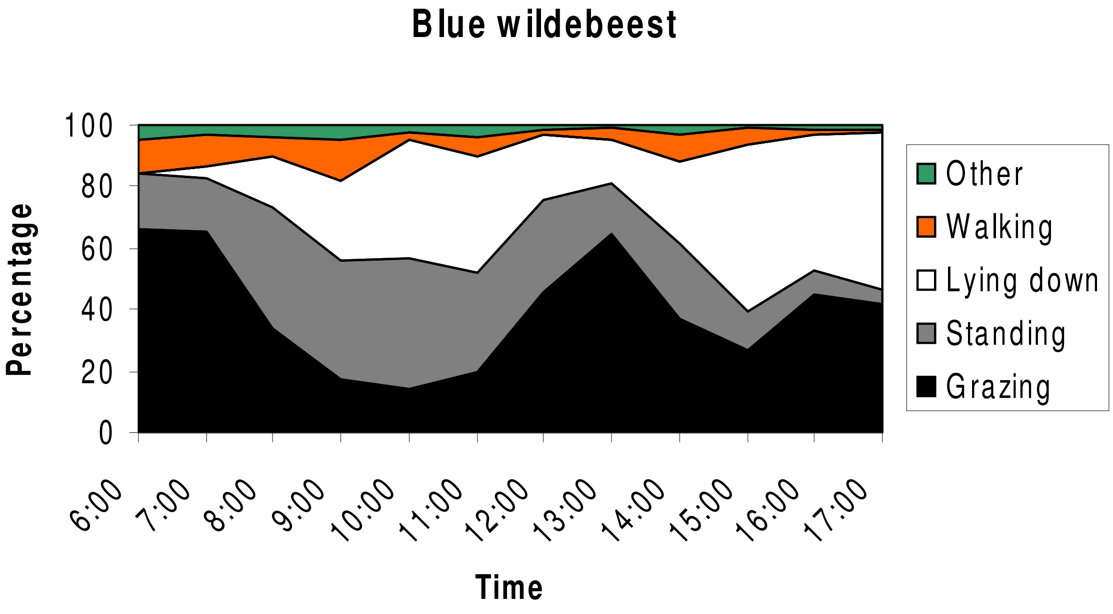


Figure 8.6: Diurnal activity patterns expressed as a percentage of time spent, of the black and blue wildebeest for the late growing season at Ezemvelo Nature Reserve.

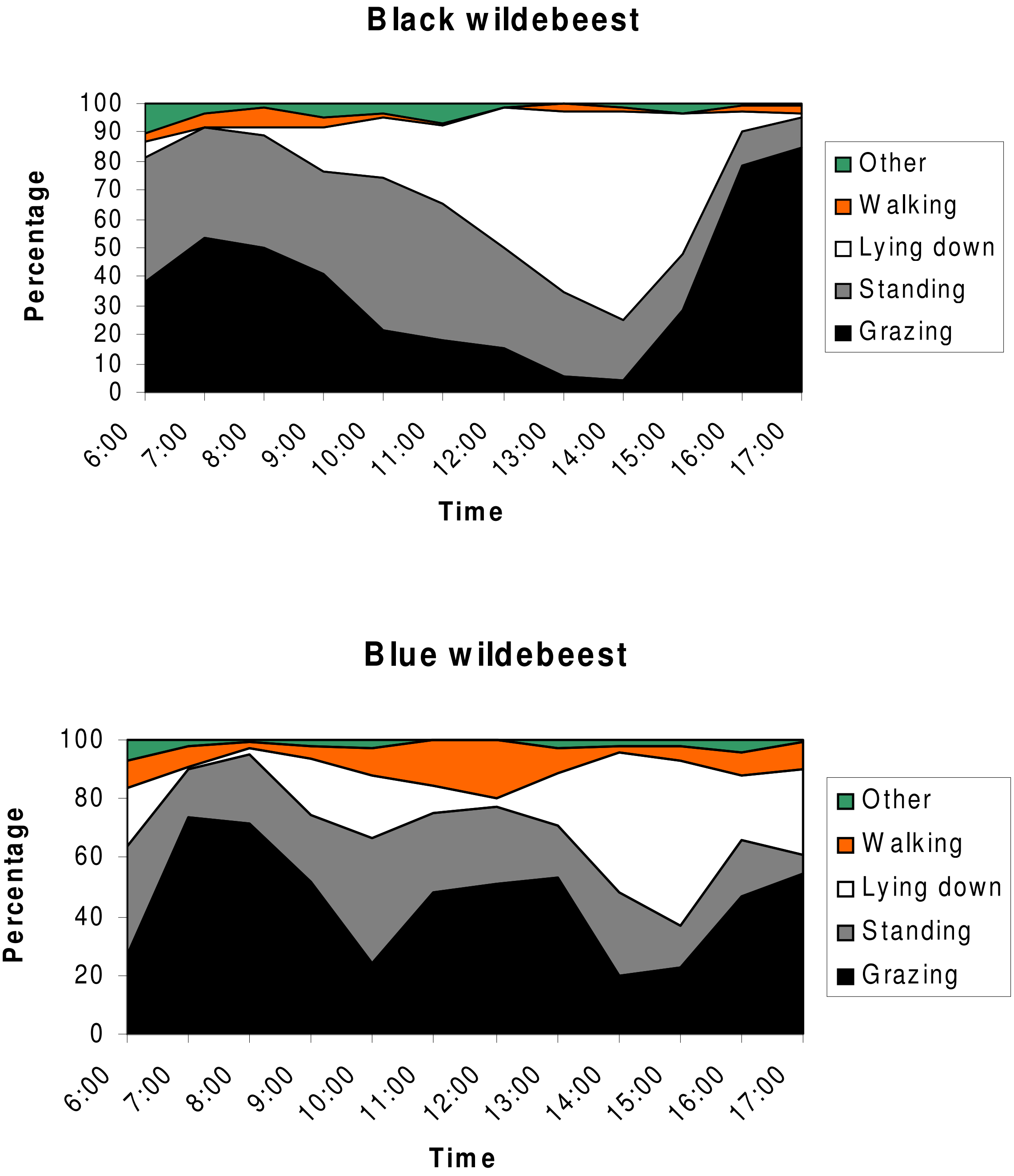


Figure 8.7: Diurnal activity patterns, expressed as a percentage of time spent, of the black and blue wildebeest for the dormant season at Ezemvelo Nature Reserve.

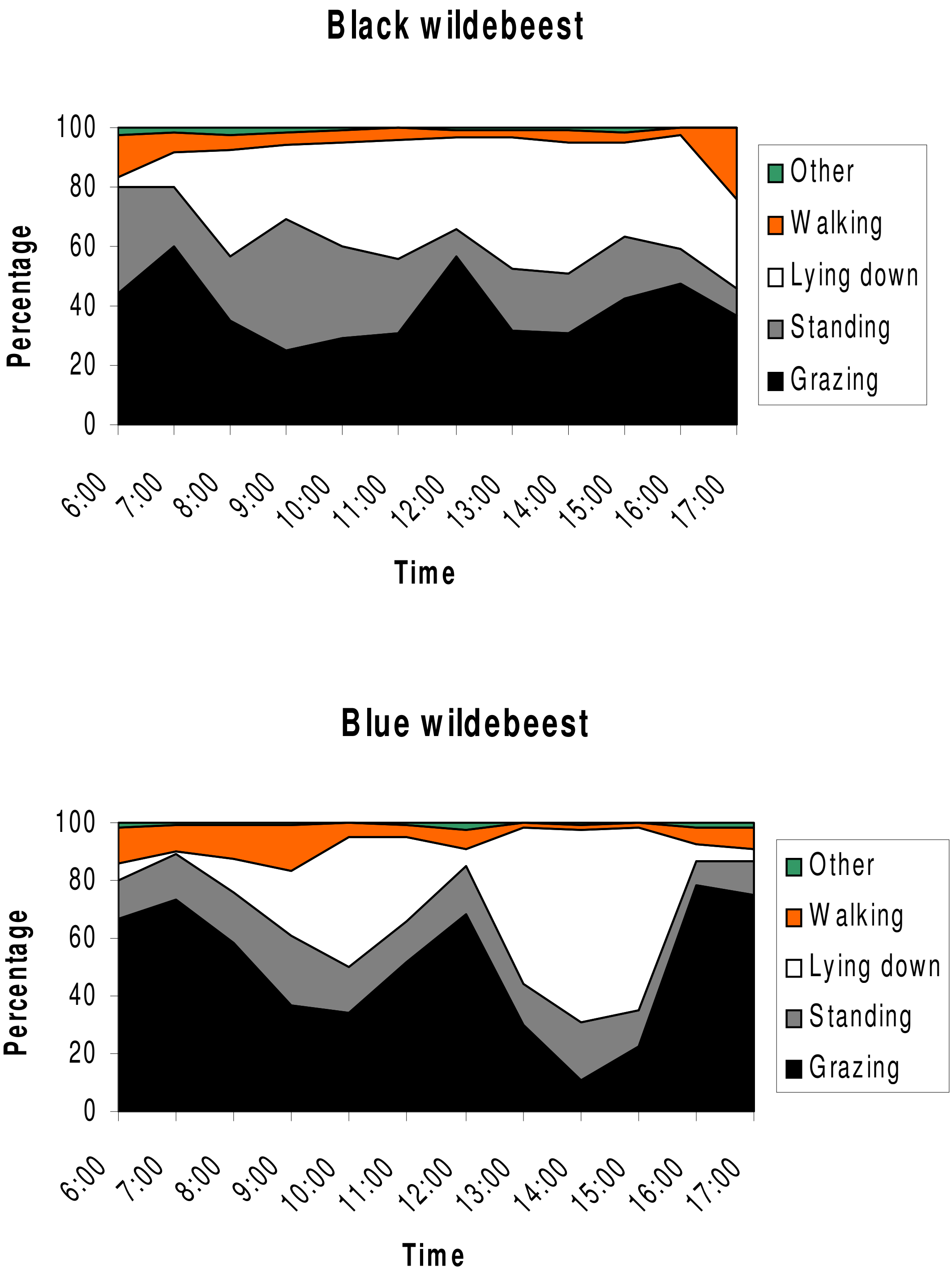


Figure 8.8: Diurnal activity patterns, expressed as a percentage of time spent, of the black and blue wildebeest for the early growing season at Ezemvelo Nature Reserve.

During the late growing season the black wildebeest had two main peaks of grazing when more than 40% of the herd was found grazing. These occurred from 06:00 to 08:00 and again in the evening from 16:00 to 18:00.

Another less intense grazing peak occurred from 10:00 to 13:00. During the dormant season no small grazing peak occurred at midday and most grazing was concentrated in the hour before sunset. During the early growing season there are three main grazing peaks through the diurnal period where more than 40% of the herd was found grazing. The first was from 06:00 to 08:00, the second from 12:00 to 13:00 and the last from 15:00 to 17:00.

During the late growing season one marked resting period occurred in the day where more than 40% of the herd was lying down. This occurred from 13:00 to 15:00 in the afternoon. Another less distinct grazing period occurred from 08:00 to 12:00. During the dormant season only one marked peak in resting activity occurred from 12:00 to 16:00 where more than 40% of the animals were lying down. Lying down was less than 10% for the rest of the day during this season. During the early growing season no major peaks in resting activity occurred and lying down featured evenly throughout the day accept for from 06:00 to 08:00 when few animals were lying down.

In the late growing and early growing seasons, walking was concentrated in two main bouts, one in the early morning and another in the late afternoon just before sunset. This pattern was not distinct during the dormant season. No drinking behaviour was observed by black wildebeest during any of the activity budget surveys, indicating that drinking must be restricted to night time in the study area.

During the late growing, season the blue wildebeest showed three main peaks of grazing activity when more than 40% of the herd was grazing. The first peak was from 06:00 to 09:00, the second from 12:00 to 14:00 and a smaller peak from 16:00 to 18:00. Three main but slightly longer, grazing peaks were also found in the dormant season. The first occurred from 07:00 to 10:00, the second from 11:00 to 14:00 and the last from 16:00 to 18:00. The early growing season showed the same pattern as that of the late growing season with three main grazing peaks from 06:00 to 09:00, from 11:00 to 13:00 and another from 16:00 to 18:00.

In the late growing season, the blue wildebeest were found to spend more time walking in the mornings than the black wildebeest (χ^2 = 4.44; *df* = 1; p = 0.0350). Blue wildebeest spent significantly more time in grazing and walking during midday than the black wildebeest (χ^2 = 3.333; *df* = 1; p = 0.0679 and χ^2 = 4.0333; *df* = 1; p = 0.0446 respectively) during the late growing season. During the dormant season, the black wildebeest spent significantly more time standing in the mornings than the blue wildebeest (χ^2 = 3.1527; *df* = 1; p = 0.0758). Blue wildebeest spent significantly more time walking in the afternoons than black wildebeest during the dormant season (χ^2 = 4.0833; *df* = 1; p = 0.0433). During the early growing season the only significant difference indicated by the Kruskal Wallis test was that black wildebeest spent significantly more time standing in the mornings than the blue wildebeest (χ^2 = 4.800; *df* = 1; p = 0.0285).

Periods of activity and rest

Blue wildebeest were found to be significantly more active than the black wildebeest throughout the entire study period (χ^2 = 11.1727; *df* = 1; p = 0.0008) (Figure 8.8). Blue wildebeest spent 53% of their daily time being active while black wildebeest were only active for 43% of their overall daily time. Blue wildebeest were also found to be significantly more active than the black wildebeest during the late growing season and the early growing season (χ^2 = 6.4821; *df* = 1; p = 0.0109 and χ^2 = 3.6923; *df* = 1; p = 0.0547 respectively). No significant difference between the black and blue wildebeest in terms of time spent active was found for the dormant season.

DISCUSSION

Like the blue wildebeest, the black wildebeest was a migratory animal that occurred in large herds when totally wild (Von Richter 1971b). The black wildebeest has never been studied in its natural habitat while interacting with its natural predators. This opportunity is lost in South Africa as migration is no longer possible, and probably will never be again. Therefore, the social organisation of both types of wildebeest in most parts of South Africa (blue wildebeest in the Kalahari still migrate from time to time) reflects a permanently sedentary phase, consisting of a pattern of permanently established territories, with separate and small (in relation to the migratory herd) female herds and segregated bachelor herds (Jarman 1974). A single male defends a territory. A central trampled and heavily grazed core area of use occurs in each territory, and it is associated with much dung deposition (Estes 1969).

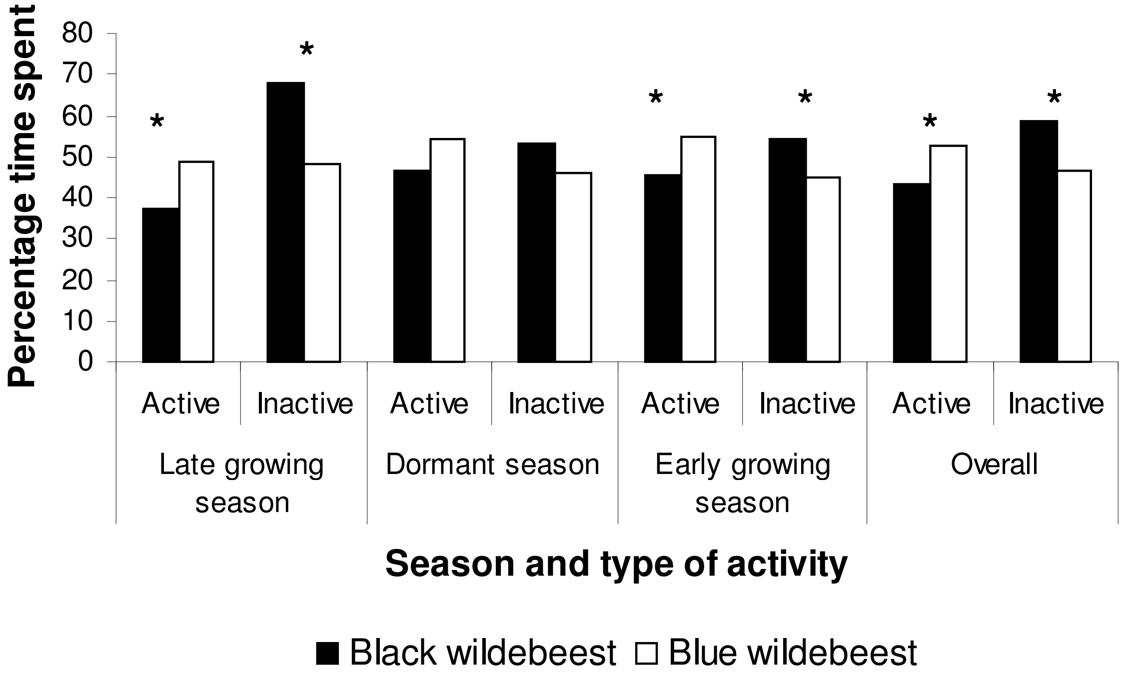


Figure 8.9: Periods of activity (grazing and walking) and rest (lying down and standing), expressed as percentage of time spent, for the black and blue wildebeest for the entire study period and for each ecological season at Ezemvelo Nature Reserve. * Indicates significant differences between the black and blue wildebeest within the seasons and periods of activity.

Territorial behaviour in the blue wildebeest was studied by Estes (1969) and in the black wildebeest by Von Richter (1971a). Their studies and others indicate that the blue wildebeest may have a much more fluid breeding behaviour than the black wildebeest. This may, however, be because most blue wildebeest studies have been conducted on large migratory herds in eastern Africa. Studies on sedentary populations are few. The last study was conducted by Knight (1991) on a blue wildebeest population in the Kalahari, which still has the ability of migrating from time to time.

The activity patterns of the black wildebeest have been studied in detail by Vrahimis and Kok (1993). Direct observations were conducted on a monthly basis from sunrise to sunset in both the dry and the wet season. Black wildebeest were found to spend most of the day lying down, followed by grazing (Vrahimis and Kok 1993). Territorial and bachelor males spent more time in grazing, standing and performing other activities but less time in lying down than the females.

The time that was devoted to grazing by the blue wildebeest as it was studied by Berry *et al.* (1982) was 33%. The predicted foraging time in relation to body mass is 28% (Owen-Smith 1982). Both black and blue wildebeest foraging time at Ezemvelo Nature Reserve was greater than this percentage. The lower foraging time for the black wildebeest (30%) compared with the blue wildebeest (40%) could be as a result of the smaller stomach size of the black wildebeest, resulting in more time spent in ruminating.

The physiological limitations of the blue wildebeest result in the effective use of the woodland areas within the study area where shade is available (Ben-Shahar and Fairall 1987), while the black wildebeest can survive on open grass plains with no shade. Ambient temperature can be related to changes in activity (Ben-Shahar and Fairall 1987). In the present study, the black wildebeest seemed to be more inactive than blue wildebeest during the day and spent equal proportions of their time in grazing and lying down while ruminating. The blue wildebeest spent more time in grazing than in lying down. While the blue wildebeest responds to environmental pressure in the form of heat stress (Ben-Shahar and Fairall 1987) the black wildebeest does not. The thicker, darker coat of the black wildebeest enables it to tolerate greater heat stress than is allowed by the thinner pelage of the blue wildebeest.

The major differences between the two types of wildebeest as was found in the present study relate to the amount of time spent in grazing, and the tendency of the blue wildebeest to be more active than the black wildebeest. While the blue wildebeest seemed to respond to environmental pressure in the form of heat stress, the black wildebeest did not.

In both types of wildebeest, the mean time spent feeding per day was longer in the adult females than in the calves. Calves of both types of wildebeest spent more time lying down than the adults. Adult females spent more time grazing than territorial bulls for both types of wildebeest, but the differences were more marked for black wildebeest than for blue wildebeest. Black wildebeest tended to be more territorial than blue wildebeest and hence it would be expected that black wildebeest territorial bulls would spend less time feeding and more time standing and viewing their territories (Vrahimis and Kok 1993). The results of the present study suggest sex-related differences in either the mode of food-gathering and processing and/or in food and nutrient requirements (Leuthold and Leuthold 1978).

It is also possible that the differences found in feeding time between the black and blue wildebeest reflected the lack of nocturnal observations. Compensation for any feeding deficit incurred during the day could have been made during the night (Leuthold and Leuthold 1978).

The majority of animals preferred to lie down rather than stand during the heat of midday in the present study as was also observed by Vrahimis and Kok (1993). This could be a result of the wildebeest attempting to reduce the impact of reflected radiation from the ground (Jarman 1977). Berry *et al.* (1984) and Vrahimis and Kok (1992) found that body orientation was related to sun and wind direction in both the black and blue wildebeest.

Connochaetes species have precocial young which show a well-developed following response and the calves accompany their mothers from the moment when they first gain their feet, and are able to run within minutes of birth (Estes 1966; Von Richter 1971a). Calving is also strictly seasonal and highly synchronised, with the bulk of the young being dropped within a 3-week period (Estes 1966; Von Richter 1971a; Skinner and Chimimba 2005). Vrahimis and Kok (1994) studied the diurnal activity of early post-natal black wildebeest calves and found that they spent most of their time lying down. The results of the present study agreed with these observations for the black wildebeest. However, the blue wildebeest calves spent more time feeding than lying down. These differences may be related to an innate means of predator avoidance in the black wildebeest that tends to occur in more open habitats than the blue wildebeest (Vrahimis and Kok 1994). The tawny coat of the young calf of both types of wildebeest is completely different from that of the older animals, thereby improving its concealment in its natural environment (Estes 1974).

The black wildebeest in the present study spent less time lying down (33%) than the black wildebeest that were studied by Vrahimis and Kok (1993) (40%). The black wildebeest in the present study also spent more time standing (27%) than in the study of Vrahimis and Kok (*op. cit.*) (12%). Less time was also spent grazing (35%) in the present study than in the study of Vrahimis and Kok (*op. cit*) (40%).

Interspecific differences could be an inherent part of each species' behaviour but they may also be linked to the climatic factors prevailing in different areas of study (Vrahimis and Kok 1993). An increase in static activities such as lying down and standing usually appears under conditions of high heat load (Leuthold 1977; Berry *et al.* 1982).

According to Owen-Smith (1982), foraging time tends to increase with increasing body mass in large herbivores, but factors such as the location of the study area, the availability of grazing and the foraging behaviour of the different species may all play a vital role in the amount of time spent grazing (Vrahimis and Kok 1993). The time spent in standing by ungulates may be influenced by a variety of circumstances, including weather conditions (Leuthold 1977) and external disturbances. Territorial bulls show a long time spent in standing. When standing, territorial males have an improved view of the surrounding terrain, making it easier to spot potential intruders or possible mating partners (Vrahimis and Kok 1993).

The small proportion of the time that was spent in walking by the black wildebeest in the present study can partly be attributed to the pronounced tendency of black wildebeest to remain in their concentration areas (Vrahimis and Kok 1993).

Blue wildebeest tended to spend more time grazing than black wildebeest. This may be attributed to black wildebeest concentrating in areas where the grass layer has been modified to such an extent that its standing biomass is less and thus the black wildebeest do not need to graze as much to obtain the same nutritional intake. Also the smaller body size may require less food intake. The open environment may require more time to be spent lying down to reduce heat gain than in the more shaded habitats of the blue wildebeest.

Seasonal differences indicate that the time spent grazing is greater in the dormant season when the grasses are dormant and low in nutritional value. More time is spent lying down in the hotter seasons than in the cooler seasons. More time is spent walking in the early growing season than the late growing season and dormant season.

CONCLUSION

The activity patterns of the black and blue wildebeest at Ezemvelo Nature Reserve differed significantly in terms of the time spent being active and resting. This has been attributed to the differences in size between the two types of wildebeest and the area selectivity of the black wildebeest that did not require much moving about. Movement of the black wildebeest during the night requires further study. The activity patterns differed from the same type of wildebeest as found in other study areas where similar categories were used. This could be attributed to human disturbance in the study area affecting the activity patterns to a certain degree. It could also be attributed to differences in the quality of the vegetation available to the two types of wildebeest at Ezemvelo Nature Reserve.

CHAPTER 9: NICHE BREADTH, OVERLAP AND EXPLOITATIVE INTERSPECIFIC COMPETITION

INTRODUCTION

The niche, as defined according to the Hutchinsonian concept (Hutchinson 1957), is accepted as the region in n-dimensional space where the fitness of an individual of a species is said to be positive. The utilisation of multiple resources allows for resource partitioning between the species occupying a specific area. Resource partitioning would in turn, result in niche differentiation and therefore the coexistence of a number of different species in an area would be facilitated (Schoener 1974b).

Resource partitioning patterns in ungulate communities have been extensively studied (Gordon and Illius 1989; Voeten and Prins 1999; Forsyth 2000; Johnson *et al*. 2000; Bagchi *et al*. 2003; Hemami *et al*. 2004; Namgail *et al.* 2004), but the mechanisms that produce such partitioning remain poorly understood.

The observed pattern of resource partitioning between two co-evolved species could be ascribed to ecological forces (i.e. inherent ecological requirements, current competition and / or predation) and evolutionary history (Connell 1980). The pattern can, however, only be tested and interpreted in terms of current ecological forces as the past processes cannot be determined in co-evolved ecosystems (Namgail *et al.* 2004). This has elicited much criticism of studies that have concluded that competition was a main mechanism of resource partitioning (Forsyth 2000).

Animals partition resources in three fundamental ways: temporally, spatially and trophically (Pianka 1973). They may differ in the times when they are active, the places which they exploit and even the foods which they eat. Such differences, separate niches, reduce competition and presumably allow for the coexistence of a variety of species in one area. The various niche dimensions along which partitioning may take place include habitat, diet, temporal activity and spatial distribution. Habitat is the most common niche dimension to be partitioned, followed closely by food resources (Hemami *et al*. 2004). Temporal partitioning becomes important in environments where resources are renewed rapidly (Bagchi *et al*. 2003).

In studies of species interactions it is useful to quantify the degree to which two species overlap in their use of space, habitat or other resources (Hurlbert 1978).

Overlap indices measure the similarity of two species' use of resources (Loman 1986). Many studies have cited overlap in the use of resources as evidence for competition between ungulates (e.g. Gordon and Illius 1989). However, interpreting these studies is problematic for a number of reasons, the most important being that a high degree of overlap will result in competition only when that resource becomes limiting (Forsyth 2000). The role of competition in ungulate communities has been the subject of considerable debate (Putman 1996). The relative lack of evidence for the effects of interspecific competition among ungulates arises largely from the difficulty of conducting replicated manipulations of density in the field (Caughley and Sinclair 1994). Hence, interspecific competition is difficult to prove (Putman 1996).

Interspecific competition between two species is possible only when three separate conditions are met (Putman 1996; Traill 2004):

- There is habitat overlap
- There is overlap in forage consumed by the two species within those shared habitats
- The shared dietary resources are limiting.

Therefore, to prove that interspecific competition is occurring a reduction of fitness of one of the competitors needs to be demonstrated with the above conditions being met.

To demonstrate that competition is occurring, a reduction in fitness of one of the competitiors needs to be found, and mere overlap may not indicate the presence of competition.

The seasonal context is also extremely important since it is essential to understand resource partitioning between two species during the critical season when resources are limiting (Riney 1982; Traill 2004).

When competition seems to occur as a result of extensive overlap in the use of a limiting resource, a finer level of analysis may reveal separation being achieved by a more fine-grained division of the environment (Dunbar 1978). Ecological overlap may be reduced in quite subtle ways, which may not be obvious and immediately apparent. In addition, species may be able to tolerate much greater levels of ecological overlap in more diverse or richer habitat types than in simple and resource poor ones (Dunbar 1978).

Competition is not expected to play a role in two species that have a low resource overlap. Such species may separate spatially or overlap extensively in a random manner and depending on the distribution of their preferred resources (Hofer *et al.* 2004). Where a high degree of resource overlap is evident ecological competition hypotheses can be formulated.

It is predicted that if two species were similar on any one of the resource dimensions (e.g. habitat, diet, spatial distribution), they would be segregated on some other dimension (Pianka 1973). For coexistence, segregation has to occur on at least one dimension. Therefore, if they showed similarity in habitat use, they may differentiate along another dimension, such as spatially or behaviourally, or even in terms of diet in order to coexist successfully.

Taking into account the historical distributions, occasionally overlapping populations and the morphological, ecological and physiological similarities between the black and blue wildebeest, interspecific competition is expected to occur between the two types of wildebeest in areas where they have been confined together. Interspecific competition is here defined as the act of two species seeking the same space and food (exploitation), which are in short supply, or interacting in such a way that their growth and survival are affected (interference) (Anthony and Smith 1977). Interference competition includes active or passive social interactions such that one or both species avoids the other, whereas exploitative competition exists when one species uses a resource, making it unavailable to another species (Putman 1996).

This chapter explores the evidence for exploitative competition between the black and blue wildebeest and Chapter 10 explores evidence for interference competition. It is hypothesised that exploitative competition between the black and blue wildebeest will take place.

The objectives of this part of the present study were therefore to:

- Describe quantitatively the respective niches of the two types of wildebeest along the habitat, spatial distribution and dietary dimensions
- Explore the potential for exploitative interspecific competition between the two types of wildebeest based on their overlap in the respective niche dimensions.

METHODS

Habitat niche dimension

Niche breadth was calculated for each type of wildebeest by using the different habitat types as resource states and for a separate analysis the different habitat factors were also used as resource states. The following equation of Levins (1968) was used to calculate the niche breadth and hence to quantify the niches of the black and blue wildebeest along the habitat dimension:

$$B=1/\sum^{n}{}_{i}p_{j}^{2}$$

where B is Levin's measure of niche breadth, p_j the proportion of the observations found in resource state j. B is maximum when the observation percentages are similar in each resource state and would be minimal if all observations occur only in one resource state. B was standardised to B_A, ranging from 0 to 1, based on the following equation of Hurlbert (1978):

$$B_A = B-1/n-1$$

where n is the number of resource states.

Overlap in resource use was assessed by using Pianka's niche overlap index (Pianka 1973):

$$O_{rm} = \sum^{n}(p_{jr} \times p_{jm}) / (\sum p_{jr}^{2} \times \sum p_{jm}^{2})^{1/2}$$

where O_{rm} is the index of niche overlap between black and blue wildebeest; p_{jr} is the black wildebeest proportionate use of the resource unit j (calculated as: percentage of the observations that were in habitat j, as a proportion of the total observations across all habitat types); p_{jm} is the blue wildebeest proportionate use of resource unit j; n is the total number of habitat types. This is a symmetrical measure that ranges from 0 when no habitats are used in common to 1 when there is complete habitat overlap.

For comparison another measure of niche overlap was utilised. The Sorenson's Quotient of Similarity (QS) as used by Churchfield *et al.* (1999) was therefore also applied to the habitat type data and the individual habitat factor data. The equation used was as follows:

$QS = 2j/(a+b)$

where j = the total number of resource states common to both types of wildebeest being compared; a = the total number of resource states found in species a (black wildebeest); b = the total number of resource states found in species b (blue wildebeest).

Spatial distribution niche dimension

It was difficult to provide quantitative measurements of the distributions of the black and blue wildebeest at Ezemvelo Nature Reserve as individuals were not identified. A descriptive analysis has therefore been provided to give some indication of the spatial overlap between the two types of wildebeest at Ezemvelo Nature Reserve. The study area was divided into grids of equal size and the number of black and blue wildebeest within each grid was calculated and converted to a percentage of the total number of animals of that type of wildebeest. To calculate indices of spatial overlap by using these percentages the method as described by Anthony and Smith (1977) was applied. For each grid, if for example the black wildebeest occurrence was 5% and the blue wildebeest occurrence was 7%, then the overlap, $Y_{i,}$ would be 5%. The total overlap in spatial distribution for a particular season was calculated from the sum of the overlaps for each individual grid according to the following equation:

$$\sum_{i=1} Y_{i},$$

where n equals the total number of grids utilised. Sorenson's Quotient of similarity was also applied to this data to indicate the degree of similarity between the areas utilised by the black and blue wildebeest.

Estimated dietary niche dimension

Since results from a detailed faecal analysis of the diet of the black and blue wildebeest were not yet available, the diet of both types of wildebeest had to be inferred from floristic data at the sites of their occurrence. It was assumed that a large proportion of the diet would be made up of the dominant plant species that were found within the feeding sites of each type of wildebeest. During the habitat surveys

(Chapter 4), data were collected at each site of occurrence of a black or a blue wildebeest on the dominant and sub-dominant plant species present within a 5 m radius of the site where the wildebeest was observed. Only data for the grazing observations were extracted to estimate the diet. Further data from the vegetation surveys that were done at the feeding sites of the black and blue wildebeest (Chapter 6) were also utilised to indicate the grass species with the highest percentage occurrence in the chosen feeding site of either type of wildebeest. This estimated diet was then used to determine the estimated dietary overlap between the black and blue wildebeest. Overlap in diet was calculated by using the same method as was described for spatial overlap. Sorenson's Quotient of similarity was also applied to this data to indicate the percentage of shared plant species in the diets of the black and blue wildebeest.

RESULTS

Habitat type niche dimension

Habitat type niche breadth and overlap indices of black and blue wildebeest for each ecological season are given in Table 9.1. Niche breadths of all the black wildebeest social groups combined differed significantly from that of blue wildebeest as assessed by the paired t-test ($t = -12.19$; *df* = 2; $p = 0.007$). Niche breadths also differed significantly between the female herds of the black wildebeest and those of the blue wildebeest ($t = -5.27$; *df* = 2; $p = 0.034$). Black wildebeest female herds tended to have a significantly lower niche breadth than the blue wildebeest female herds (0.27 vs 0.53). The territorial bulls of the black wildebeest did not have a significantly lower niche breadth than those of the blue wildebeest ($t = -3.15$; *df* = 2; $p = 0.087$). Territorial bulls had a higher niche breadth than both bachelor herds and female herds for both types of wildebeest.

Niche breadth was the lowest during the dormant season (0.25) and the highest during the early growing season (0.37) for the black wildebeest for all social groups combined. For the blue wildebeest, niche breadth was maximised during the early growing season (0.63) and at its lowest during the late growing season (0.50) for all social groups combined.

Niche overlap between the two types of wildebeest was least during the late growing season (0.77), while maximal niche overlap occurred during the early growing season (0.94) for all social groups combined. Territorial bulls had the highest niche overlap during the late growing season (0.94), while female herds had the highest overlap during the early growing season (0.94). The lowest overlap for female herds was during the late growing season (0.73).

In terms of habitat type utilisation, overlap between the black and the blue wildebeest was generally high for all the seasons (0.87). Similarly, the Sorenson's Quotient of Similarity indicated a degree of similarity of 0.89 in terms of the habitat type utilisation of the black and blue wildebeest.

Habitat factor niche dimension

Niche breadth and overlap indices for the habitat factors for black and blue wildebeest appear in Tables 9.2 and 9.3. Niche breadth of the black wildebeest only differed significantly from that of the blue wildebeest in terms of distance to water ($t = 4.94$; *df* =2; $p = 0.039$), woody vegetation cover ($t = -14.76$; *df* = 2;$p = 0.005$), total grass height ($t = -7.84$; *df* =2; $p = 0.016$), and geomorphology ($t = 11.7$; *df* = 2; $p = 0.007$). The black wildebeest (0.87) were more likely to utilise a wider variety of distances from water than the blue wildebeest (0.83) and had a narrow niche breadth in terms of different woody vegetation covers (0.00), while the blue wildebeest tended to utilise a wider variety of woody vegetation covers (0.53). The blue wildebeest (0.88) was less selective in terms of the total grass height at the site of occupation than the black wildebeest (0.47), and the black wildebeest (0.88) utilised a wider range of geomorphology than the blue wildebeest (0.35). Although they were not found to be significantly different between the black and blue wildebeest, the rock cover and exposure habitat factors also indicated that the blue wildebeest had a higher niche breadth than the black wildebeest (Table 9.2).

Table 9.1: The index of Levin (1968) of niche breadth for each type of wildebeest, and that of Pianka (1973) of niche overlap for each season and social group for the habitat type choices of the black and blue wildebeest at Ezemvelo Nature Reserve from January 2004 to August 2005. The t-values are based on the paired t-test

	Late growing season	Dormant season	Early growing season	Entire study period	t-value	P-value
Niche breadth						
All data						
Black wildebeest	0.30	0.25	0.37	0.31	-12.13	0.007
Blue wildebeest	0.50	0.52	0.63	0.59		
Female herds						
Black wildebeest	0.26	0.20	0.36	0.27	-5.27	0.034
Blue wildebeest	0.39	0.47	0.57	0.53		
Bachelor herds						
Black wildebeest	0.51	0.34	0.43	0.46	-1.74	0.225
Blue wildebeest	0.54	0.48	0.83	0.63		
Territorial bulls						
Black wildebeest	0.55	0.13	0.23	0.36	-3.15	0.087
Blue wildebeest	0.73	0.64	0.74	0.71		
Niche overlap						
All data	0.77	0.89	0.94	0.87		
Female herds	0.73	0.90	0.95	0.87		
Bachelor herds	0.76	0.55	0.85	0.72		
Territorial bulls	0.94	0.79	0.80	0.87		

Table 9.2: The index of Levin (1968) for niche breadth for each type of wildebeest for each season and for the entire study period for the abiotic and biotic habitat factor choices of the black and blue wildebeest at Ezemvelo Nature Reserve from January 2004 to August 2005 obtained from the habitat survey data (Chapter 4) and based on the paired t-test

Habitat variable	Type of wildebeest	Late growing season	Dormant season	Early growing season	Entire study period	t-value	p-value
Aspect	Black wildebeest	0.83	0.99	0.98	0.97	2.49	0.130
	Blue wildebeest	0.74	0.48	0.64	0.65		
Slope	Black wildebeest	0.61	0.58	0.69	0.63	1.80	0.213
	Blue wildebeest	0.58	0.52	0.48	0.52		
Landscape position	Black wildebeest	0.38	0.52	0.37	0.43	0.62	0.597
	Blue wildebeest	0.40	0.46	0.38	0.42		
Distance to water	Black wildebeest	0.84	0.78	0.98	0.87	4.94	0.039
	Blue wildebeest	0.76	0.65	0.91	0.83		
Woody vegetation cover	Black wildebeest	0.01	0.00	0.00	0.00	-14.76	0.005
	Blue wildebeest	0.54	0.46	0.58	0.53		
Grass cover	Black wildebeest	0.48	0.76	0.65	0.73	-1.69	0.233
	Blue wildebeest	0.82	0.73	0.98	0.88		
Rock cover	Black wildebeest	0.45	0.50	0.66	0.53	-3.48	0.074
	Blue wildebeest	0.57	0.75	0.76	0.62		
Total grass height	Black wildebeest	0.43	0.46	0.50	0.47	-7.84	0.016
	Blue wildebeest	0.69	0.81	0.91	0.88		
Grass leaf height	Black wildebeest	0.56	0.60	0.98	0.76	-0.74	0.538
	Blue wildebeest	0.81	0.85	0.80	0.88		
Plant utilisation	Black wildebeest	0.50	0.35	0.68	0.52	-0.10	0.927
	Blue wildebeest	0.55	0.68	0.36	0.58		
Visibility	Black wildebeest	0.53	0.51	0.49	0.70	-2.19	0.160
	Blue wildebeest	0.55	0.68	0.76	0.74		
Distance to shade	Black wildebeest	0.45	0.50	0.26	0.41	-0.53	0.647
	Blue wildebeest	0.38	0.44	0.59	0.48		
Erosion	Black wildebeest	0.29	0.36	0.44	0.37	-2.21	0.157
	Blue wildebeest	0.43	0.37	0.60	0.47		
Altitude	Black wildebeest	0.86	0.88	0.87	0.93	-1.15	0.369
	Blue wildebeest	0.95	0.96	0.84	0.94		
Exposure	Black wildebeest	0.00	0.00	0.00	0.00	-3.99	0.058
	Blue wildebeest	0.12	0.06	0.15	0.11		
Geomorphology	Black wildebeest	0.92	0.80	0.89	0.88	11.70	0.007
	Blue wildebeest	0.39	0.35	0.28	0.35		
Forb : grass ratio	Black wildebeest	0.42	0.47	0.39	0.57	-2.95	0.099
	Blue wildebeest	0.46	0.63	0.54	0.64		
Drainage	Black wildebeest	0.05	0.15	0.33	0.18	1.89	0.200
	Blue wildebeest	0.04	0.05	0.15	0.08		
Combined niche breadth	Black wildebeest	0.48	0.51	0.56	0.55	-7.00	0.020
	Blue wildebeest	0.54	0.55	0.60	0.59		

The combined niche breadth (considering all habitat factors together) of the blue wildebeest was significantly higher than the black wildebeest (t = -7.00; *df* = 2; p = 0.020) (Table 9.2).

For the black wildebeest, the highest niche breadth was in aspect (0.97) and altitude (0.93), while for the blue wildebeest the highest niche breadth occurred in the grass leaf height (0.88) and grass cover (0.88) habitat factors. Black wildebeest had their lowest niche breadth in the woody vegetation cover (0.00), exposure (0.00) and drainage (0.19) habitat factors. Blue wildebeest similarly had the lowest niche breadth in the drainage (0.08) and exposure (0.11) habitat factors.

The highest niche breadth in terms of all habitat factors combined was during the early growing season for both the black and blue wildebeest. The lowest niche breadth for both black and blue wildebeest was found during the late growing season. This is an almost identical pattern to that found for the habitat type analysis in the previous section. The only significant habitat factor that differed from this pattern was geomorphology where the highest niche breadth for both black and blue wildebeest was during the late growing season.

Niche overlap between the black and blue wildebeest was complete for the plant utilisation (1.00), erosion (1.00), exposure (1.00) and drainage (1.00) habitat factors, and very high for the visibility (0.99), forb : grass ratio (0.98), grass cover (0.98), grass leaf height (0.96), slope (0.96), and landscape position (0.95) habitat factors. Niche overlap for the black and blue wildebeest was lowest for the distance to shade (0.46) habitat factor. The highest niche overlap between the black and blue wildebeest was during the dormant season followed closely by the late growing season and the lowest niche overlap was during the early growing season (Table 9.3).

The Sorenson's Quotient of Similarity between the black and blue wildebeest for each habitat factor was very high and mostly equalled 1 as the categories for each habitat factor were subjectively constrained based on wildebeest occurrence and thus these values have not been presented here.

Table 9.3: The index of Pianka (1973) of niche overlap for each season and for the entire study period for the abiotic and biotic habitat factor choices of the black and blue wildebeest at Ezemvelo Nature Reserve from January 2004 to August 2005 obtained from the habitat survey data (Chapter 4)

	Late growing season	Dormant season	Early growing season	Overall
Aspect	0.79	0.83	0.86	0.85
Slope	0.94	0.96	0.94	0.96
Landscape position	0.96	0.94	0.96	0.95
Distance to water	0.84	0.90	0.95	0.93
Woody vegetation cover	0.92	0.92	0.89	0.91
Grass cover	0.96	0.99	0.87	0.98
Rock cover	0.74	0.72	0.94	0.74
Total grass height	0.93	0.95	0.76	0.92
Grass leaf height	0.97	0.97	0.88	0.96
Plant utilisation	1.00	0.93	0.85	1.00
Visibility	0.99	0.94	0.94	0.99
Distance to shade	0.45	0.53	0.39	0.46
Erosion	0.99	1.00	0.98	1.00
Altitude	0.95	0.93	0.89	0.94
Exposure	1.00	1.00	1.00	1.00
Geomorphology	0.86	0.77	0.82	0.82
Forb : grass ratio	0.97	0.98	0.97	0.98
Drainage	1.00	1.00	0.98	1.00
Combined overlap	0.90	0.90	0.88	0.91

Spatial distribution niche dimension

It is evident that there is a high degree of spatial separation between the two types of wildebeest. The overall spatial overlap between the black and the blue wildebeest at Ezemvelo Nature Reserve was only 14%. Black wildebeest were primarily found on the open plains on the northwestern side of the reserve on the high-lying areas. The only place where the blue wildebeest did not occur in large numbers was on these open plains that were favoured by the black wildebeest. Overlap between the black and blue wildebeest occurred primarily on the edges of the open plains where blue wildebeest territorial bulls were invading territories that were favoured by the black wildebeest bulls.

Since there were some seasonal changes in the spatial distributions of both types of wildebeest, the data were also analysed on a seasonal basis. The total spatial overlap for the late growing season was 11%, for the dormant season 8% and for the early growing season 13%. Thus spatial overlap was highest during the early growing season and the lowest during the critical dormant season. Only 60% of the study area was utilised by any type of wildebeest. The remaining 40% is made up of unsuitable habitat for both types of wildebeest, consisting mainly of rocky slopes that are covered with dense woodland.

The degree of similarity of the areas occupied by the black and blue wildebeest based on the Sorenson's Quotient of Similarity indicated that it was 23% during the late growing season, 21% during the dormant season and 27% during the early growing season.

Estimated dietary niche dimension

The plant species present in the feeding sites and their relative percentage frequency of occurrence are shown in Figure 9.1 and 9.2. The niche breadth of the black wildebeest was found to be 0.64, which was higher than the niche breadth for the blue wildebeest, which was found to be 0.39. The most common plant species in the feeding sites of the black and blue wildebeest was *Eragrostis curvula,* and the dominant plant species in the sites occupied by the black wildebeest was *Cynodon dactylon* and *Eragrostis curvula* for the sites occupied by the blue wildebeest. Black wildebeest had a larger variety of plant species than the black wildebeest (Figure 9.2) in their feeding sites indicating the possibility of a more diverse diet.

An overall overlap in the species composition of the feeding sites of the black and blue wildebeest was found to be 55%. Assuming that the composition of the feeding sites gives an indication of the diet of the black and blue wildebeest, the estimated dietary overlap is therefore 55%. It is acknowledged that a quantitative Sorenson's Index may have provided more accurate results.

The shared plant species in the diet of the black and blue wildebeest as calculated by the Sorenson's Quotient of Similarity was 88% for the feeding sites (Chapter 6). According to the dominant plant species in the areas occupied by the black and blue wildebeest and determined in the habitat surveys (Chapter 4) the shared plant species in the diet of the black and blue wildebeest was 81%.

DISCUSSION

The present study has shown that the niche breadth of the black wildebeest is smaller than that of the blue wildebeest in terms of the spatial and habitat dimensions. However, preliminary results on the possible diet of the two types of wildebeest indicate that the black wildebeest has a higher niche breadth than the blue wildebeest in terms of the dietary dimension. This is supported by other studies that have indicated that the natural distributional range of the two types of wildebeest tends to follow differences in their habitat tolerances that do not reflect differences in their trophic behaviour (Codron and Brink In press).

Black and blue wildebeest have not until recently been studied in the same area before and therefore details on their joint resource partitioning are lacking. The knowledge that is available which can be utilised to predict the outcome of competition between the two types of wildebeest is based on overall physiology, morphology and individual habitat choices, all of which have been studied in isolation. Codron and Brink (In press) conducted a study on the feeding niches and trophic ecology of the black and blue wildebeest using stable carbon and nitrogen isotope data from faeces and tooth dentine collagen and concluded that speciation of the black and blue wildebeest was not driven by resource competition. The results of this study, however, indicated that there were different trophic behaviours between the two types of wildebeest but that sympatric coexistence of the two types of wildebeest was facilitated by differential niche occupation at herd levels rather than between species.

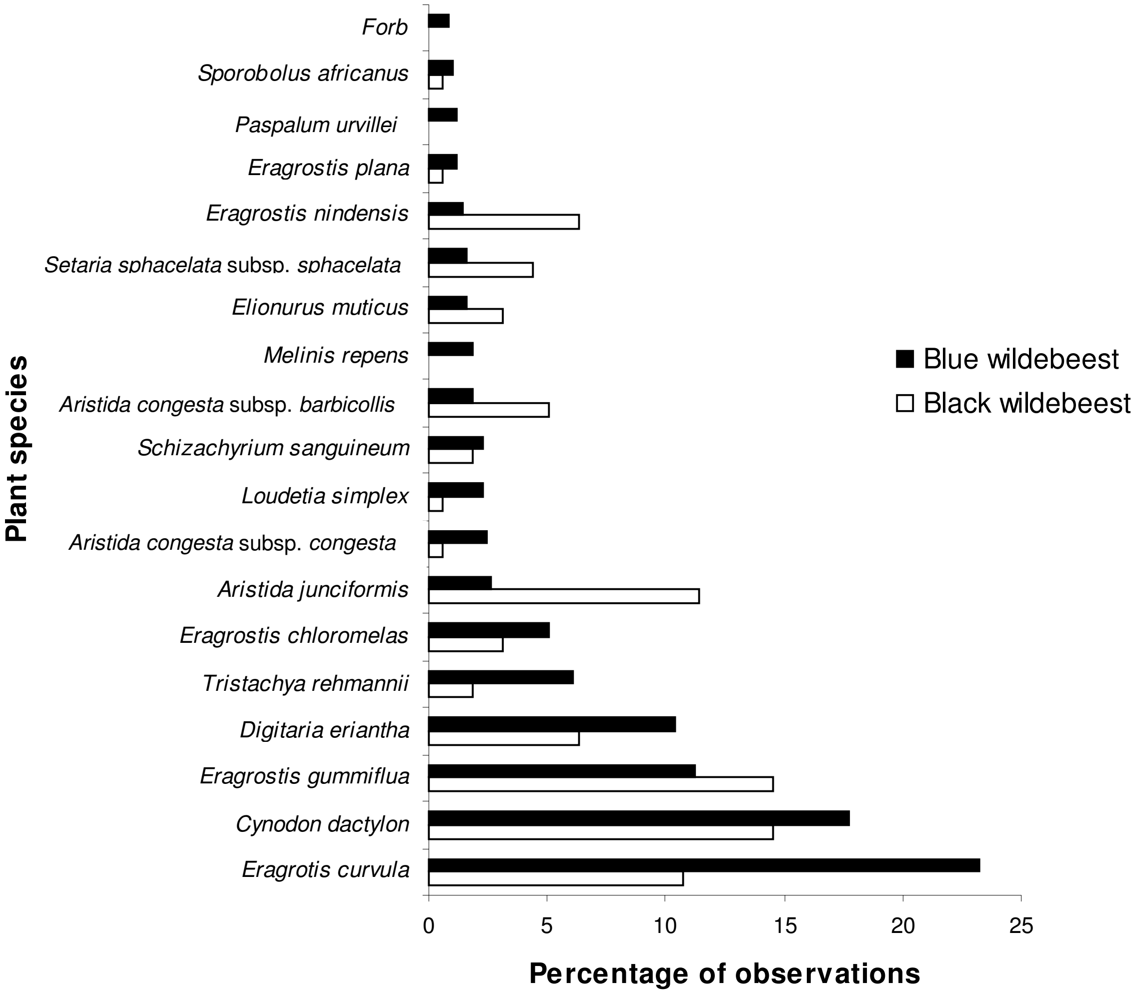


Figure 9.1: Percentage frequency of occurrence of the dominant plant species at the sites of occupation of the black and blue wildebeest at Ezemvelo Nature Reserve from January 2004 to August 2005. Data obtained during the habitat survey collection period (Chapter 4).

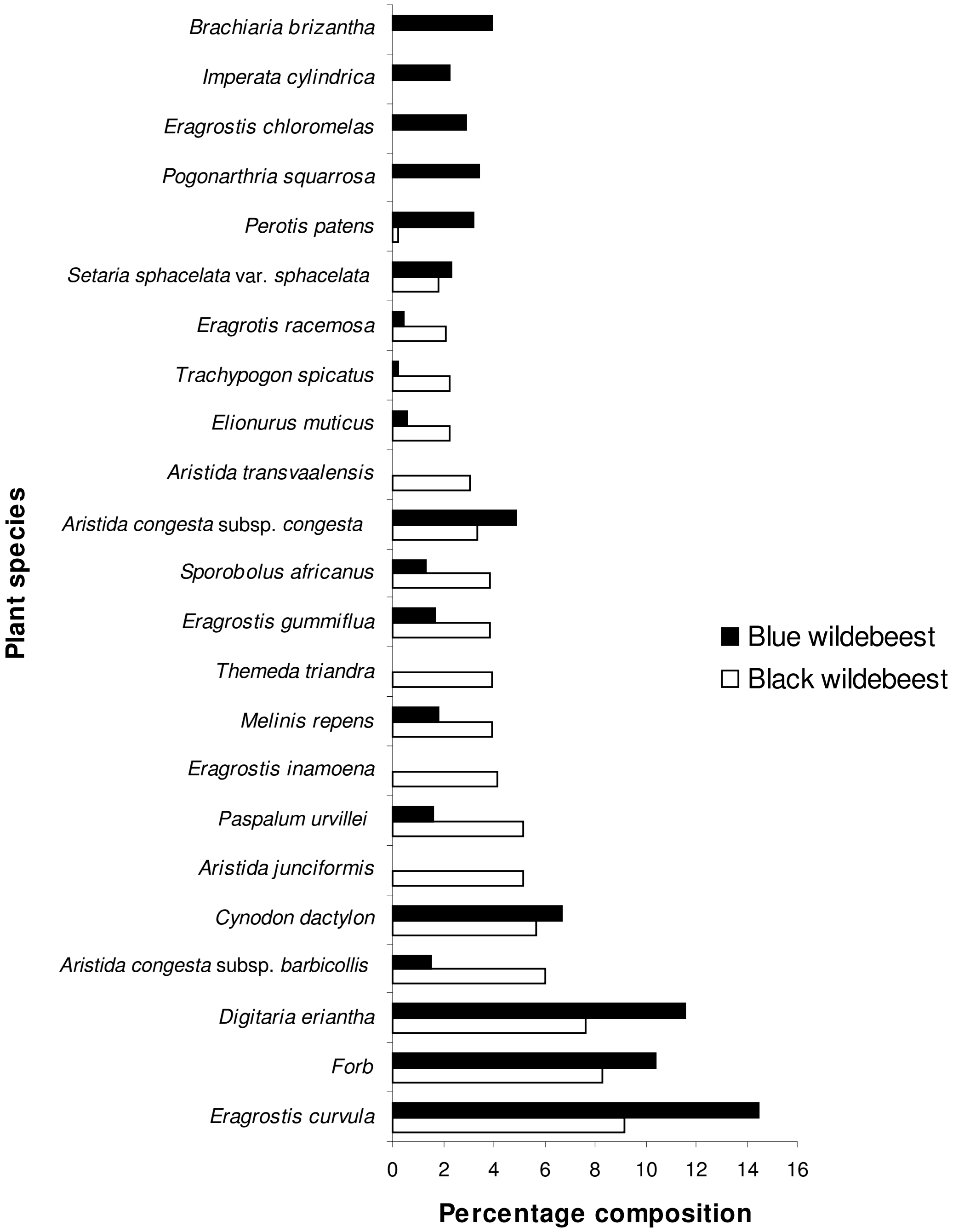


Figure 9.2: Species composition at the feeding sites of the black and blue wildebeest at Ezemvelo Nature Reserve for all plant species contributing more than 2% to the overall species composition in the feeding sites sampled in March 2004. Data obtained from vegetation surveys in the feeding sites of the black and blue wildebeest (Chapter 6).

Black wildebeest are smaller than blue wildebeest, both are ruminants with similar mouth morphologies and are selective short grass feeders. The present study has so far indicated that there is a large degree of habitat and dietary overlap and spatial separation is high. In addition it appears that the black wildebeest population in the study area has been decreasing over the last 3 years (2003 to 2005), while the blue wildebeest population has increased in density over the same time period. Does the above information indicate the presence of sufficient ecological separation between the two types of wildebeest to reduce competition to such an extent that they can coexist successfully when confined together? The response of two ecologically similar types of wildlife to habitat heterogeneity through time and space may be adequately dissimilar to result in an overall shift in trophic position (Cordon and Brink 2006). Therefore, the answer to the question posed would depend on the heterogeneity of the habitat in which the two types of wildebeest are confined and whether that habitat is able to cater for the specific requirements that separate the two types of wildebeest.

The two types of wildebeest may be able to tolerate greater levels of ecological overlap in more diverse or richer habitats (Dunbar 1978) as such habitats would have more niches available for exploitation that could allow for their coexistence even if most of those niches are utilised by both types of wildebeest. In richer habitats there will always be some niche that could be utilised by one type but not by the other.

Had black and blue wildebeest evolved sympatrically, they may have been expected to have diverged or occupied different niches at such an extent that they were able to coexist. However, being brought together recently, their similarity may be testing the limits of coexistence (Bryce *et al.* 2002), especially in areas with low habitat heterogeneity.

Codron and Brink (In press) conclude that since trophic partitioning is an important mechanism allowing sympatric species to avoid competition, it is anticipated that a trophic shift would have accompanied the divergence of the black from the blue wildebeest. However, as has been stated previously trophic adaptation between the black and blue wildebeest do not differ. Therefore it is thought that the two types of wildebeest may have been able to co-exist in some areas by temporally shifting their feeding niches over short time scales (Brink *et al.* 1999; Codron and Brink In press).

Studies of niche overlap and ecological separation amongst coexisting shrews concluded that body size has an important role in effecting ecological separation in multi-species communities where a high degree of morphological and ecological similarity occurs between members (Churchfield *et al.* 1999). Black wildebeest are smaller than blue wildebeest and therefore would be expected to require a higher energy diet due to increases in metabolic rate (Codron and Brink In press). This has been disproven and studies have shown that the feeding ecology of the black wildebeest is not dissimilar to the blue wildebeest.

Black wildebeest evolved in the high-lying open treeless grasslands of South Africa, while the blue wildebeest evolved in the savannas of the low-lying portions of southern Africa. Therefore, from their evolutionary histories, it may be expected that the black and blue wildebeest would have different habitat preferences. Both types of wildebeest are selective grazers of short grass and therefore it would be expected that they would utilise the grass species that are available in a similar way. The black wildebeest has a dark, thick coat which is adapted to continual exposure to full sun, while the blue wildebeest has a thin, dark pelage that is less adapted to sun exposure. Hence the blue wildebeest will seek shade when it is available. Therefore, these physiological differences indicate that there may be differences in the way in which the two types of wildebeest distribute their activities during the daytime and that would influence the temporal distribution of their active periods.

Niche breadth indices based on habitat type (Table 9.1) indicated that the blue wildebeest had more generalist habitat associations than the black wildebeest. The more detailed analyses of habitat selection incorporating the various abiotic and biotic factors of the habitat also suggested that, at the spatial scales considered in the present study, blue wildebeest showed fewer preferences than black wildebeest. Although the two types of wildebeest showed different preferences in their habitat use, their use of the habitat types and factors showed considerable overlap. At the time of the present study the spatial overlap between the two types of wildebeest was low. However, there was an indication that the blue wildebeest bulls were moving into the areas that were traditionally occupied by the black wildebeest, at least during periods of the year when the heat load was not as high, therefore allowing the blue wildebeest to venture into areas where shade was not in the near vicinity.

Table 9.4 summarises the indices of overlap and quotients of similarity calculated in the present study. The indices of niche overlap that were found in the present study indicated that the overlap in spatial distribution was low for the entire study period (14%) but was lowest during the dormant season (8%). This critical season was when food shortage may play the greatest role. Black wildebeest may be able to maintain themselves in their chosen habitats, but the invading blue wildebeest may be unable to maintain their body weight in these areas. Such areas may also be too exposed to the cold during the dormant season and thus also make them unsuitable for the blue wildebeest. Since only the blue wildebeest encroaches on the black wildebeest habitats, it is the blue wildebeest that are the cause of the observed spatial overlap. The reasons why the blue wildebeest bulls have been entering this habitat need to be elucidated. Possible explanations include that it is only bachelors with no territory that have been forced out of the preferred blue wildebeest habitat into the black wildebeest habitat; or that the sex ratio of the blue wildebeest is skewed and hence blue wildebeest bulls are seeking potential territories in other habitats; or that the population size of the blue wildebeest has outgrown its preferred habitat and hence is expanding into less favourable habitat. The highest spatial overlap is during the early growing season. This is the season when the calves are born and fresh grass is sprouting after the first rains.

Spatial segregation is less at finer spatial scales than that of broad habitat types. If competition is a strong structuring force, then a non-random spatial distribution can be expected (Hofer *et al.* 2004). The spatial overlap in the present study was lower than expected by chance. This could be as a result of interspecific competition for similar resources, and the result of this reduction of spatial overlap would decrease the intensity of competition (Hofer *et al.* 2004).

Overall, indices of niche breadth indicate that black and blue wildebeest habitat resources were likely to be very similar at the study area and the overlap indices indicated that the two types of wildebeest overlapped considerably in terms of habitat choices. Regardless of the scale, the extent of overlap was considerable and greater than the 0.5 proposed by Levins (1968) to prohibit coexistence.

Table 9.4: Summary of the indices of overlap and quotients of similarity in spatial distributions, habitat type selection and diet between black and blue wildebeest at Ezemvelo Nature Reserve from January 2004 to August 2005. Table adapted from Anthony and Smith (1977). (QS is the quotient of similarity)

Season	Spatial overlap (S)	QS for shared areas of occupation	Habitat type selection (H)	QS for shared habitat types	Diet overlap (F)	QS for shared plant species in diet
Late growing season	0.11	0.23	0.77	0.89	0.55	-
Dormant season	0.08	0.21	0.89	0.89	0.55	-
Early growing season	0.13	0.27	0.94	0.89	0.55	-
Seasonal mean	0.11	0.24	0.86	0.89	0.55	0.88

The indices utilised to calculate niche breadth and overlap in the present study may have reduced biological interpretability and their suitability as a foundation for discussion of resource utilization strategies, competition, and species packing (Hurlbert 1978). An index and its interpretation depends on a number of factors as listed by (Hurlburt *op. cit.)* as: how the resource states were defined: whether they are arbitrary units or discrete natural entities; and whether or not empty resource states are excluded from the analysis. Overlap indices often fail as measures of competition and this needs to be taken into consideration when interpreting the results of the present study.

Comparing these results with the results of the logistic analysis, which separated the habitats of the black and blue wildebeest (Chapter 7), it is possible to conclude that habitat differentiation and spatial differentiation between the two types of wildebeest provide the main mechanism for coexistence at Ezemvelo Nature Reserve and trophic differences play little or no role.

The black and blue wildebeest need to differ on one dimension for ecological separation to occur. This dimension was found to be the habitat factor dimension of distance to shade. The tools required to measure this dimension properly may not have been applied correctly in the present study and hence further detailed analysis of this dimension is required.

CONCLUSION

Although black wildebeest are more selective than blue wildebeest, resource partitioning between the two types of wildebeest was found to be incomplete. Considerable overlap in the use of key resources such as habitats and possible food species, but little overlap in spatial distribution and temporal activities was found. Overlap in resource use tended to be lowest during the dormant season when food resources were most limiting. The results of the present study indicated that exploitative competition was being avoided at the current population levels at Ezemvelo Nature through the partitioning of mutually exclusive resources such as woody vegetation cover and altitude and space. This partitioning was relaxed during the late growing and early growing seasons when the food resources were less limiting than during the dormant season.

CHAPTER 10: BEHAVIOURAL INTERACTIONS, SPECIES ASSOCIATIONS AND INTERSPECIFIC INTERFERENCE COMPETITION

INTRODUCTION

Interactions with other species may indicate facilitative or competitive behaviour between individuals (Arsenault and Owen-Smith 2002). An investigation into the interspecific behaviour of coexisting black and blue wildebeest may reveal evidence of interference which may further indicate that competition could play a role in the continued existence or decline of one or both of the two types of wildebeest at Ezemvelo Nature Reserve. Instances of both intolerance and mutual tolerance and their evaluation in terms of random expectation may help in revealing such competition (Krämer 1973). Avoidance behaviour may allow antagonistic species to coexist in common habitats without stressful interactions (Anthony and Smith 1977). Observations of interspecific behaviour are expected to reveal interspecific dominance if present (Krämer 1973) and to shed some light on the question of hybridisation between the black and blue wildebeest.

Evidence for intolerance or mutual tolerance of the two types of wildebeest has not been investigated. Only anecdotal reports of associations between black and blue wildebeest are available (Vrahimis 2004 pers. comm.)[13].

It has already been found that spatial overlap between the black and blue wildebeest at Ezemvelo Nature Reserve is low (11%) (Chapter 9). Overlap occurred where blue wildebeest bulls have entered the preferred areas of the black wildebeest during times of high food abundance. No cases of black wildebeest entering blue wildebeest areas were observed. It was hypothesised that interference competition would be evident between the two types of wildebeest

The objectives of this part of the present study were therefore to:

- Investigate the interspecific behaviour of the coexisting black and blue wildebeest at Ezemvelo Nature Reserve for evidence of interference competition
- Determine the associations of each type of wildebeest with other wildlife species present within the study area.

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METHODS

Behavioural interactions

When black and blue wildebeest were located within 45 m of each other in the present study, notes were taken on any behavioural interactions between the two types of wildebeest. Behavioural interactions between black and blue wildebeest were evaluated in only those encounters in which individuals or groups of individuals of the two types of wildebeest came close enough for antagonism or avoidance to be displayed by either type (Anthony and Smith 1977). Passive dominance refers to those situations in which one type of wildebeest was dominant but no overt aggression was observed. Active dominance refers to those situations in which one type of wildebeest was dominant by way of overt aggression. Overt aggression was displayed by horning and other territorial displays as described by Von Richter (1971a) and Estes (1969). In addition, in the habitat surveys (Chapter 4), whenever a wildebeest was located, any association with other species was also recorded if the two involved were within 100 m of each other.

Temporal activity overlap

The diurnal distribution of activity (grazing and walking) data obtained during the activity budget surveys (Chapter 8) was used to determine the likelihood of mutual interference among the two types of wildebeest by averaging the conjoint probabilities of being active at the same time across the hours of the day as was described by Dunbar (1978).

Species associations

The Chi-squared goodness of fit was used to statistically compare species associations of the two types of wildebeest and the number of individuals of each species present on the reserve (Thomas and Taylor 1990; Manly *et al.* 1993). Expected frequencies were calculated from the available proportions of types of wildlife obtained from the counts conducted within the study area. If the Chi-squared test was found to be significant, the null hypothesis that all the associations were in proportion to the number of individuals of the associated species on the reserve (no selection) was rejected. Subsequently, the cell Chi-squared values for each species category were calculated. If these were significant the difference between the observed and expected values was examined. If the observed value was greater than the expected value, a positive association with that species was concluded. If the expected value was more than the observed value, it was concluded that that species category was avoided by the relevant type of wildebeest.

RESULTS

Behavioural interactions

Encounters between the two types of wildebeest were most frequent during the rutting season (30%) (Table 10.1). In 49% of the encounters between black and blue wildebeest, dominance could not be determined. When dominance could be determined (51% of the encounters), blue wildebeest were dominant in all but one encounter. Dominance of the blue wildebeest over the black wildebeest did not appear to depend upon the sex or group composition of either species (Table 10.1). The dominance of blue wildebeest over black wildebeest was displayed mostly by passive mechanisms (68%) and occasionally by active mechanisms (32%). Passive dominance usually occurred when the two types of wildebeest were grazing together.

Temporal activity overlap

The diurnal distribution of activity (grazing and walking) for the overall data and by season is shown in Figures 10.1 and 10.2. The mean conjoint probability that black and blue wildebeest will be active at the same time during the day was 0.225 for all the data, 0.170 for the late growing season, 0.229 for the dormant season and 0.283 for the early growing season. These results indicated that the likelihood of interference between the black and blue wildebeest when feeding was low and that direct competition for forage was thus relatively unlikely. Black wildebeest tended to concentrate their active periods during the early mornings and the late afternoons. Additional observations have indicated that the black wildebeest was more active at night than the blue wildebeest, which may allow for further separation in the active period of each type of wildebeest. Blue wildebeest were much more likely to be active over the midday period (12:00 to 14:00) than the black wildebeest.

Table 10.1: Summary of the behavioural interactions between the black and blue wildebeest at Ezemvelo Nature Reserve as recorded from April 2004 to August 2005. M = males; F = females; C = calves

Date	Black wildebeest	Blue wildebeest	Dominant species	Type of dominance
21/04/2004	1M, 8F, 2C	1M	Blue wildebeest	Passive
26/04/2004	5M	1M	Blue wildebeest	Passive
27/04/2004	9M	1M	Not determined	
20/07/2004	1M	1M, 20 F, 6 C	Blue Wildebeest	Passive
16/08/2004	5 M	1 M	Blue wildebeest	Passive
17/08/2004	1 M, 25 F, 6 C	1 M	Not determined	
20/08/2004	1 M	1 M	Not determined	
21/08/2004	4 M, 25 F, 5 C	1M	Blue wildebeest	Active
03/09/2004	1M, 7F, 2C	1M	Black wildebeest	Active
05/09/2004	4M	1M	Not determined	
16/09/2004	2M	1M	Blue wildebeest	Passive
21/09/2004	9 M	1M	Blue wildebeest	Active
30/09/2004	1M, 16F, 3C	1M	Not determined	
26/10/2004	1M	1M, 16F, 7C	Blue wildebeest	Passive
10/11/2004	1M	1M	Blue wildebeest	Passive
13/11/2004	1M, 9 F, 1C	1M	Blue wildebeest	Passive
04/01/2005	2M, 1F, 1C	1M	Not determined	
04/01/2005	1M	1M	Blue wildebeest	Passive
10/01/2005	1M, 28F, 7C	1M	Not determined	
11/01/2005	2M, 1F	1M	Not determined	
13/01/2005	2M, 9F, 3C	1M	Not determined	
02/02/2005	1M, 18F, 3C	1M	Not determined	
25/02/2005	1M	1M	Blue wildebeest	Passive
01/03/2005	1M	1M	Blue wildebeest	Passive
15/03/2005	1M, 10 F, 3C	1M	Not determined	
18/03/2005	2M	1M	Blue wildebeest	Passive
15/04/2005	3 M, 1F	1M	Not determined	
18/04/2005	1M	1M	Blue wildebeest	Passive
22/04/2005	1M	1M	Blue wildebeest	Passive
22/04/2005	1M	2M	Not determined	
11/05/2005	1M	1M	Not determined	
23/05/2005	1M, 4F	2M	Not determined	
10/06/2005	3M, 1F	1M	Not determined	
18/06/2005	3M	2M	Not determined	
23/07/2005	2M	2M	Blue wildebeest	Passive
26/08/2006	1M, 7F, 1C	3M	Blue wildebeest	Active
30/08/2006	1M, 7F, 1C	2M	Not determined	

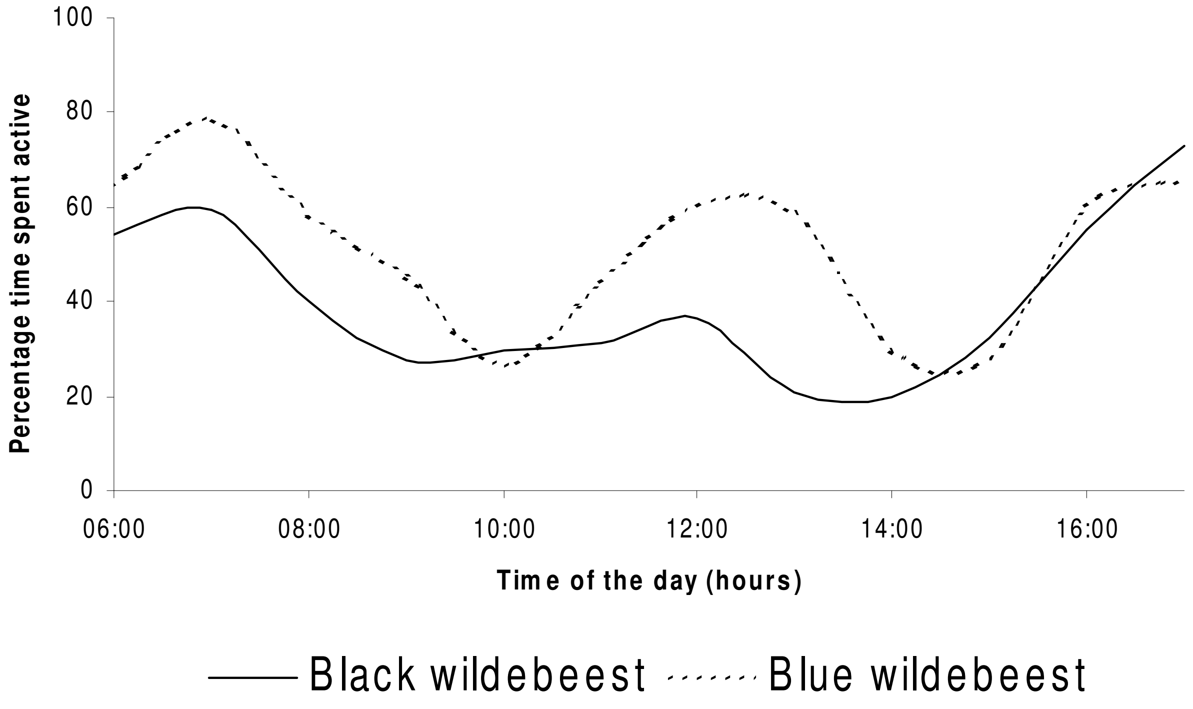

Figure 10.1: Diurnal patterns, expressed as percentage time spent active (grazing and walking), for black and blue wildebeest based on scan samples of activity taken at 5-minute intervals throughout the daytime at Ezemvelo Nature Reserve from March 2004 to August 2005.

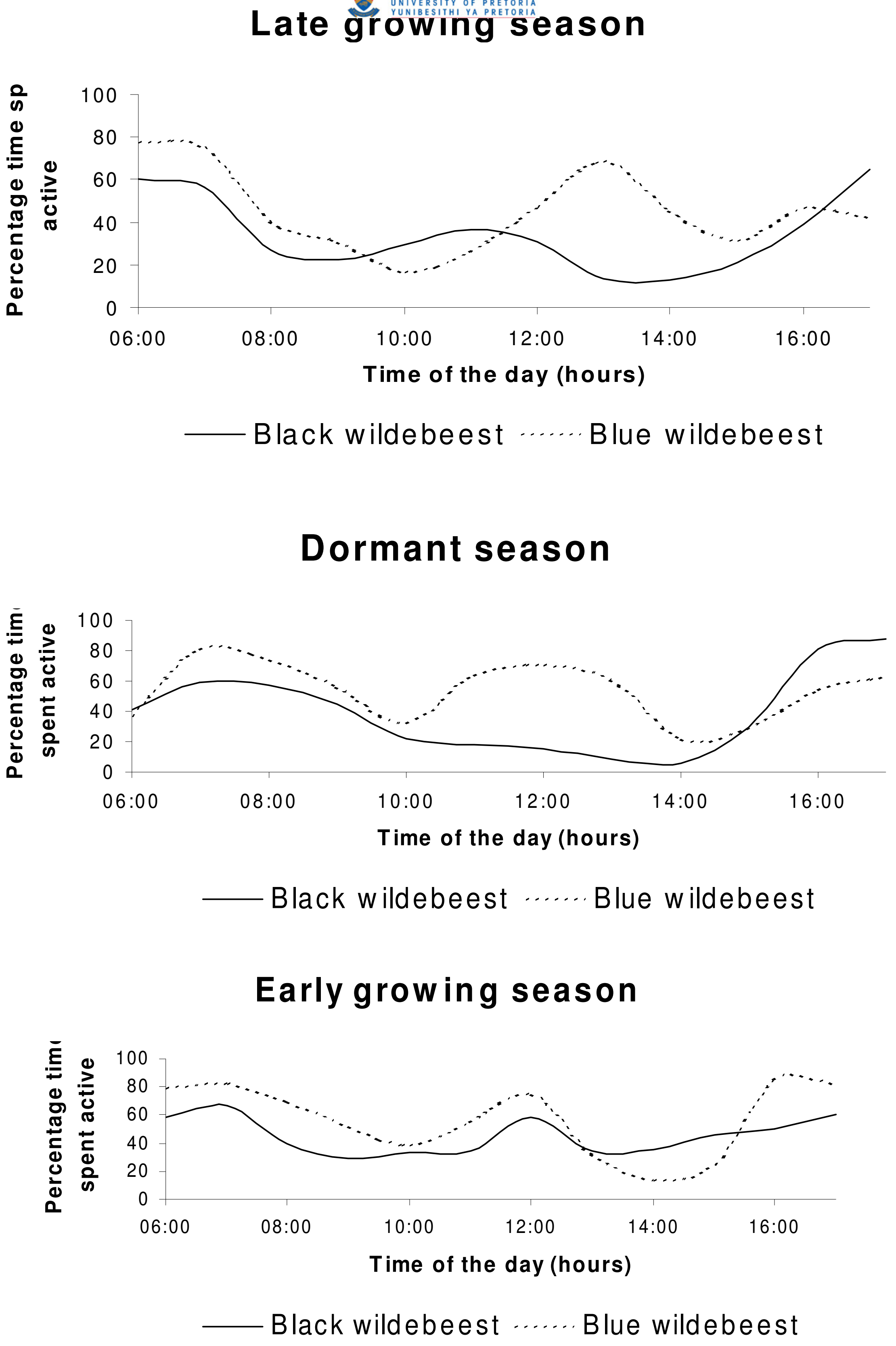

Figure 10.2: Seasonal diurnal patterns, expressed as the percentage of time spent active (grazing and walking), for the black and blue wildebeest based on scan samples of activity taken at 5-minute intervals throughout the daytime at Ezemvelo Nature Reserve from March 2004 to August 2005.

Blue wildebeest were least active around 10:00 in the morning and from 14:00 to 15:00 in the afternoon. Black wildebeest, however, tended to be least active from 09:00 to 14:00.

Species associations

Black wildebeest were observed not to be associated with any other species in 45.3% of the observations while blue wildebeest occurred alone in 61.0% of the observations (Figure 10.3). On those occasions where wildebeest were associated with other species, the black wildebeest was most likely to be associated with the blesbok (28.9%), while the blue wildebeest was most likely to be associated with Burchell's zebra (19.6%). In general blue wildebeest were associated with a wider diversity of species (13) than the black wildebeest (9). No seasonal variations in this pattern were observed (Figure 10.4).

Blue wildebeest were less likely to be associated with black wildebeest than black wildebeest were likey to be associated with blue wildebeest. This is indicated by the result that, of all the blue wildebeest association observations, only 4.2 % were with black wildebeest and of all the black wildebeest association observations, 7.2 % were with blue wildebeest. The results also indicated that either a black or a blue wildebeest was more likely to associate with the other type of wildebeest (i.e. a black wildebeest was more likely to associate with a bluek wildebeest or a blue wildebeest was more likely to be associated with a black wildebeest), than with the greater kudu, common eland, gemsbok *Oryx gazella*, ostrich, springbok *Antidorcas marsupialis*, waterbuck, common warthog *Phacochoerus africanus*, red hartebeest *Alcelaphus buselaphus caama* and impala. This observation is most likely due to different habitat choices of these wildlife and due to the varying number of individuals of these species available for association.

The Chi-squared tests indicated that black wildebeest were associated with blesbok to a much higher degree than what was expected (Table 10.2). The results also indicated that black wildebeest were associated with the common warthog, Burchell's zebra, impala and red hartebeest to a much lesser extent than what was expected. Blue wildebeest tended to associate with Burchell's zebra to a much greater extent than what was expected, and also with the blesbok and interestingly with the black wildebeest. Blue wildebeest tended to avoid most other species.

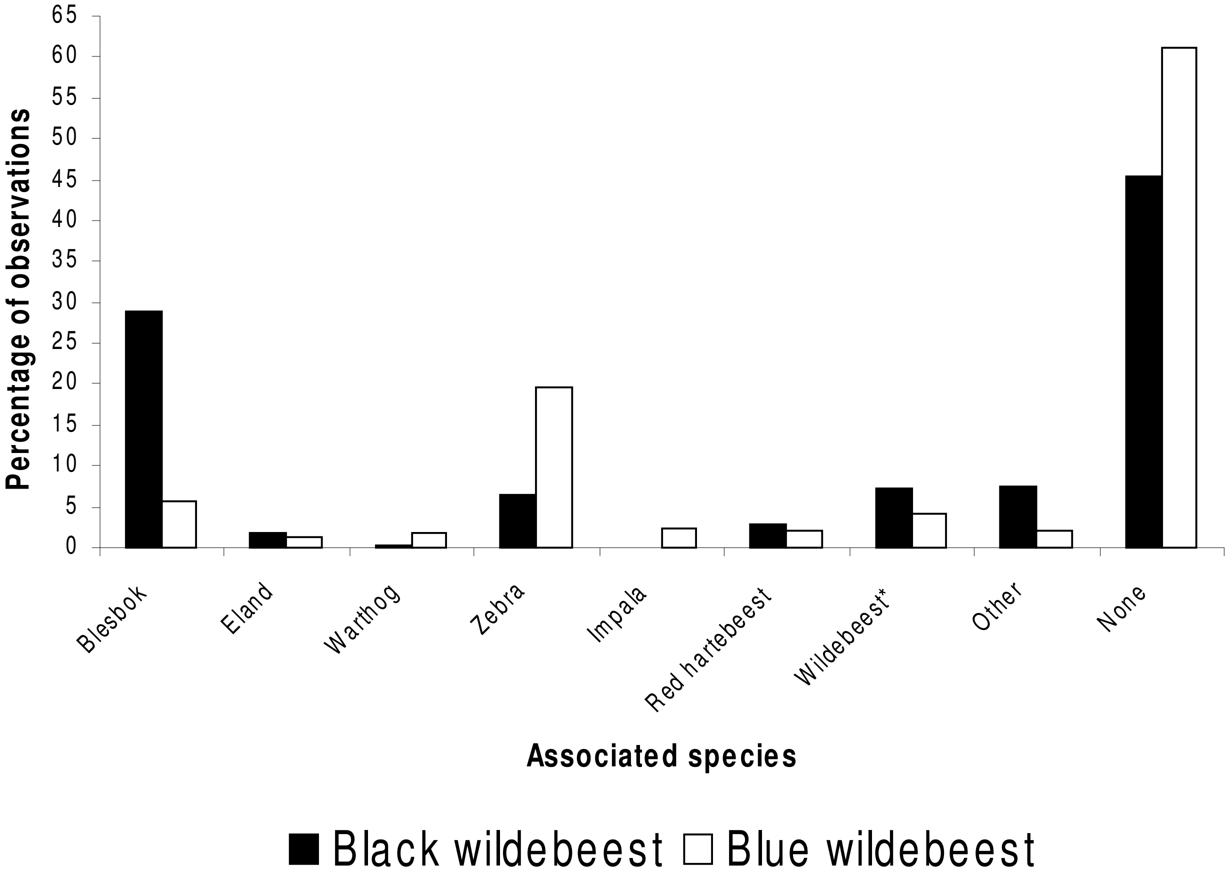

Figure 10.3: The association of the black and blue wildebeest with other types of wildlife at Ezemvelo Nature Reserve as observed from January 2004 to August 2005. * Indicates a black or blue wildebeest depending on the type of wildebeest under analysis. (Eland = common eland; warthog = common warthog; zebra = Burchell's zebra).

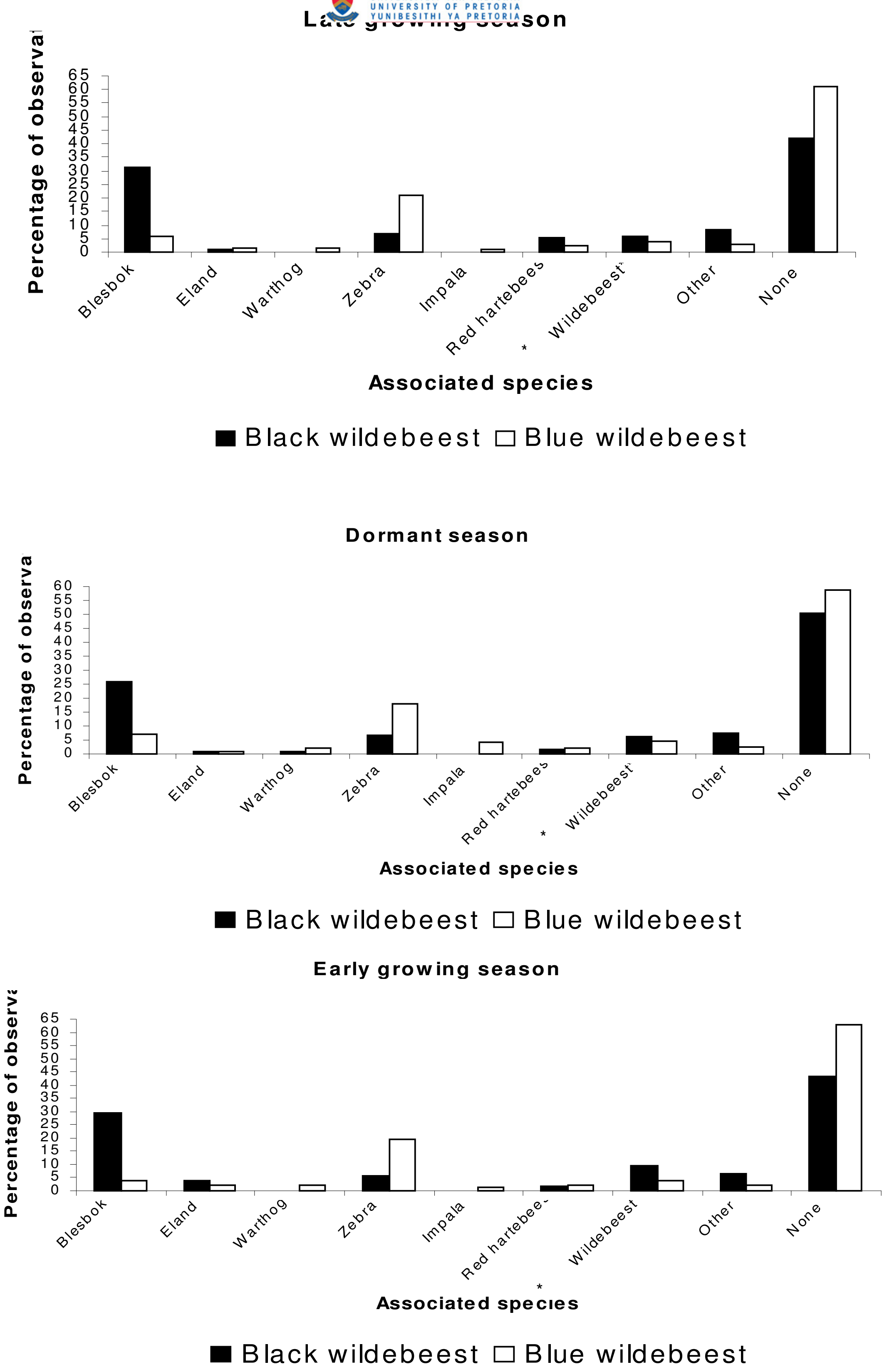

Figure 10.4: The association of the black and blue wildebeest with other types of wildlife at Ezemvelo Nature Reserve for the three ecological seasons as observed from January 2004 to August 2005. * Indicates black or blue wildebeest depending on the type of wildebeest under analysis. (Eland = common eland; warthog = common warthog; zebra = Burchell's zebra).

Minimal seasonal differences in this pattern were observed and hence seasonal analyses were not repeated here.

DISCUSSION

The dominance of the blue wildebeest over the black wildebeest in many of the interspecific encounters observed throughout the present study was not surprising as the blue wildebeest is almost 1.5 times the size of the black wildebeest (Furstenburg 2002a and b). This size difference may account for the blue wildebeest's dominance in all but one circumstance observed during the present study, but other factors such as age, period of sexual cycle and group composition may also influence dominance in interspecific interactions (Anthony and Smith 1977).

Many encounters between black and blue wildebeest involved either a single blue wildebeest bull with a female herd of black wildebeest, or a number of blue wildebeest bulls with a number of black wildebeest bulls (Table 10.1). It appears that the blue wildebeest tends to be the instigators of such interspecific encounters.

Competitive interference is operative only if it affects one or both species by their exclusion from an area or by detrimental behavioural interactions (Miller 1967). No evidence of either of these effects could be found on Ezemvelo Nature Reserve.

The extent to which population densities and species ratios affected the results of this analysis remains undetermined. However, it can tentatively be concluded that interference competition appears not to play a significant role in the association between the black and blue wildebeest at Ezemvelo Nature Reserve.

Blue wildebeest tended to be associated with Burchell's zebra, a roughage and bulk grass feeder, which accepts both tall and short grasses and does not have a patch-selective feeding style (Bothma *et al*. 2002). Blue wildebeest themselves are selective grazers who prefer short grass and have a patch-selective feeding style as do black wildebeest (Bothma *et al*. 2002). Black wildebeest were associated with the blesbok on many occasions, also a selective grazer, which prefers short grass and has a patch selective feeding style. These differences in the species associations may be indicative of differences in the degrees to which black and blue wildebeest are able to tolerate areas with tall bunch grasses.

Table 10.2: Summary of the Chi-squared tests performed to evaluate the hypothesis that black and blue wildebeest at Ezemvelo Nature Reserve associated with other species in proportion to their occurrence. Values in brackets indicate association frequencies of <5 and therefore the Chi-squared test may not be valid. + indicates a positive selection, 0 indicates random selection, - indicates a negative selection

		Late growing season			Dormant season			Early growing season			Overall		
Type of wildebeest	Species	Chi-square	df	Selection	Chi-square	df	Selection	Chi-square	df	Selection	Chi-square	df	Selection
Black wildebeest	Blesbok	179.60	1	+	139.61	1	+	151.14	1	+	470.19	1	+
	Common eland	(2.39)	1	0	(1.74)	1	0	0.40	1	0	1.68	1	0
	Common warthog	(3.87)	1	-	(1.54)	1	0	(3.53)	1	0	(8.74)	1	-
	Burchell's zebra	9.16	1	-	5.89	1	-	9.89	1	-	24.76	1	-
	Impala	(7.96)	1	-	(6.64)	1	-	(7.25)	1	-	(21.85)	1	-
	Red hartebeest	0.009	1	0	(2.70)	1	0	(3.20)	1	0	3.97	1	-
	Wildebeest*	0.86	1	0	0.17	1	0	0.36	1	0	0.19	1	0
	Other	0.32	1	0	0.07	1	0	1.27	1	0	1.29	1	0
Blue wildebeest	Blesbok	7.10	1	+	16.72	1	+	0.73	1	0	20.36	1	+
	Common eland	1.72	1	0	(4.64)	1	-	0.00	1	0	4.23	1	-
	Common warthog	1.24	1	0	0.00	1	0	0.05	1	0	0.23	1	0
	Burchell's zebra	26.95	1	+	9.12	1	+	21.70	1	+	55.51	1	+
	Impala	(9.60)	1	-	0.07	1	0	6.73	1	-	10.29	1	-
	Red hartebeest	2.04	1	0	2.86	1	0	1.96	1	0	6.72	1	-
	Wildebeest*	6.22	1	+	9.74	1	+	8.49	1	+	24.57	1	+
	Other	20.48	1	-	25.21	1	-	21.48	1	-	71.23	1	-

* Indicates one of the two types of wildebeest depending on which comparison is involved

Black wildebeest occurred in areas on the reserve that were not favoured by Burchell's zebra. Burchell's zebra therefore occurred in similar habitats to the blue wildebeest and thus they may facilitate the feeding behaviour of blue wildebeest by reducing the height of the grass layer in areas that may not seem suitable for a patch-selective grazer (Bell 1970; McNaughton 1976). Therefore, the close association of the blue wildebeest and Burchell's zebra may be facilitative rather than competitive. In contrast, the close association between the black wildebeest and blesbok, often seen grazing selectively on the same patch within a bunch grass community, may be a competitive one. Black wildebeest and blesbok have both evolved similar feeding styles and similar tolerances for open habitats and thus competition between the two species may be high (Skinner and Chimimba 2005).

It is clear that the social behaviour of wildebeest, especially the habit of male blue wildebeest to associate with animals of other species, predisposes them to opportunities of hybridisation when confined with black wildebeest (Vrahimis 2003a). Of all the blue wildebeest observations where an association with another wildlife species was recorded, 40% of these were of a lone territorial bull. Of all recorded cases it appears that disruption of the normal demographic or social structure was involved, as was seen at the Spioenkop Nature Reserve in 1995 (Langley 1995). At Ezemvelo Nature Reserve there has not been any disruption of the normal demographic or social structure of the black or blue wildebeest. However, lone blue wildebeest bulls are in excess (26% of the blue wildebeest population) (Chapter 12). These bulls tend to be forced into less favourable habitats by the breeding territorial bulls, especially during the rutting season (Von Richter 1971a). This will cause increased encounters between these bulls and the black wildebeest herds. During the rut, these bulls may find themselves in a suitable position to mate with the black wildebeest females since the black wildebeest males would either be too small to fend them off, or too few to prevent mating from occurring. The large number of lone blue wildebeest bulls at Ezemvelo Nature Reserve is an indication that all the suitable territories have been occupied. From this it can be inferred that the maximum stocking density for blue wildebeest has been attained or exceeded. These lone bulls relegated to unfavourable habitats may interfere with the social structure of the black wildebeest. These bulls have to be removed from the black wildebeest habitat on an annual basis to ensure that hybridisation does not take place.

It is believed that hybridisation only occurs under artificial conditions, where the two species are forced together in a confined area (Vrahimis 2003a). This may become the situation at Ezemvelo Nature Reserve if the population size of the blue wildebeest is allowed to increase beyond acceptable levels.

It was already stated in Chapter 3 of the present study that it was currently thought that the only way to ensure that hybridisation between the black and blue wildebeest does not occur, was to prevent any contact between the two types. This was because conservationists and scientists could not clearly identify the factors that resulted in hybridisation. It was suggested that in order to identify these factors, an understanding of the ecological and behavioural differences between the two types of wildebeest needed to be attained.

The present study has gone some way towards reaching an understanding of these differences and has shown that the ecological requirements of the black and blue wildebeest differ to such an extent that the chances of the two types of wildebeest cross-breeding is reduced. This is, however, dependent on the population sizes of the wildebeest present in an area, the level of habitat heterogeneity available, and in providing a mixture of open grassland and savanna as habitat. The underlying premise for this conclusion is that the two types of wildebeest are ecologically separated and pose little threat of crossbreeding under natural conditions.

CONCLUSIONS

The present study has indicated that there was little evidence for interference competition between the black and blue wildebeest at Ezemvelo Nature Reserve. Black wildebeest were most commonly associated with a possible competitor, the blesbok, while the blue wildebeest was most commonly associated with a possible facilitator, Burchell’s zebra. In the future, the threat of hybridisation between the black and blue wildebeest at Ezemvelo Nature Reserve could increase unless the population size of the blue wildebeest is reduced and blue wildebeest lone bulls are removed from the black wildebeest core habitats.

CHAPTER 11: GRAZING CAPACITY AND STOCKING DENSITY

INTRODUCTION

To develop an effective grazing management policy for wildlife on a reserve, detailed information on the veld condition, grazing capacity and the response of plant species to grazing pressure is required (Bredenkamp and Theron 1978). This information provides a basis for the calculation of recommended stocking densities for an area. The ecological capacity of an area is the potential of that area to support herbivores through grazing and/or browsing over an extended period without the deterioration of the ecosystem (Bothma *et al*. 2004). It is a characteristic of the entire habitat of which the vegetation, herbivores and their predators all form a part.

Grazing capacity and browsing capacity are used to determine the stocking density for a wildlife ranch or nature reserve. Stocking density is an important management aspect on any reserve and relies on reliable predictions of the grazing and browsing capacities of the specific area under investigation (Vorster 1999). The stocking density is an estimate of an allowable land to animal relationship which would provide the most beneficial returns in terms of a given management objective.

The ecological capacity is a product of the quantity and quality of the natural resources present, while the stocking density is based on personal preference and the objectives of an area (Von Holdt 1999). The stocking density should, however, never exceed the ecological capacity (Bothma *et al*. 2004) and should preferably be conservative to allow for variable rainfall conditions and changes in the quality and quantity of the natural resources in an area during the critical time of the year.

Veld condition assessments should thus be conducted on a regular basis to evaluate the vegetation’s response to current management practices such as the stocking density (Donaldson and Vorster 1989; Trollope 1990). Management practices can then be adapted, if necessary, according to the observed trends in the different plant communities.

Animal-plant interactions in terms of habitat preference, grazing ecology and the feeding category of a specific herbivore species, play an important role in the setting of appropriate stocking densities. Some herbivores posses the ability to change vegetation in order to provide in their specific habitat needs (Van Rooyen 2002).

Specific animals prefer specific types and structures of vegetation. These preferences usually correlate with the various anatomical adaptations of a herbivore species, which enables it to optimally utilise the preferred stratum or structure of a vegetation type. The feeding habit of one animal can change the vegetation to such an extent that it is more suitable for another herbivore species with different feeding requirements and preferences (Van Rooyen 2002).

To ensure the continued survival and coexistence of the black and blue wildebeest at Ezemvelo Nature Reserve it was necessary to determine the quality and quantity of grazing available to the grazers at Ezemvelo Nature Reserve. The aims of this study were therefore to determine the potential grazing capacity and hence to see whether the current stocking density in the study area was optimal or whether it was overstocked. It was hypothesised that Ezemvelo Nature Reserve was overstocked in terms of the number of grazing wildlife present.

The objectives of this study were:

- To quantify the frequency of occurrence of the different ecological classes of the grasses present in order to compile a veld condition index for every habitat type
- To use the data from the veld condition index to calculate a realistic prediction of the grazing capacity for every habitat type
- To determine the potential black and blue wildebeest stocking density at Ezemvelo Nature Reserve based on the grazing capacity, veld condition and stocking density of the present wildlife in the reserve during a year with a mean or near mean rainfall.

METHODS

Veld-condition assessment

A veld condition index was calculated according to procedures laid out by Bothma *et al.* (2004). To determine the percentage of occurrence of each grass species in the herbaceous layer for each habitat type, the step–point technique as described by Donaldson and Vorster (1989) and Vorster (1982) was used. At each site a transect consisting of two parallel lines of 200 m long and 20 m apart along a north to south direction were surveyed. At every second pace, the end of a measuring staff was grounded and the grass plant that was nearest to the point was identified. If no herbaceous plant occurred within 0.5 m of the step-point, the point was classified as bare soil. The grass species were grouped into five ecological classes as described by Bothma *et al*. (2004) and as repeated in Chapter 5. All non-grassy herbaceous species were classified as forbs. These classes were based on a subjective assessment of the grazing value, phytomass production and palatability and response to grazing of each grass species (Bothma *et al.* 2004).

A total of 102 step–point surveys were conducted throughout the five habitat types that were available to the black and blue wildebeest at Ezemvelo Nature Reserve in order to get a reliable estimation of the relative frequency of the different grass species and the cover of the herbaceous layer. These habitat types covered a large proportion of the reserve and most of the other wildlife present utilised these five habitat types almost exclusively. The remaining areas on the reserve were inaccessible to most types of wildlife accept for perhaps the greater kudu, due to steep slopes and dense vegetation.

Once every grass species was allocated to a specific ecological status class, the total percentage frequency for every ecological class in each sample plot could be calculated from data collected during the step–point survey. This percentage was multiplied by the grazing value of that specific ecological class. These weighted constants were 10 for class 1, 7 for class 2, 5 for class 3, 4 for class 4, 1 for class 5 and 0 for bare soil (Bothma *et al.* 2004). When added, the sum of all the values calculated for every ecological class gave a veld condition score with a maximum value of 1000.

The veld condition score was converted to a veld condition index by expressing it as a percentage of the maximum score. Veld condition indices can be interpreted as follows (Bothma *et al.* 2004):

- <40% - veld in an extremely poor condition
- 40–59% - veld in a poor to moderate condition
- 60–80% - veld in a good condition
- >80% - veld in an excellent condition

Grazing capacity

Grazing capacity refers to the production potential of veld and was originally defined as the area of veld needed to sustain a livestock unit for a year in a good productive condition without being detrimental to the vegetation (Fourie *et al*. 1985). Grazing capacity can therefore be expressed either as hectare per Large Stock Unit (LSU), or as Large Stock Units per hectare. In the past this concept was also applied in wildlife ranching (Bothma *et al*. 2004).

Recently, grazing capacity for wildlife has been redefined by Bothma *et al.* (2004) for better application in wildlife ranching. The concept reflects the ecological production potential of the grazeable portion of a homogeneous vegetation unit. Grazing capacity for wildlife is expressed as the area of land (hectares) that is required to maintain a single Grazer Unit over an extended number of years without deterioration to the vegetation or soil. A Grazer Unit refers to a blue wildebeest with a mass of 180 kg. The grazing capacity for wildlife is expressed as the number of Grazer Units per 100 hectares.

The ecological capacity for herbivores of a habitat generally refers to the maximum number of grazers that the given habitat can sustain (Bothma *et al.* 2004). When stocked at ecological capacity, neither the animals nor the vegetation on an area will be in a particular good condition (Behnke and Scoones 1993). Therefore, it is often reduced by 20 to 30% to achieve an economic grazing capacity (Bothma *et al*. 2004).

The equation as used in the present study to calculate grazer units is based on the relationship between the recent and mean annual rainfall, veld condition, percentage grass cover, habitat accessibility and the influence of fire on plant production and is described as follows (Bothma *et al*. 2004):

$$\text{Grazer Units per 100 ha} = 0.547 * [(c+(r-500) * 0.23 * a * f * (\log (g)-1)^{0.4}]$$

c = veld condition index
r = rainfall over the past two years at the site (mm)
g = percentage grass cover
a = accessibility of habitat to plains wildlife on a scale of 0.1 to 1, with 0.1 = totally inaccessible and 1 = totally accessible
f = fire factor on a scale of 0.8 to 1, with 1 = absence of fire

500 = mean annual rainfall (mm) for the larger region based on long-term means for the rocky highveld grassland vegetation type (Low and Rebelo 1996).

A mean annual rainfall of 675 mm was used for Ezemvelo Nature Reserve in the calculation. The accessibility of the habitat to plains wildlife was taken as 1 on the scale as explained above for basically all the terrain described by the five habitat types identified to be available to both types of wildebeest on Ezemvelo Nature Reserve is accessible for all wildlife. Since fire has been excluded from most habitats for more than 3 years on Ezemvelo Nature Reserve, the fire factor (f) was set at 1 for the sandy grasslands, old lands and moist grasslands. An accidental fire passed through a large proportion of the rocky grasslands and *Burkea* woodlands in late 2004 and hence the fire factor was set at 0.8 for these two habitat types

Stocking density

A preliminary stocking density for the habitat types potentially available to the black and blue wildebeest at Ezemvelo Nature Reserve was calculated from the grazing capacity of the potential wildebeest habitats.

Herbivores were categorised according to their feeding behaviour, into the following categories (Van Hoven 2002):

- Bulk or low selectivity feeders
- Highly selectivity feeders
- Mixed feeders
- Browsers

The feeding category of a specific animal is a good prediction of the ratio of browse:graze in the animal's diet. Bulk feeders mostly graze, whereas browsers feed almost exclusively on leaves, twigs and seedpods of fodder trees. Bulk and browse feeders are the two extremes, with concentrate- and mixed feeders in between. However, the graze:browse ratio varies considerably between species. Therefore, following Bothma *et al.* (2004) the percentage grazing and browsing in the diet was considered and GU equivalents calculated based on the relevant diets to set stocking densities for each type of herbivore.

For productive wildlife ranching the economic grazing capacity for an area is usually set at 70% of the ecological grazing capacity (Bothma *et al.* 2004). Therefore the economic grazing capacity was also calculated for the present study.

For comparison the rainfall method of Coe *et al.* (1976) was applied to calculate the possible large herbivore biomass in kg/m^2 based on a mean annual rainfall of 675 mm for Ezemvelo Nature Reserve utilising the following equation:

Large herbivore biomass (kg/km^2) = 8.684 x mean annual rainfall (mm) – 1205.9

RESULTS

Ecological grazing capacity

All the grass species recorded and identified on Ezemvelo Nature Reserve during the step–point survey were classified into their different ecological classes and listed in Appendix 3.

The characteristics of the five habitat types that were utilised by the black and blue wildebeest at Ezemvelo Nature Reserve have been described in Table 11.1 The veld condition index of each of these habitat types ranged from 31 to 45%, indicating that the overall veld condition at Ezemvelo Nature Reserve was poor. The *Burkea* woodlands had the highest veld condition score (448), while moist grasslands had the lowest veld condition score (313).

According to the rainfall method of Coe *et al.* (1976), a total of 26 GU/100 ha could be supported at Ezemvelo Nature Reserve. This estimate is a first approximation of the ecological capacity of an area for herbivores and does not consider local temporal and spatial variations in the habitats within a specified area (Van Rooyen 2002). Therefore, the ecological grazing capacity was calculated separately for each of the five habitat types available to the wildlife at Ezemvelo Nature Reserve by using the method of Bothma *et al.* 2004. The value obtained was decreased by 30% to provide an economic grazing capacity for Ezemvelo Nature Reserve.

Table 11.1: Veld condition index and ecological grazing capacity calculation in Grazer Units (GU) for Ezemvelo Nature Reserve, a grassland reserve in South Africa, based on the condition of the vegetation in 2004 and calculated by using the methods that were described by Bothma *et al*. 2004

Characteristics	Habitat types				
	SG	RG	OL	MG	BW
Size (ha)	2933	2540	744	658	123
Contribution of the ecological classes[a]					
Class 1	7	19	18	4	26
Class 2	12	19	2	17	3
Class 3	0	0	0	0	0
Class 4	43	17	44	25	32
Class 5	33	22	28	49	37
Bare soil	4	21	6	2	5
Veld condition score (maximum 1000)	363	414	418	313	448
Veld condition index (%)	36.3	41.4	41.8	31.3	44.8
Grass cover (%)	80	60	72	90	83
Mean rainfall (mm/year)	675	675	675	675	675
Topography index of accessibility [b]	1	1	1	1	1
Fire factor [c]	1	0.8	1	1	0.8
Economic grazing capacity at mean annual rainfall:					
GU/100 ha	28.1	22.6	29.6	26.9	25.2
Total GU	825	575	220	177	31

SG = Sandy grasslands, RG = Rocky grasslands, OL = Old lands, MG = Moist grasslands, BW = *Burkea* woodlands

[a] Ecological classes

1. Valuable and palatable tufted or stoloniferous grass species with a high productivity and high grazing value
2. Tufted, perennial grass species with an intermediate productivity and moderate grazing value
3. Tufted, tall perennial grass species with a high productivity but low grazing value
4. Generally unpalatable annual and perennial tufted or stoloniferous grass species with an intermediate productivity and low grazing value
5. Unpalatable annual grass and forb species with an intermediate productivity and low grazing value

[b] Topography index of accessibility: 0.1 = Inaccessible to plains wildlife, 1.0 = fully accessible to plains wildlife

[c] Fire factor: 0.8 = recent fires; 1.0 = No recent fires.

The old lands could therefore support the most Grazer Units per 100 hectares (30 GU/100 ha) of all the habitats available. For all the habitat types available to both types of wildebeest in the study area, a total of 1 823 GU could be supported, giving a mean economic grazing capacity of 27 GU/100 ha for Ezemvelo Nature Reserve (Table 11.1). This value compares well with the recommendation obtained from the rainfall equation suggested by Coe *et al.* (1976).

It was estimated that these five habitat types encompassed 90% of the grazing available in the reserve for utilisation by grazing herbivores. The remaining habitats (rocky slopes and riverine vegetation) that were considered to be inaccessible to the majority of the wildlife on the reserve, consisted mainly of steeply sloping rocky areas covered in shrubs and trees and dense riverine vegetation. These inaccessible were not included in any calculations of the grazing capacity in this part of the present study.

Stocking density

During the study period Ezemvelo Nature Reserve was stocked at 26 GU/ha (1475 GU) (Table 11.2). This figure compares favourably with the economic grazing capacity of 1823 GU for the accessible habitats. The wildlife at Ezemvelo Nature Reserve that utilised the grazing resources were made up of 34% low selectivity feeders, 38% high selectivity feeders and 28% mixed feeders. The Burchell's zebras at Ezemvelo Nature Reserve, which are bulk feeders, utilised 39% of the available grazing capacity. Black wildebeest utilised 4% of the available grazing, while the blue wildebeest utilised 12% of the available grazing in the study area. Therefore black and blue wildebeest combined utilised 16% of the available grazing in the study area.

DISCUSSION

The recommended stocking density of 1 828 GU for Ezemvelo Nature Reserve was an estimate and the veld condition, rainfall and physical condition of the wildlife should be monitored to make fine adjustments through active adaptive management (Bothma *et al*. 2004). This should be repeated yearly. By comparing the actual wildlife numbers present on the reserve with those that are recommended based on the available plant resources, any overstocking observed can be corrected (Bothma *et al*. 2004).

Table 11.2: Estimated current numbers of herbivore grazers after the calving season, and stocking densities calculated for the herbivore grazers at Ezemvelo Nature Reserve for December 2004

Type of wildlife	Number of animals	Grasses in the diet (%)	Mean mass (kg)	Number of grazing animals	Grazer units (GU / animal)	Number of. GU	Percentage of grazing capacity
Low selective grazers							
White rhinoceros	2	100	1727	2	5.5	11	1
Burchell's zebra	583	93	260	542	1.32	716	39
Ostrich	93	80	69	74	0.5	37	2
Total	678					764	42
High selective grazers							
Blesbok	166	90	65	149	0.5	75	4
Blue wildebeest	250	87	180	218	1.0	218	12
Black wildebeest	93	90	160	84	0.8	67	4
Gemsbok	18	75	210	14	1.1	15	1
Red hartebeest	178	75	120	134	0.7	93	5
Waterbuck	62	84	205	52	1.1	57	3
Total	767					525	29
Mixed Feeders							
Springbuck	96	32	37	31	0.3	9	1
Common eland	121	50	460	61	2.0	121	6
Impala	249	45	41	112	0.3	34	2
Common warthog	106	70	30	74	0.3	22	1
Total	572					186	10
All grazing herbivores	2017					1475	81

The vegetation at Ezemvelo Nature Reserve is classified as grassland with Bankenveld areas in the koppies. This means that there will be little browse available to browsers on the reserve, especially during the winter (dormant season) when the trees lose their leaves. The number and type of wildlife that can be supported at Ezemvelo Nature depends on the availability of browse during the dormant season. The present wildlife on the reserve makes up 589 BU, which would require a browsing capacity for the reserve of 8 BU/100ha. The only habitat types that would support this browsing pressure would be the rocky grasslands, *Burkea* woodlands and the rocky slopes and the riverine vegetation habitats, which make up 38% of the surface area of the reserve.

The calculations as stipulated here indicate that Ezemvelo Nature Reserve is presently under-stocked. These values should be examined with caution, as there are large areas within the reserve where the grazing capacity would be considered to be almost zero. There is a large amount of evidence indicating that large portions of the habitat available to the grazing herbivores are not suitable. These include:

- The appearance of distinct overgrazed patches in many of the old lands in the study area
- The loss of condition of the high-selective feeders during the dormant season.

Approximately 35% of the sandy grasslands are unavailable for grazing due to the presence of dense stands of *Stoebe vulgaris* in this habitat type. This would severely reduce the grazing capacity of this habitat and needs consideration. If this factor is taken into account then the grazing capacity of the reserve will be reduced to 1 539 GU. Other factors that would have a negative influence on the grazing capacity calculation include the following:

- The encroachment of *Stoebe vulgaris* in many of the previously overgrazed grassland areas of the reserve. This encroachment is estimated at 35% of the grassland areas from aerial photographs
- The rocky grasslands constituted 2 540 ha of the study area (36%) and were not readily utilised by the black and blue wildebeest (Chapter 5) due to the relative inaccessibility of the terrain within this habitat type
- The *Burkea* woodlands constituted only 2% of the area available to the black and blue wildebeest but were heavily utilised by the blue wildebeest due to its high grazing value and provision of cover. It therefore suffered severe

overgrazing by wildlife at Ezemvelo Nature Reserve, making it unavailable during the dormant season.

- Large areas of the study area within the delineated habitats were invaded by alien plants such as *Acacia mearnsii* and *Acacia dealbata*. These areas were estimated to cover 25% of the area that would otherwise be available to grazers.

Black and blue wildebeest only formed part of the grazing community at Ezemvelo Nature Reserve, but their stocking densities in the study area could have an influence on the ability of the two types of wildebeest to co-exist as well as an influence on the condition of the habitats which they utilize.

Black wildebeest

Black wildebeest prefer open grassland areas where water is freely available. They prefer short grass, both for feeding and visibility (Apps 1996). They are natural migraters and pose a severe threat of patch overutilisation when their numbers are too high and they are confined to fenced land. Black wildebeest can also be productive with a mean population growth rate of 30 to 38% (Bothma *et al.* 2002).

Black wildebeest on Ezemvelo Nature Reserve are already posing a threat of patch overutilisation. Preferred areas within the herd's territory are being utilised intensively and are often similar to a blesbok's preferred grazing spots. There are only a certain number of suitable habitat areas for the black wildebeest on the reserve. Black wildebeest are also not dependent on shade during the hot time of the day like most other herbivore species (Apps 1996).

During the study period, Ezemvelo Nature Reserve was stocked with 93 black wildebeest, which equates to 74 GU. Territorial behaviour sets a limit to the numbers of competing black wildebeest that can co-exist in an area. According to Furstenburg (2002a), the range size for a black wildebeest bull is approximately 400 ha while that for a cow varies from 200 to 500 ha. A territory for a bull is 2 to 6 ha in size. The stocking density of black wildebeest should not exceed 10 animals per 100 ha and the minimum group sex ratio is recommended at one bull for every 10 cows (Furstenburg 2002a).

Blue wildebeest

The habitat of the blue wildebeest consists of open woodland, scrub and grassland, with access to permanent water (Apps 1996). Blue wildebeest seek shade during the midday heat and will stand under a tree during this time (Apps 1996; Bothma *et al.* 2002). They prefer short grass up to 15 cm tall, but browse can consist of up to 13% of the diet (Bothma *et al.* 2002). Blue wildebeest are selective of plant parts, but to a lesser extent of the plant species if the majority of the species are sweetveld species. In marginal habitat, blue wildebeest will overutilise preferred grass species, which can result in severe vegetation damage (Furstenburg 2002b).

During the study period, Ezemvelo Nature Reserve was stocked with 250 blue wildebeest, which equates to 250 GU. According to Furstenburg (2002b), the range size for a blue wildebeest bull varies from 600 to 1 800 ha while that for a cow varies from 1000 to 2500 ha. A territory for a bull is 0.5 to 1.5 ha in size. The stocking density of blue wildebeest should not exceed 7 animals per 100 ha (Furstenburg 2002b) and the minimum group sex ratio is recommended at one bull of more than 4 years for every 6 to 10 cows of more than 2 years of age. Many wildlife species are limited by territorial behaviour. It sets a limit to the number of competing bulls that can co-exist in an area (Bothma *et al.* 2004).

CONCLUSION

The results of this part of the present study indicated that the total ecological grazing capacity of Ezemvelo Nature Reserve was not exceeded. This conclusion needs to be considered carefully along with a number of other habitat factors that may influence the grazing capacity. The populations of black and blue wildebeest at Ezemvelo Nature Reserve have reached saturation levels based on grazing capacity and social behaviour. The populations of both types of wildebeest should not be allowed to increase. However, only through active adaptive management where the veld condition is monitored and the stocking density adjusted can trends in the vegetation be related to the stocking density and correction measures be made.

CHAPTER 12: POPULATION DYNAMICS

INTRODUCTION

Berryman (1981) defined a population as a group of individuals of the same species that occur together in the same place and at the same time. The individual animal is the distinct unit used for providing the basic information to determine the dynamics in a population of animals (Delany and Happold 1979). The dynamics of a population are determined from the birth and mortality rates as well as from immigration, emigration and the interaction of these parameters with the population's age and sex ratio. A change in any of these parameters tends to influence population size and the rates at which these change will impact the rate of increase or decrease in a population (Herbert 1970; Caughley and Sinclair 1994). Therefore, by noting changes in the rate of population size change, changes in the fecundity rate, mortality rate and age distribution of the population may also be identified (Caughley and Sinclair 1994).

In areas where predation is not a significant population regulatory factor, it has been suggested that the main mechanisms of population regulation in ungulates may be a reduction in reproductive success or juvenile survival (Turchin 1995). The quality and quantity of food in an animal's habitat may affect birth rates as nutritional stress can lead to decreases in pregnancy rates and rebreeding frequency (Shaw 1985). Recruitment and overall population changes can be used to measure survival rate (Krebs 1999).

The sex ratio of a population corresponds with the type of reproduction system and the bond between the sexes (Leuthold 1977). An imbalance in the sex ratio of animals often leads to poor mating frequency, especially in species where males have a harem of females such as impalas and territorial species such as both types of wildebeest. Age structure is also important since the reproductive potential of an individual depends on its age (Bothma 2002b).

In nature, populations of wild animals have developed a social structure that promotes the optimum production of young (Bothma 2002b). However, within fenced nature reserves, this natural social structure may be modified due to predation or inadequate food supply (Tambling and Du Toit 2005). Biological monitoring of the population dynamics of a species is essential to ensure that populations are maintaining demographic and genetic viability within a reserve situation (Walpole *et al.* 2001) and is essential for management decisions for a particular species (Bothma 2002b).

Changes in the growth rate of a population may be as a result of the detrimental effect of interspecific competition acting through a combination of fecundity and survivorship and the effects are expected to be density dependent (Begon *et al.* 1996). Therefore, competition between the black and blue wildebeest may result in the decrease of the weaker competitor, which in the present study is thought to be the black wildebeest due to its smaller size and area dependence. Evidence of population decline in one of the types of wildebeest may provide some support for the hypothesis that competition between the two types of wildebeest at Ezemvelo Nature Reserve happens and from that, the further inference that no ecological separation exists between the two types of wildebeest, if all the other factors have been considered. These other factors may include the possibility that the habitat is not suitable for one or both types of wildebeest as described in Chapter 1. It was hypothesised here that the population size of the black wildebeest is negatively affected by the blue wildebeest population.

The objectives of this part of the study were therefore to:

- Determine the size and growth rate of the black and blue wildebeest populations at Ezemvelo Nature Reserve
- Determine the sex ratio of the black and blue wildebeest populations at Ezemvelo Nature Reserve
- Determine the age structure of the black and blue wildebeest populations at Ezemvelo Nature Reserve
- Determine the grouping behaviour and mean herd sizes of the black and blue wildebeest populations at Ezemvelo Nature Reserve
- Make inferences based on the above results on evidence for competition and hence evidence for ecological separation between the black and blue wildebeest.

METHODS

A monthly count was conducted on the reserve to count all animals of all types of wildlife present. Animals were sexed and aged during these counts by using binoculars. These counts used the road transect technique (Collinson 1985) and provided a repeatable count with repeatable results. This technique, according to Collinson (1985), is able to provide precise counts but may be inaccurate as the population size may be under- or overestimated. However, due to the high visibility on the reserve and the detailed knowledge of all wildebeest herds on the reserve these inherent inaccuracies of the method were regarded to be negligible in this study. Additional population data were obtained from the habitat survey data as described in Chapter 4. These counts provided information on the population sizes and growth rates, group composition, sex ratios and age structure of the populations of black and blue wildebeest at Ezemvelo Nature Reserve.

The differences between the sexes in the adults were determined by using a combination of horn structure, presence or absence of a penile sheath, and general build (Von Richter 1971a; Attwell 1977; Skinner and Smithers 1990; Estes 1991). Young calves were difficult to sex and therefore were not sexed for both types of wildebeest.

Age structure and group composition were established by determining the number of males, females and juveniles in each group encountered. Juveniles were classified as such until the next breeding season when new calves were dropped. Therefore, all animals over 1 year of age were classified as adults during these counts.

Population performance is expressed as the reproductive success rate (Riney 1982) or annual birth rate (calf:cow ratio) (Caughley and Sinclair 1994). The mean calf:cow ratio was calculated for both black and blue wildebeest to determine the reproductive success rates of the populations of black and blue wildebeest at Ezemvelo Nature Reserve. Calves were taken as less than 1 year of age and adult females as > 1.5 years based on mean first ages for calving by wildebeest. Sexual maturity in blue wildebeest is reached at 3.5 years and in black wildebeest at 1.2 years of age (Furstenburg 2002a and b).

RESULTS

Population size and growth

There were 2.4 times more blue wildebeest on Ezemvelo Nature Reserve than there were black wildebeest (Table 12.1). With their larger body size the blue wildebeest formed 3.2 times more biomass on Ezemvelo Nature Reserve than did the black wildebeest.

Figure 12.1 shows the trend in population growth of the black and blue wildebeest over the period May 2003 to August 2005. The blue wildebeest population showed a finite growth rate of 3% while the black wildebeest population decreased by 2% over the period. No wildlife capture operations had taken place on Ezemvelo Nature Reserve since 2002, except for five black wildebeest males which were removed in July 2004 to be taken to the Voortrekker Monument Reserve in Pretoria as they were donated by the owners of Ezemvelo Nature Reserve (Tau 2004 pers. comm.)[14]. Eight blue wildebeest bulls were culled in 2005, three of these due to injury and the rest for biltong production.

Sex ratio

The results of investigating sex ratios of adult blue and black wildebeest are presented in Table 12.2. Sex ratios were based on breeding animals. Since the entire population of both black and blue wildebeest was known on the reserve, the sex ratio for the entire population was calculated for the whole study period and the sex ratio for the separate herds was calculated for each season.

The mean ratio of females per male at Ezemvelo Nature Reserve for the entire population of both black and blue wildebeest was 1.56:1 during the study period. Blue wildebeest were observed in herds where the mean female to male ratio was 9.73:1, while the black wildebeest were observed in herds where the mean female to male ratio was 9.93:1.

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Table 12.1: Population statistics for the black and blue wildebeest at Ezemvelo Nature Reserve in 2005

Wildebeest type	Population size	Mean mass (kg)	Biomass (kg)	Percentage change in 3 years
Black wildebeest	98	150	14 700	-2
Blue wildebeest	236	200	47 200	3

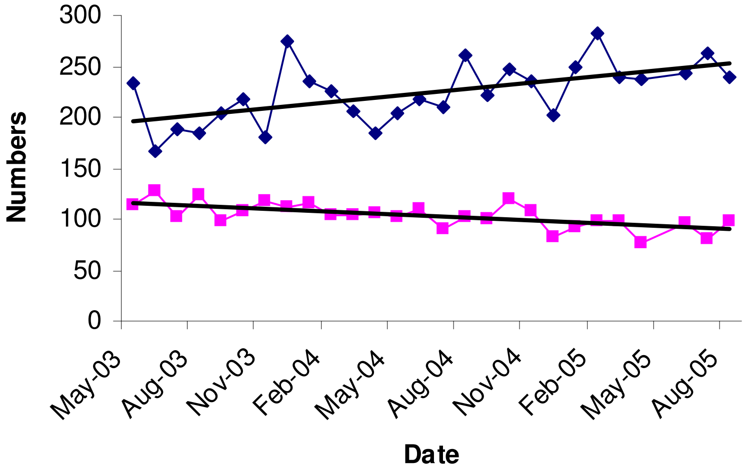

Figure 12.1: Population trends of the black and blue wildebeest at Ezemvelo Nature Reserve as obtained from monthly counts from May 2003 to August 2005. The black lines indicate trend lines, while the blue diamonds inficate blue wildebeest and the pink squares indicate black wildebeest.

Table 12.2: The ratio of females per male in herds of black and blue wildebeest at Ezemvelo Nature Reserve over the three ecological seasons in 2004 and 2005

Wildebeest type	Late growing season	Dormant season	Early growing season
Black wildebeest	9.03:1	10.58:1	10.19:1
Blue wildebeest	9.53:1	11.17:1	8.50:1

Age structure

Both types of wildebeest had populations consisting of fewer than 40% young individuals (Figure 12.2). According to Bothma (2002b) a productive wildlife population consists of 40% young individuals. As seen in Figure 12.2, 89% of the black wildebeest population were adults and only 11% were young individuals. The blue wildebeest population had 83% adults and 17% young individuals.

Grouping behaviour and herd size

Territorial blue wildebeest bulls tended to be more solitary than black wildebeest territorial bulls. Only 33% of the black wildebeest observations were of a black wildebeest territorial bull on its own, while 66% of the blue wildebeest observations were of a single blue wildebeest territorial bull. Therefore, most black wildebeest bull territories were occupied by female herds and the bull would closely associate with the herds throughout the year. In contrast, most blue wildebeest bull territories were not occupied by female herds, and therefore there was generally no close association between the territorial bulls and the female herds except during the rutting season.

The herd sizes of black wildebeest tended to remain relatively constant throughout the year, while the blue wildebeest tended to have a more fluid herd size and groups tended to separate and regroup on various occasions. Blue wildebeest had larger herds than black wildebeest in the late growing season and the dormant season. There was no difference between the herd sizes of black and blue wildebeest in the early growing season. Black wildebeest herd size did not differ over the seasons and remained constant at a mean of 12 animals throughout the year. The mean blue wildebeest herd size was largest during the late growing season (17 animals) and lowest during the early growing season (12 animals). During the dormant and late growing season, the black wildebeest maximum herd size was 35 animals, and 39 during the early growing season. Blue wildebeest maximum herd size during the late growing season was 45, 37 during the dormant season and 42 in the early growing season (Figure 12.3).

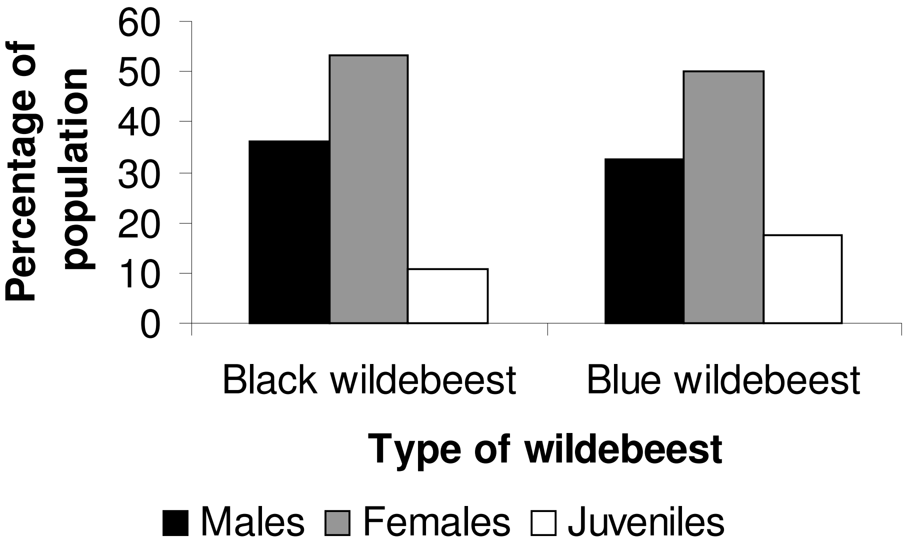

Figure 12.2: The broad population structure of the black and blue wildebeest populations at Ezemvelo Nature Reserve, South Africa for the period January 2004 to August 2005.

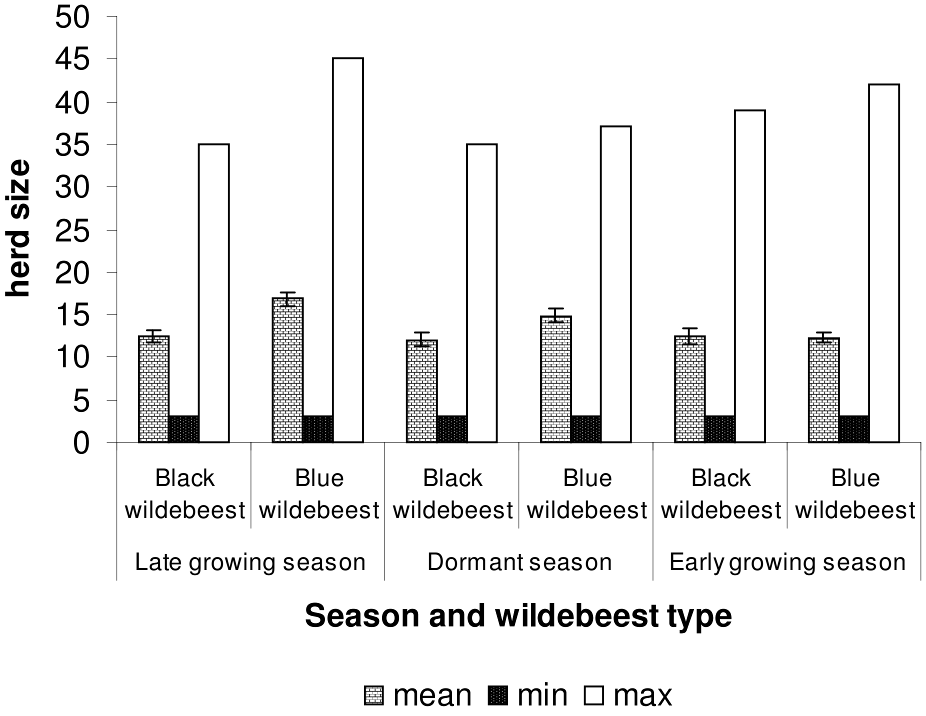

Figure 12.3: Mean, minimum and maximum herd sizes of black and blue wildebeest over three seasons on Ezemvelo Nature Reserve from January 2004 to August 2005. The bars on the mean columns represent the standard errors, which are small due to the large sample sizes that were used for these calculations.

Recruitment rate

The mean blue wildebeest calf:cow ratio was 0.52:1 while the black wildebeest had a much lower mean calf:cow ratio of 0.21:1 (Table 12.3).

DISCUSSION

The current negative rate of increase of the black wildebeest population at Ezemvelo Nature Reserve suggests that the population has probably reached its optimum stocking density. Calf mortality through food limitation during the dormant season and some predation by leopard could be limiting growth in this population.

The calving rate of the black wildebeest was also relatively low (21%). Ezemvelo Nature Reserve is situated in sour grassland with inferior nutrition during the winter months and is considered marginal habitat for both black and blue wildebeest. Populations of black wildebeest in the Giant's Castle Game Reserve and Golden Gate National Park, all with marginal habitat, showed a reproductive rate for black wildebeest of between 47% and 68% (Von Richter 1971a). The values of Von Richter (1971a) represent a population that at best is maintaining itself. Blue wildebeest at Ezemvelo Nature show a positive rate of increase of 3% but their low reproductive rate of 52% is an indication that this population is just managing to sustain itself. Blue wildebeest in the Serengeti were reported to have a reproductive rate of 96% (Watson 1969). The Serengeti is in optimal habitat under natural conditions unlike the habitat at Ezemvelo Nature Reserve.

The breeding potential of a wildlife population can be indicated by its sex ratio (Giles 1978). Under natural circumstances the number of females per male at adulthood for black wildebeest is 1.5:1 to 2.0:1 and for blue wildebeest it is 1.5:1 to 2.2:1 (Bothma 2002b). At Ezemvelo Nature Reserve the ratio was in accordance with this ratio and therefore the breeding potential based on the sex ratio is adequate. Estes (1969) listed a number of territorial species which consistently showed a dominance of females in a variety of habitats, suggesting that vigorous condition-depleting rutting activities may have adverse effects on the survival of males during the winter months (Von Richter 1971a). Unmanaged herds in suitable habitats showed a sex ratio of close to parity in studies conducted by Von Richter (1971a) while herds in marginal habitats showed a strong preponderance of males. One would expect a preponderance of males at Ezemvelo Nature Reserve due to the marginality of its habitats but the results showed that there was a dominance of females over males for both types of wildebeest. This may indicate that the habitat is not as marginal as may have been thought. However, the blue wildebeest population did have a greater percentage of its population being made up of territorial bulls than did the black wildebeest population (Table 12.3), indicating that there may be more suitable habitat available and more open niches for blue wildebeest to utilise than there is for black wildebeest in the study area.

In addition to sex ratio, the age structure is also important for assessing the productivity of a population. For the population to remain productive, a stable age structure made up of 30 to 40% young should be maintained in a natural area (Bothma 2002b and c). The low percentage of young in the black wildebeest population at Ezemvelo Nature Reserve indicates that the black wildebeest are not highly productive. The low calf:cow ratio of the black wildebeest could indicate that the black wildebeest population is mainly made up of old individuals past their reproductive peak (pers. obs.) and this could be the reason for the declining population of black wildebeest in the study area. Young animals in the Golden Gate National Park formed 33% of the population (Von Richter 1971a).

The black and blue wildebeest at Ezemvelo Nature Reserve were strict seasonal breeders and the majority of the calves were dropped within 3 weeks from the beginning of December. This agrees with studies on black wildebeest as done by Von Richter (1971a and b) and on blue wildebeest by Estes (1966).

The black wildebeest population at Ezemvelo Nature Reserve has been decreasing since both black and blue wildebeest were kept together (Chapter 2). No records on the population trends of the black wildebeest on the eZemvelo section of the reserve were available and therefore it cannot be known for sure whether this population was increasing or decreasing before blue wildebeest began invading the area due to the lowering of fences.

The reserve has no supplemental feeding programme (Tau 2005 pers. comm.)[15] and only salt licks are distributed throughout the reserve during the dormant season.

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Table 12.3: Population size and density of the black and blue wildebeest at Ezemvelo Nature Reserve as calculated from the mean monthly count data for the entire study period from January 2004 to August 2005

Item	Black wildebeest	Blue wildebeest
Size of available area (ha)	8 468	8 468
Population size	98	236
Wildebeest per ha	0.01	0.03
Wildebeest: percentage of total	6	14
Wildebeest in breeding herds (% of total population)	66	60
Wildebeest in the bachelor herds (% of total population)	16	8
Territorial bulls (% of total population)	10	28

Thus being in a marginal habitat with no supplemental food and no management burns has created a habitat where the black wildebeest population is decreasing. With the addition of possible competition from the blue wildebeest, which is showing an increasing population trend, the black wildebeest population at Ezemvelo Nature Reserve may not recover and may possibly become extinct in the future.

There can be a number of possible reasons for the black wildebeest decline at Ezemvelo Nature Reserve. These range from food shortages as a result of competition with other grazers, changed rainfall patterns (Dunham *et al*. 2003), and habitat degradation (Harrington *et al*. 1999) due to *Stoebe vulgaris* invasion in the preferred habitat of the black wildebeest. It is unknown whether this decline is restricted to Ezemvelo Nature Reserve as little information was available from nearby areas that had populations of black wildebeest. Renosterpoort Nature Reserve, which is on the southern boundary of Ezemvelo Nature Reserve, also had a decline in their black wildebeest numbers but this was thought to be due to the initial herd size that was introduced being too small to form a viable population, rather than there being any form of food shortage (Anon 2004). No sick animals or carcasses of black wildebeest were found during the study period in the study area.

There is evidence that an increase in the density of the shrub *Stoebe vulgaris* could be contributing to the decline of the black wildebeest at Ezemvelo Nature Reserve. Shrubs compete with grasses for water and thus reduce the grass standing crop (O'Connor 1985). *Stoebe vulgaris* cover has almost doubled over the last 10 years in the areas inhabited by the black wildebeest (Tau 2004 pers. comm.)[16]. These shrub invasions have decreased the area of grassland and increased the grazing pressure on the grasslands remaining, without a decrease in the stocking density of the wildlife in the study area. There is no work available on the affect of shrub invasions on the dry season availability of green grass (Dunham *et al*. 2003).

The potential competitors for black wildebeest at Ezemvelo Nature Reserve were blue wildebeest, blesbok, Burchell's zebra, red hartebeest, common warthog, common eland, ostrich, springbok and impala as they all tended to occur in the same habitats as the black wildebeest and grass formed a large proportion of their diets (Skinner and Chimimba 2005). An increase in the number of one species causing the

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decline of another species can be an indication of interspecific competition if there is overlap in diet, this overlap occurs in a shared habitat and the food supply is limited (Borner *et al.* 1987). Black wildebeest numbers were negatively correlated with blue wildebeest (r = -0.32), Burchell's zebra (r = -0.36), impala (r = -0.12) and ostrich (r = -0.28) numbers. None of these correlations were found to be significant. Therefore it can be concluded that the decline of black wildebeest is not solely caused by interspecific competition with other grazers. The type of wildlife that the black wildebeest was most commonly associated with was the blesbok, and the number of blesbok in the study area was also decreasing over the last 3 years. The correlation of black wildebeest with blesbok was negative (r = -0.23).

All bones and carcasses of black wildebeest that were found on the reserve were of old individuals and therefore it was concluded that there was only a limited young adult black wildebeest mortality on the reserve. The reason for the low recruitment of black wildebeest should therefore lie in the low fecundity levels. This could be a result of low nutrition of the adult females and age (Owen-Smith 1990; Harrington *et al*. 1999). From the evidence that the veld condition is poor to medium (Chapter 5) and the invasion of Karoo shrubs that is decreasing the grazing capacity further, it appears that nutritional stress may well be the reason why the black wildebeest numbers are declining. Due to their need for an open habitat, they are unable to move to other areas of the reserve where the shrub invasion is lower because the visibility, altitude, aspect and openness of these habitats would not be suitable for their territorial behaviour.

Black and blue wildebeest have coexisted on Ezemvelo Nature Reserve for a number of years (Chapter 2). Their continued coexistence will rest on their different habitat requirements and preferences, the correct population size of each of the two types of wildebeest at Ezemvelo Nature Reserve as well as on habitat improvement of the areas that have been invaded by *Stoebe vulgaris* in the preferred habitats of the black wildebeest.

CONCLUSION

This study investigated possible reasons for the decline of the black wildebeest population at Ezemvelo Nature Reserve. The possible factors for this decline could be marginal habitat in association with competition with the blue wildebeest. The strength of the competition between the black and blue wildebeest has been discussed in chapter 10 and 11 and found to be present but weak in nature. Without corrective management action the black wildebeest may not be able to withstand both pressures and may become locally extinct at Ezemvelo Nature Reserve. However, to substantiate this, more detailed investigations of the age-specific mortalities and age structure of both types of wildebeest have to be made.

CHAPTER 13: MANAGEMENT IMPLICATIONS

INTRODUCTION

Some individuals and agencies operate on the premise that a population's persistence can be ensured with the simple protection of a suitable portion of the preferred habitat of an animal population. However, the conservation of biodiversity, or any part of it, usually requires active adaptive wildlife management. Wildlife management is a science and an art of making land produce populations of wildlife (Bailey 1984) and has confines set by legislation and official policy. Operating on the "look after itself" premise has resulted in overutilisation and land degradation (Cromhout 2006). Wildlife population numbers can increase to such levels within confined reserves that they may change the vegetation composition and cover to the detriment of other species. This further results in soil erosion followed by a reduction in grazing for grazer species. Wildlife- proof fences and the lack of predators prevent natural migrations and natural population degradation and areas with these characteristics can by no means be considered as natural self-sustaining systems. Therefore management is essential.

Management can be of two types: conservation management and preservation management (Thomson 1992). Conservation management includes the sustainable utilisation of wildlife for the benefit of man, while preservation management includes the protection of endangered species and does not allow sustainable utilisation of the wildlife resources in the protected area. Utilisation can be consumptive and non-consumptive. Ezemvelo Nature Reserve currently obtains most of its income from ecotourism. This is a non-consumptive type of utilisation. Little consumptive utilisation of the wildlife has taken place on the reserve over time, except for some wildlife sales and the harvesting of a few animals for biltong production. The aesthetic value of healthy wildlife is important from a tourism point of view. A delicate balance exists in managing for both abundance of healthy large herbivores and maintaining the scenic beauty of the vegetation. To achieve this balance, conservation management is required.

The purpose of this section is to present some broad management recommendations for Ezemvelo Nature Reserve, with specific guidelines for the management of the black and blue wildebeest. These recommendations are based on the results of the present study. All the recommendations on stocking densities, habitat manipulation and general management should be made from a balanced holistic perspective (Von Holdt 1999).

MANAGEMENT OBJECTIVES

Well-defined management objectives are essential for any wildlife management plan (Mentis and Collinson 1979). Management is futile if unambiguous goals are not defined. The objectives for the black and blue wildebeest at Ezemvelo Nature Reserve were to maintain a free-ranging, self-sustaining population of each type of wildebeest on the reserve while at the same time ensuring that hybridisation between the two types did not occur at any time. Black and blue wildebeest are water-dependent selective grazers and therefore both water and forage quality may limit their populations. However, where water is abundantly available, forage quality would be the main limiting factor. Since the two types of wildebeest have been confined together artificially, and since they are able to hybridise, special attention should be given to the active management of both populations of wildebeest.

ACTIVE ADAPTIVE MANAGEMENT

Adaptive management is a term that is used to describe the system of making management decisions by learning from one's past mistakes (Stuart-Hill 1989). It is a useful form of management where management decisions have to be made without having all the facts at hand. Adaptive veld management depends on three important monitoring programmes:

- Recording environmental conditions and the management systems that are being applied
- Measuring the performance of the animals
- Measuring changes in the vegetation.

MONITORING

Monitoring of the habitat aims at the purposeful and repeated examination of the state or condition of the habitat in relation to external stress, and involves the frequent testing of the differences between baseline or initial surveys and follow-up surveys (Bothma and Van Rooyen 2002). Obtaining regular, repeatable ecological data is important for the successful management and utilisation of any wildlife area. The aim of monitoring is to observe trends in animal populations and the habitat over time. A monitoring programme serves as an early warning system and it aims to detect changes or trends that occur as a result of management actions or natural events. It is important to adapt the management programme in good time when and where it is necessary. The influence of the management strategy on the following should be monitored regularly (Bothma and Van Rooyen 2002): veld condition, grazing capacity, browsing capacity, affects of water provision, affects of bush encroachment and its control, and the affects of habitat reclamation measures such as soil erosion control. Opportunistic management has to be undertaken and continual monitoring and flexibility in the management plan is essential.

Monitoring is the most important aspect of any wildlife management programme and should therefore be standard procedure on any wildlife area. Monitoring and adaptive wildlife management go hand in hand and allow wildlife managers to make proper decisions. Long-term monitoring allows for the measurement of changes over time and these changes can be evaluated against the area's long-term objectives to provide an indication as to whether a specific management action needs to be altered. The following section discusses the three important monitoring programmes which should form the basis of a wildlife management plan for Ezemvelo Nature Reserve.

Environmental monitoring

Certain components of the habitat can be regarded as key components as they are reliable indicators of the condition of the habitat. Aspects related to these key components should be monitored regularly. The key components on a wildlife area are: rainfall, soil erosion, permanent natural surface water, fire, aspects of vegetation structure, plant biomass production, vegetation cover and composition, and the productivity, growth rate and numbers of the animal population (Bothma and Van Rooyen 2002). In practice it is difficult to monitor all these components annually. Therefore, for practical management purposes the following components should be regularly monitored: rainfall, temperature, water quality, soil erosion, habitat (herbaceous component, woody component) and animals.

Rainfall

Long-term rainfall is important for the determination of trends. The graph of the long-term rainfall is supplied for Ezemvelo Nature Reserve (Figure 2.3). Rainfall received should be monitored daily if possible. Rainfall figures for over 20 years are required to make reliable deductions for a specific area (Bothma and Van Rooyen 2002). Rainfall has the greatest influence on the productivity of vegetation and ecological capacity of a reserve (Coe *et al.* 1976). Rainfall records are important for the adjustment of stocking densities. There are currently 10 rainfall gauges placed at strategic spots at Ezemvelo Nature Reserve. Another two rain gauges are recommended for the high-lying northern plateau areas on the eZemvelo section and another gauge in the low-lying areas near the bridge crossing the Wilge River to provide a more even spread of rain gauges throughout the reserve. Accurate records should be kept and trends in the rainfall patterns analysed regularly.

Temperature

The minimum and maximum temperature should be measured daily at 08:00 at a standard height of 1 to 2 m above the ground surface in a shaded and well-ventilated area (Bothma and Van Rooyen 2002). This could be done at the reception area on the reserve. A Stevenson screen weather station could be set up to record this information, which could be made available for future researchers and for burning purposes.

Relative humidity

Relative humidity of the air and air temperature has major affects on fire intensity (Trollope *et al.* 2004). The use of these two factors can be used to determine optimum periods for management burns for the creation of quality forage for grazing herbivores. This becomes extremely important during the fire season and when firebreaks are being burnt and will help ensure that runaway fires do to inappropriate burning times are avoided. Relative humidity of the air can be measured by using a hygrometer.

Water quality

Inorganic and organic constituents in water can supplement an animal’s mineral requirements or aggravate/induce a mineral imbalance in an animal (Meyer and Casey 2002). The susceptibility of toxic and palatability hazards differs from animal species to animal species.

It is recommended that key watering points be monitored on a quarterly basis. The Institute for Soil, Climate and Water of the Agricultural Research Council[17] of South Africa offers a water analysis package that gives information on a wide range of water constituents (Meyer and Casey 2002). Water quality assessments should also be performed regularly.

At Ezemvelo Nature Reserve, there are no artificial watering points at present. The wildlife utilise the banks of the Wilge River to drink as well as the various streams that cross the reserve. There are a number of points that are regularly utilised and the quality of the water at these points should be measured in order to determine what is present in the water. This information will aid in the setting up of future supplementation programmes.

Soil erosion

Many wildlife areas experience some form of soil erosion, especially if they originated from trampled livestock ranches. Soil erosion is generally caused by wind and water. Wildlife are also known to cause localised erosion. The main culprits are dassies, arid-zone mongooses, ground squirrels, yellow mongooses, bat-eared foxes, porcupine, field mice, rats and moles (Snyman 1999). Insects may also be blamed for some localised erosion. The springbok is one of the herbivores, excluding small stock, which has the greatest influence on the vegetation. It is responsible for bare patch formation, pan formation and general erosion (Roux and Opperman 1986). At Ezemvelo Nature Reserve there are a number of areas that have been severely eroded due to the action of wildlife. Black wildebeest and blesbok are responsible for creating bare patches in the sandy grasslands where the herds intensively concentrate their grazing in one patch for an extended period of time. Blue wildebeest territorial bulls also tend to create bare patches that could potentially result in erosion but the population is much less patch selective than the black wildebeest.

The nature and quality of the vegetation plays an important role in preventing soil erosion. Vegetation provides a protective layer that is responsible for holding the soil in place and protecting it against the erosive activity of wind and water. The erosion process is accelerated if this protective layer is damaged. Stands of perennials are

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much more effective than stands of annuals at preventing erosion (Snyman 1999). Grasses are more effective at preventing erosion than shrubs because grasses have a larger basal cover and a network of roots close to the surface that bind the soil. In veld where grass has been replaced by bushes, erosion is prevalent. The areas at Ezemvelo Nature Reserve that have been invaded by *Stoebe vulgaris* may become vulnerable to erosion in the future due to the reduction in the grass cover. This is another reason why this invader should be controlled in the study area.

Different soil types react differently to erosion. Van Schalkwyk (1984) lists the main factors that have an influence on the erodability of a soil as:

- Texture: soils containing a high percentage of fine sands and silts are more erodable than those with a high percentage of clay and coarse sands.
- Structure: soils with a coarse blocky, platey or massive structure are more prone to erosion than those with a fine granular structure.
- Organic material: soils with a high organic content are more resistant to erosion than those with a low organic content. The organic matter in the soil is important for soil structure and water infiltration and it has been found that in semi-arid rangelands it is normally below 2.5% and decreases with veld degradation and increased aridity (Snyman 1999).
- Profile permeability: soils with a high permeability are more resistant to erosion than those with a low permeability.

The deep sandy soils at Ezemvelo Nature Reserve have a high percentage of sands and are thus expected to be easily erodable. The soils are adequately aerated and consist of a loose granular structure that is easily affected by wind erosion. The organic material content in the soils at Ezemvelo Nature Reserve is generally low, as the soils tend to dry out quickly and not retain their moisture. The profile permeability is high due to the sandy nature of the soils, which causes the soils to be highly leached.

Soil erosion at Ezemvelo Nature Reserve varies from moderate to severe. The main types of erosion include sheet erosion, gully erosion and channel erosion. Bare patches are the starting point of sheet erosion and erosion gullies. Episodic floods sometimes contribute to serious sheet erosion, the incision of pediments, and gully formation.

Gullies are visible manifestations of land-use malpractices and lead to increased denudation of the soil and increased runoff (Van Schalkwyk 1984). Gullies are caused by the destruction of the vegetation in drainage ways by fires or overgrazing and animal trails, labour paths or vehicle tracks. Dongas usually occur near the bottom of slopes. There are a number of deep gullies at Ezemvelo Nature Reserve. Serious attention needs to be paid to these gullies. It is recommended that the wildlife be attracted to the edges of these gullies with molasses so that their hooves can break down the sides of these gullies. They should be filled with debris and stabilised with gabions. A programme needs to be implemented for the stabilisation of the gullies at Ezemvelo Nature Reserve to prevent them from increasing in size.

The consequences of erosion can be measured by the development of microtopography: sheet erosion, gulley and drainage systems, accumulation of sediment, decrease in soil fertility, changes in soil structure and texture, changes in soil moisture status, salinization and compaction of the soil, water runoff and lowering of the water table (Roux and Opperman 1986). These factors should be measured regularly at Ezemvelo Nature Reserve.

The management of the reserve should do all that is possible to prevent man-made erosion. It is important to have knowledge of the areas on the ranch that may be sensitive to erosion, as well as areas that are already degraded due to erosion. Veld reclamation programmes should be in place for the prevention and reclamation of eroded areas. Roads should not be placed in erosion sensitive areas of the reserve. Vehicles should only be allowed on the designated roads. Bare patches and any signs of erosion should be carefully monitored so that any erosion can be prevented in the early stages of development. To ensure the continued stability of an ecosystem, the loss of abiotic components such as mineral nutrients (and soil) must be minimised (Bothma 1996).

Habitat monitoring

To conduct monitoring surveys of the habitats, fixed points sites should be established in each habitat. Thirty-four fixed points were established during the present study. It is recommended that at least three representative sites from these 34 sites be selected in each habitat at Ezemvelo Nature Reserve. The species composition and biomass of the herbaceous vegetation should be surveyed annually. The same methods as described in the present study should be utilised to provide information on these parameters. Such data will also provide information on fuel load for fires and allow the detection of any changes in species composition. Aerial photographs taken at constant intervals and altitudes will also provide an effective way of evaluating the impact of herbivores on the vegetation over time. Fixed-point photography at the selected sites can also be used to provide a subjective evaluation of the trends in vegetation of the area over time.

Monitoring of wildlife

In order to have a thorough knowledge of the wildlife populations at Ezemvelo Nature Reserve a number of factors related to the wildlife populations need to be measured. The seasonal distribution and numbers of wildlife should be recorded continually and population growth rates calculated (Bothma and Van Rooyen 2002). The age and sex ratio of the animals should be monitored annually, as well as the natural rate of mortality and the cause of death. The physical condition (at the end of the wet and dry seasons), diseases and parasites of animals should also be recorded (Bothma and Van Rooyen 2002). For the purpose of determining trends in the populations, repeatable counts should also be conducted.

The current wildlife censusing techniques utilised at Ezemvelo Nature Reserve should be continued. These should be complemented with annual aerial counts and drive counts in the rocky areas for rare animals. Night spotlight counts for nocturnal species should also be conducted regularly. These counts will assist in determining population trends of the wildlife. To reduce the growth rate of a wildlife population, the most productive females and the mature males could be removed. The populations of black and blue wildebeest need to be monitored carefully and the growth rate of the blue wildebeest population curbed.

It is also important to monitor the habitats that are preferred by the different types of wildlife in an area. Seasonal wildlife movements can have a considerable impact on the habitat and knowledge of such movements will aid in setting realistic stocking densities.

With Ezemvelo Nature Reserve not being optimal habitat for both black and blue wildebeest, black and blue wildebeest may be more susceptible to disruptive pressures especially in confined areas where they cannot escape harmful ecological factors. It would be advantageous if some form of rotational grazing could be encouraged. Local movements at Ezemvelo Nature Reserve tended to be controlled by availability and quality of forage. Selection by the blue wildebeest was further enhanced by the presence of burnt areas. The breeding female component of the population is the most important component (Caughley and Sinclair 1994). They often select the best grazing areas while the bachelor herds are forced into sub-optimal areas by the territorial bulls. Habitat selection by the female herds would therefore be a good indication of optimal habitats within the confines of the reserve. The present study showed that the female herds of the blue wildebeest were highly selective for the old lands and the black wildebeest for the sandy grasslands during the early growing season. To optimise Ezemvelo Nature Reserve for the coexistence of the black and blue wildebeest, the vegetation should be managed specifically to suit the needs of both types of wildebeest. The habitats should be monitored for structural and nutritional adequacy (Dörgeloh 1998). Patch burning throughout winter would improve forage quality during the critical dry period.

A population viability analysis should be conducted on the black wildebeest at Ezemvelo Nature Reserve. A comprehensive and accurate population composition analysis needs to be conducted. Herds could be attracted to an artificial feeding site during the winter of each year and age-specific sex ratios, fecundities and mortalities monitored. Replacement of some animals with unrelated subadult females to maintain the demographic balance and genetic variation should be implemented.

SPECIFIC MANAGEMENT RECOMMENDATIONS

Ecological capacity and stocking density

As was discussed in detail in Chapter 11, the ecological grazing capacity of Ezemvelo Nature Reserve has not yet been exceeded. However, the populations of the grazing ungulates need to be monitored to ensure that the capacity is not exceeded in the future. The browsing component in the study area is limited and a detailed study of the browsing capacity needs to be conducted to determine stocking densities for the browsers that are present on the reserve. The browsing component on the reserve is currently made up of mainly greater kudu and common eland. These animals tend to jump the fences in winter to search out areas where browse is more readily available. If adjustments to the stocking density are to be made the first animals that could be removed include Burchell’s zebra, blue wildebeest, red hartebeest and common eland.

Habitat manipulation

It is clear that some form of ecological separation exists between the black and blue wildebeest at Ezemvelo Nature Reserve. In addition, the loss of grazing areas due to the encroachment of *Stoebe vulgaris* and the increase in the blue wildebeest population has also led to the increased potential for competition for food resources between the two types of wildebeest. Keeping in mind that one of the objectives of Ezemvelo Nature Reserve is to prevent hybridisation between the black and blue wildebeest, such competition should be removed. This can be done by maintaining conservative stocking densities, by habitat manipulation or by a combination of both methods.

In addition, manipulation of the habitat to suite specific species can be considered. This would involve removing trees to provide more grassland for grazers and also the mowing of grassland to simulate fire. Habitat diversity is essential for providing a variety of habitats for different species of wildlife and the greater the habitat diversity, the more the different types of wildlife that can be kept on the reserve.

The following specific steps are recommended to assist in the manipulation of certain habitats on Ezemvelo Nature Reserve so as to increase the grazing capacity of the area and to reduce the potential for competition between the black and blue wildebeest:

- The most important action is the control of the blue wildebeest stocking densities as well as the total grazer stocking densities. Specific recommendations have been given in Chapter 11.
- Fire can be used as a habitat manipulation tool by drawing animals away from overgrazed patches and creating areas of better quality forage during critical times of the year.
- The enlargement of the property may provide further suitable habitat for the black wildebeest if chosen in such a way.
- A *Stoebe vulgaris* control and monitoring programme should be implemented in an attempt to regain the large portions of grazing land lost to this encroaching shrub.

- Roads have important ecological effects in any wildlife area and therefore consideration needs to be given to road placement and construction as well as road use (Du Toit and Van Rooyen 1996). A road is a disturbance to the natural vegetation as it compacts the soil, increases runoff in such areas and causes soil erosion in those soils prone to erosion (Du Toit and Van Rooyen 1996). Poorly planned roads lead to soil erosion and habitat degradation. They also lead to disturbance of the wildlife in certain areas.
- Removal of all alien and problem plants from waterways and from open areas should be conducted to improve the grazing capacity in these areas. The plants of concern are black wattle *Acacia mearnsii*, grey poplar *Populus x canescens*, silver wattle *Acacia dealbata*, *Argemone ochroleuca*, and *Sesbania punicea*.
- The survival of the *Burkea* woodlands shoud be ensured through their protection from fire, and their establishment should be encouraged.

Genetics management and hybridisation

Inbreeding leads to the loss of genetic fitness, increased mortality in young animals, reduced fertility and depressed growth (Du Toit *et al*. 2002). The number of breeding animals in the herd influences the rate of inbreeding at each generation. The sex ratio also plays an important role in the flow of genetic material in a population (Du Toit *et al.* 2002). For healthy population growth to occur, a genetically viable population is essential. It therefore, remains sound policy to obtain breeding males from another genetic source from time to time as reserve fences prevent the exchange of genetic material between animals of bordering reserves.

The random nature of genetics and the lack of previous genetic studies on wildlife, makes it extremely difficult for researchers to recommend genetic management policies (Bothma 2002a). The genetic norm among different species varies greatly and some animals are naturally interbred. In formulating a management strategy for the maintenance of genetic diversity in wildlife populations on reserves, it is suggested that the conservation of pure populations should take precedence over the maintenance of high diversity values (Anon 2003a). Genetic diversity should be considered as an integral part of biodiversity. Maintaining large-scale biodiversity is essential in keeping an ecosystem healthy.

The principle of managing several smaller populations as a meta-population with artificially induced gene flow remains a viable strategy (Grobler 2003). Gene flow needs to be maintained in order to prevent inbreeding and thus avoid detrimental genetic effects. The first step towards meta-population management is to identify suitable subpopulations elsewhere (Bothma 2002a). Artificially induced gene flow requires a critical selection of which populations should be part of the programme. Ideally, only populations that have been analysed through molecular methods and proven to be pure individuals, should be used for new genetic material when exchanging animals between different populations (Grobler 2003). The smaller an animal population, the more frequently would the stock have to be translocated to mimic natural migration patterns (Bothma 2002a).

It is therefore recommended that since it is thought that the reason for the low productivity of the black wildebeest is the large proportion of older animals in the herds, new young black wildebeest cows and bulls should be brought in to increase this productivity. This will hopefully halt the population decline of the black wildebeest at Ezemvelo Nature Reserve while at the same time increasing the genetic diversity of the population.

Reserve management should only keep those wild animals that are ecologically adapted to a region and are known to have occurred previously in that region (Du Toit *et al*. 2002). This will ensure that competition between ecologically equivalent animals is eliminated. Therefore it is recommended that only black wildebeest should be kept at Ezemvelo Nature Reserve.

It is advisable never to mix animals of different subspecies. Wild animals will hybridise on a wildlife area when the area is too small and minimum herd sizes are not maintained (Du Toit *et al.* 2002). Black and blue wildebeest hybridise and produce fertile hybrids. Red hartebeest and blesbok can also hybridise to give infertile hybrids.

Supplementary feeding

In order to balance their diets and meet their nutritional requirements, wild herbivores evolved over time with the behaviour of migrating as the seasons change. However, today wild herbivores are increasingly being confined to reserves (Maskall and Thornton 1996; Thornton 2002). Wild herbivores are therefore dependent on the vegetation in a relatively small area to provide their required nutrients for normal reproduction and physiological processes (Thornton 2002). To balance a system in terms of nutrient flow (inputs versus outputs) the correct nutrient supplementation on nature reserves is becoming all the more essential (Maskall and Thornton 1996; Whitehead 2000). However, the size of Ezemvelo Nature Reserve is sufficient to allow for some movement of wildlife and supplementary feeding should only become necessary when the area is overstocked or when the habitat is not suitable for the particular species that requires the feeding.

Ezemvelo Nature Reserve is characterised by sourveld plant species, which generally lose their nutritional value during the dormant season. Most of the grass species on the reserve are unpalatable and stemmy even when available. Immediately after the rainy season in March, when enough grazing of high quality is available throughout the reserve, wildlife select their most preferred habitat types in terms of structure and plant species. At the end of the winter months the wildlife clearly select the mountainous areas within the reserve. This is especially true for Burchell's zebra that congregate on the rocky hills and mountains of the reserve, utilising just about all the available plant species during the winter months. This foraging behaviour further indicates that soil in the mountain veld is probably more fertile than soil in the sandy regions. After the depletion of available food in the mountain veld areas, wildlife will start selecting plants more for volume than for quality.

When wildlife are in a poor condition during the winter months some form of supplementation is required. During the winter months protein and energy are likely to be deficient in sourveld regions (Schmidt and Snyman 2002). Therefore it is recommended that protein licks be placed out for the wildlife at Ezemvelo Nature Reserve.

The substandard quality of the available vegetation for both types of wildebeest could lead to delayed puberty, resulting cows having their first breeding season later in life. It could also lead to females taking longer to reach the required target mass for conception, and a reproductive cycle could be skipped. Calf survival could also be impeded and abortions or stillbirths are possible. This may be one of the contributing factors to the decline of the black wildebeest population at Ezemvelo Nature Reserve causing a low calf:cow ratio as was found in Chapter 12.

Salt licks have been regularly provided for the wildlife at Ezemvelo Nature Reserve during the winter months. These licks are heavily utilised by the wildlife populations on the reserve indicating that there is a need for some form of supplementation in order to get the populations through the winter period in a good condition. Since the main objective of the reserve is for ecotourism, the presence of extremely thin and unhealthy animals is not recommended. This may detract from the aesthetic beauty of the reserve.

Disease management

The recent development of the wildlife ranching industry together with the lifting of restrictions on the movement of wildebeest in 1993 has caused concern amongst cattle producers with regards to the increased incidence of wildebeest-associated bovine malignant catarrhal fever in cattle (Cooper 2003).

There are a set of proposed control measures that have been drawn up by the Red Meat Producers Organisation and the South African Game Ranchers Organisation (SAGRO) (Cooper 2003). These include that this disease should be declared a controlled disease under the new Animal Health Act 7 of 2002. All farms presently keeping wildebeest should be registered through a statutory procedure, to be prescribed in the Regulations under the new Animal Health Act 7 of 2002. For all new registrations, applicants must obtain the written consent of all directly adjoining neighbours. All existing farms, new farms and facilities of agents, auctioneers and wildlife capturers, where wildebeest are being kept or will be kept, must be registered. A registration certificate will be issued and will be valid only for the land specified on the certificate and can be withdrawn if the holder thereof is convicted of an offence in terms of the new Animal Health Act, concerning the registration, keeping or the movement of wildebeest. Movement without state veterinary permit control will be allowed only between farms/holdings registered according to the prescribed procedure. SAGRO will apply to issue the movement permits and handle the recording and administration process as an assignee under the Animal Health Act 7 of 2002. It will be the responsibility of the buyer to produce a registration certificate before wildebeest can be purchased privately or at an auction.

Ezemvelo Nature Reserve is directly adjacent to, on a number of sides, farms which carry cattle. Possible conflict may results in the future if the wildebeest at Ezemvelo Nature Reserve are found to be the cause of a snotsiekte outbreak on adjacent properties. Therefore note should be taken by management of these proposed controlled managements to avoid any future problems.

Translocation of wildebeest

Currently legislation is also being implemented which controls the movement and keeping of wildebeest. The National Environmental Biodiversity Act of South Africa- Act 10 of 2004 (Anon 2004) regulates the translocation of indigenous species to areas where they are locally exotic in South Africa. Translocation of wildlife in South Africa has become increasingly easy and results in private landowners bringing animals together into locally exotic areas. Such practices have many associated risks. These risks include the possibility of outbreeding depression, of hybridisation between species, between subspecies, and the mixing of ecotypes with the possible resultant loss of local genetic fitness due to the modification or loss of local gene adaptations (or alleles). A further great risk is the transmission of diseases and parasites to areas where they previously did not exist and these pose considerable threats to the wildlife, and in some instances even to domestic livestock, of the areas into which they have been introduced. Yet another major risk is that an introduced taxon often has the potential to cause considerable irreversible ecological damage whether it is in the form of substrate or habitat destruction, or even outcompeting local taxa.

By introducing both black and blue wildebeest into a reserve together, the hybridisation risk is the greatest followed by habitat destruction. There is thus a need for all those interested in the maintenance of natural biodiversity to establish guidelines and principles for the translocation of biota so that no one element poses a conservation threat to any other. The guidelines state that translocated mammalian herbivore taxa must not threaten the genetic integrity of naturally occurring local taxa, i.e. they must originate from genetically identifiable and appropriate populations and not be susceptible to hybridisation. Existing hybrids should be removed. This applies directly to Ezemvelo Nature Reserve. South African endemic and threatened taxa will be afforded priority protection and will be restricted to their natural distribution ranges (for certain taxa extralimital populations may be considered). Taxa may only be translocated to areas where suitable and adequate habitat exists. Properties where wild herbivores occur will be accredited by provincial conservation authorities according to the taxa present on the property, with those supporting only historically appropriate taxa under natural conditions enjoying the highest status and qualifying for incentives.

Black wildebeest are placed in category 2 of the translocation categories for South African mammalian herbivores. This means that this type of wildebeest may be translocated within their natural geographic ranges and conditionally to areas within South Africa outside their natural range. Only individuals of approved origin will qualify. These conditions, however, will include appropriate genetic origin, adequate enclosure and registration as a zoological institution. This category includes a number of mammalian herbivore taxa that have unfortunately been extensively translocated in the past to destinations outside their natural ranges, thereby setting precedents of major numeric proportions, but which can, at least temporarily, be intensively managed through a variety of conditions, ranging from adequate enclosure prescriptions to registration of properties as zoological gardens. The aim with this category of animals is to persuade owners to remove them from the areas where they do not belong, possibly through the introduction of a system of incentives/-disincentives. If not, then the properties will be downgraded within the accreditation system, or will possibly be required to be registered as zoological gardens.

Blue wildebeest are in category 3. This is the category of South African mammalian herbivore taxa that may only be translocated within their natural geographic ranges within South Africa. This category includes mammalian herbivore taxa with a relatively wide historic range, but which have close relatives elsewhere; this implies that each related taxon is restricted to its own natural range.

Where blue and black wildebeest; or tsessebe and red hartebeest and / or blesbok; or greater kudu, nyala and bushbuck; or waterbuck and other Reduncinae, historically occurred sympatrically, they may no longer be kept on the same property in order to prevent hybridisation, unless an inspection reveals that in those areas of sympatry there is sufficient suitable habitat for each taxon, and the property itself is greater than 10 000 ha. All individuals of the taxon can be freely translocated within its natural range. Since Ezemvelo Nature Reserve is currently smaller than this size hybridisation is most definitely a cause for concern.

CHAPTER 14: CONCLUSIONS

The overall aim of the present study was to determine whether ecological separation existed between the black and blue wildebeest at Ezemvelo Nature Reserve. It was predicted that the black and blue wildebeest would be too close ecologically to be kept together in the same area without harming each other or the habitat.

Ecological separation was studied in terms of habitat separation at three different scales: macroscale, mesoscale, and microscale. Separation in habitat use was found at the macroscale and at the mesoscale but not at the microscale. The type of vegetation in the different habitats was not the factor governing habitat selection by the black and blue wildebeest. Instead the physical features of the habitat were the main driving factors of habitat selection. Factors such as distance to shade, woody vegetation cover, aspect, and altitude were the most important separating factors. The diversity of habitats at Ezemvelo Nature Reserve offers mutually exclusive areas for the black and blue wildebeest thus allowing for effective spatial separation of the two types of wildebeest on the reserve. As long as these habitats are maintained intact, the coexistence of the black and blue wildebeest at Ezemvelo Nature Reserve at the current population levels can be maintained without the threat of hybridisation. Black wildebeest are willing to trade-off nutritional quality for an open habitat and therefore may require supplementation in their preferred habitats to ensure the long-term viability of the population. The habitat offering the most high quality forage for both types of wildebeest is the old lands. This is the habitat where possible conflict between the black and blue wildebeest may occur during the critical season. Mesoscale habitat separation is the highest as it is at this scale that the physical features of the site of occupation become most important. The heightened territorial behaviour of the black wildebeest as compared to the blue wildebeest makes it dependent on high-lying open areas. Such areas will be chosen before the quality of the forage is considered. Therefore, areas with sufficient open areas at high altitudes and with high visibility are required for black wildebeest. Blue wildebeest require cover to be in the near vicinity of their feeding sites. Therefore, an area with a mosaic of open habitats and more densely vegetated areas will provide suitable circumstances for the coexistence of both types of wildebeest without competition, provided that the sizes and demographics of both populations are carefully monitored. The lack of habitat separation at the microscale was expected as it has been found that there was no difference in the way that the two types of wildebeest feed and hence no trophic difference between the two types. The feeding sites of the black and blue wildebeest were similar and showed little difference in terms of the vegetation characteristics that were measured. Slight differences in terms of grass quantity and grass species composition were found which could be attributed to the area selective nature of the black wildebeest compared to the more mobile blue wildebeest. In addition only limited suitable habitat was available for the black wildebeest on the reserve forcing them to concentrate for longer on certain patches whereas the more versatile blue wildebeest was able to utilise a wider variety of habitats.

The differences in the activity patterns of the black and blue wildebeest can be attributed to the differences in the mobility of the two types of wildebeest and to the differences in the openness of the habitats selected by either type of wildebeest. Blue wildebeest were much more active than the black wildebeest and spent less time resting than the black wildebeest. This could also be attributed to the smaller size and hence digestive capacity of the black wildebeest as compared to the blue wildebeest.

Resource partitioning between the two types of wildebeest was found to be incomplete. Considerable overlap in the use of key resources such as habitats and possible food species occurs between the black and blue wildebeest. In homogeneous landscapes with little habitat variation this finding would indicate that the two types of wildebeest would be in direct competition for their basic resources. If the study area consisted of only open plains, the black and blue wildebeest would not be able to coexist without harming each other or the habitat. The minimal overlap in terms of spatial distribution and temporal activities at Ezemvelo Nature Reserve is a direct result of the presence of a diversity of habitats that serve to provide mutually exclusive areas that can be exploited independently by either type of wildebeest.

Seasonal differences in habitat use were identified in the present study. As expected, overlap in resource use tended to be lowest during the dormant season when food resources were most limiting. This critical season prevents the members of either type of wildebeest from expanding their niche dimensions, as only a limited supply of resources is available. During the other seasons when resources are readily available it may be possible to exploit a wider breadth of resources but during the critical season niche breadth decreases and animals become more specialised. In terms of the possibility for hybridisation, the rutting period in the late growing season is the most crucial for the implementation of ecological separation between the two types of wildebeest. For hybridisation to be avoided, ecological separation should therefore be the greatest during the late growing season. Evidence for this was found in the present study.

Due to the spatial separation of the black and blue wildebeest at Ezemvelo Nature Reserve, there is little opportunity for interference competition between them. However, in a homogeneous area, interference competition could become a problem.

The encroachment of blue wildebeest bachelor males into black wildebeest habitat is a clear indication that the population size of the blue wildebeest has reached saturation levels in its suitable habitat. Population regulation of the blue wildebeest population is imperative to ensure that hybridisation does not occur.

The black wildebeest population at Ezemvelo Nature Reserve was found to be declining. No clear reason for this decline was found, but it was suggested that the quality of the available suitable habitat was declining due to encroachment by *Stoebe vulgaris*, lack of burning causing the build up of moribund material and the sourveld nature of the vegetation requiring supplementation in the critical season.

It is concluded that the introduction of both types of wildebeest into the same area is not recommended, but if done requires intensive management to prevent hybridisation and competition. Only certain areas would be suitable for such an introduction where the habitat heterogeneity is able to supply a suitable mixture of open habitats and cover. The owner of such properties has a responsibility to ensure that hybridisation does not occur and by implementing the recommendations supplied in this study with continuous monitoring may be able to conserve pure populations of black and blue wildebeest in the same area. Black and blue wildebeest are not ecologically separated to such a degree that they will be able to coexist without management action.

For the situation at Ezemvelo Nature Reserve it is recommended that one of the types of wildebeest be removed from the reserve. This will require the destruction of the animals, as live animals can no longer be sold due to provincial regulations discussed in Chapter 3. Since this action may seem too drastic, the populations at Ezemvelo Nature Reserve need to be intensively managed to ensure that suitable habitat is available for both black and blue wildebeest. This will require management action in terms of *Stoebe vulgaris* control, patch burning and population control in the form of hunting or culling. The black and blue wildebeest populations at Ezemvelo Nature Reserve cannot be left to "sort themselves out" as this will inevitably result in either hybridisation or the loss of the black wildebeest population.

FUTURE RESEARCH PERSPECTIVES

The aim of this section is to briefly outline possible future work associated with the present study that could be done at Ezemvelo Nature Reserve and on other properties where black and blue wildebeest are confined together. These include:

- A detailed study of the dietary requirements of both types of wildebeest
- Detailed age structure and population dynamics analysis of the black wildebeest population to determine the exact cause of its decline over the last three years as found in Chapter 12.
- Establishment and growth of the even cohorts of *Burkea africana* in the study area. There is a need to understand the population dynamics of these trees and how and why they grow in the areas they do. Ensure their continued survival of the woodlands as they provide an important habitat for many of the wildlife species on the reserve.
- Range size analysis of identified individuals of both types of wildebeest to show movements and activities and behaviour especially during the rutting season to continue monitoring the whether any occurrence of interbreeding between the two types of wildebeest will occur in the future.
- An in depth study of the ecological separation of the grazers because these animals compete for the same food resources, especially in terms of quantity during the dormant season.
- Genetic studies should be conducted on the black and blue wildebeest to determine the degree of genetic variation, inbreeding and whether hybridisation has taken place in the past. This detailed data could be included into a population viability analysis to predict the viability of the populations on the reserve.
- A study of coexisting populations of black and blue wildebeest in areas with low habitat heterogeneity would be able to confirm the conclusions reached in the present study.

PREDICTIONS FOR THE FUTURE OF THE BLACK AND BLUE WILDEBEEST IN SOUTH AFRICA

National policy has been implemented which will aid in discouraging landowners from keeping the black and blue wildebeest on the same property and outside of their natural distribution ranges. Recent press reports have indicated, however, that the hybridisation problem is not being taken seriously by the game industry as hybrid wildebeest were sold at a game auction in the Free State province in 2006 (African Indaba 2006). The genetic history of all populations of black and blue wildebeest is not known and it is entirely possible that many populations are the result of offspring of hybrids. This requires serious study. All populations should be analysed for genetic purity before sales are allowed. As long as there is a market for hybrids, the threat of hybridisation and doubts for the future of pure black and blue wildebeest populations in South Africa remain. Hunting regulations discouraging hunting of rare hybrids should be strongly implemented. The politics surrounding the hunting industry need regulation. This is currently being implemented at a national level. The loss of revenue due to keeping both black and blue wildebeest on the same property should not be offset from the income that may be obtained from hunting a hybrid. It is the responsibility of the hunting industry to discourage such practices.

The Stern report on global climate change indicates that climate change may also impact the black and blue wildebeest populations in South Africa. Since black wildebeest are endemic to South Africa, this type of wildebeest should be given priority protection. Climate change impacts predict that the highveld grasslands of South Africa will be encroached by Karoo vegetation in the future due to increased temperatures and lower rainfall. The decreasing size of the grasslands in South Africa will decrease the habitat available for black wildebeest. With all factors increasingly piling up against the black wildebeest all efforts should be put into conserving this type of wildebeest and the policies surrounding the prevention of hybridisation should become more strict and implemented on a fine system rather than an incentive/disincentive scheme.

The ecological separation of the black and blue wildebeest on Ezemvelo Nature Reserve in the highveld grasslands of South Africa

by

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SUMMARY

This study was conducted at Ezemvelo Nature Reserve on the boundary between the Gauteng and Mpumalanga provinces in the central grasslands of South Africa. The reserve covered an area of 8 468 ha. The area forms part of the grassland biome in the rocky highveld grassland region and receives a mean of 675 mm of rainfall annually.

The ecological separation of the black and blue wildebeest was investigated with an emphasis on habitat separation, activity patterns and feeding ecology all within a seasonal context. Habitat separation was analysed at three scales namely the macro, meso and microscales. The black and blue wildebeest showed clear resource partitioning in terms of habitat at the macro and mesoscales, but not a clear separation at the microscale.

The main factors determining the between the black and blue wildebeest separation as determined by the application of logistic regression analysis, was distance to shade, aspect and altitudes indicating that black wildebeest occupy the high-lying open north facing niches and the blue wildebeest occupy the low-lying, niches which

have a high availability of cover for protection from the heat which is not required by the black wildebeest.

Five broad habitats were delineated through the reserve and the vegetation characteristics for each habitat were measured. Black wildebeest were found to utilise the habitats which were the most open in terms of visibility and tree cover and which were high-lying. Blue wildebeest selected habitats with short grass and a history of cultivation as well as areas that ensured the close proximity to shade.

The feeding sites of the black and blue wildebeest were also analysed and compared in terms of their vegetation characteristics utilising discriminant analysis. Of the vegetation characteristics measured, only biomass and grass height proved to differentiate between the feeding sites of the black and blue wildebeest. Due to their similar trophic ecology, it was concluded that the black and blue wildebeest do not differ in terms of their microhabitat selection.

The activity budgets of the black and blue wildebeest were also compared. The black wildebeest was found to spend more time resting than the blue wildebeest. This was found to be due to the higher mobility of the blue wildebeest as compared to the extreme form of area selectivity practiced by the black wildebeest.

The population dynamics of the black and blue wildebeest was also investigated. It was found that the black wildebeest population at Ezemvelo Nature Reserve was declining over the last 3 years. The possible reasons for this decline were due to suboptimal habitat and thus decreased calf:cow ratios. The blue wildebeest population on the other hand was found to have been increasing. It was concluded that efforts needed to be made to prevent the further increase of the blue wildebeest population on the reserve so as to prevent the further encroachment of blue wildebeest bachelor males into black wildebeest territory.

Evidence for interspecific exploitative and interference competition was investigated. Due to the high spatial separation of the black and blue wildebeest at Ezemvelo Nature Reserve, little interference competition was observed accept for isolated cases where blue wildebeest bachelor males were encroaching on black wildebeest territory. Encounters between black and blue wildebeest usually showed that the blue wildebeest was dominant over the black wildebeest. Exploitative competition was found to be possible due to the high overlap in terms of habitat niche use and feeding niches.

Ecological separation between the black and blue wildebeest was not found to be complete. Certain differentiating factors such as a preference for open areas by black wildebeest and a preference for areas in the vicinity of suitable shade by blue wildebeest can be utilised to allow for the coexistence of black and blue wildebeest in an area with a high habitat heterogeneity. Homogeneous areas with low habitat diversity will not be suitable for the coexistence of black and blue wildebeest as habitat is the main differentiating mechanism between the two.

It was concluded that without the active management of the black and blue wildebeest populations at Ezemvelo Nature Reserve, the future of the black wildebeest population at least is not optimal. In the long term it was predicted that the black wildebeest population would continue to decline and the blue wildebeest would continue to increase utilising the habitats previously exclusively occupied by the black wildebeest. With the increase of alien vegetation providing further shade for the blue wildebeest in these habitats, this was considered entirely possible. Management recommendations for the black and blue wildebeest populations at Ezemvelo Nature Reserve were made and dicussed in detail.

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APPENDICES

APPENDIX 1

Habitat Selection Field Data Sheet

		1	2	3	4	5	6	7	8	9	10
Date											
Time											
Co-ordinates											
Type of wildebeest											
Group compos.	Males										
	Females										
	Subadults										
	Calves										
	Total herd size										
Activity	Grazing										
	Lying down										
	Walking										
	Standing										
	Other										
Habitat type											
Aspect											
Slope/Gradient											
Altitude											
Geomorphology											
Landscape position	Plains										
	Gentle slopes										
	Valley										
	Plateaus										
Woody density	None										
	Sparse										
	Open										
Grass cover	Sparse										
	Medium										
	Dense										
Total grass height											
Grass leaf height											
Distance to water											
Dominant plant species											
Sub-dominant species											
Vegetation structure											
Plant utilisation											
Forb : grass ratio											
Cloud cover											
Temperature											
Wind velocity											
Wind direction											
Drainage											
Exposure											
Rock cover											
Visibility											
Distance to shade											
Associations											
Erosion											
Time since last burn											

APPENDIX 2

The variables and their categories that were utilised in the PROC LOGISTIC procedure to determine the level of meso-habitat separation between the black and blue wildebeest at Ezemvelo Nature Reserve from January 2004 to August 2005

Variable	Description	Number of categories	Categories and abbreviations used
V20	Woody vegetation cover	3	1. None 2. Sparse 3. Open
V21	Grass cover	3	1. Sparse 2. Medium 3. Dense
V22	Cloud cover	3	1. 0% (Clear skies) 2. 1-50% (Partly cloudy) 3. >50% (Overcast)
		3	1. 0% 2. 1-50% 3. >50 %
V23	Temperature	3	1. <15ºC 2. ≥15-25ºC 3. >25ºC
V24	Wind speed	4	1. None (0-2 km/h) 2. Slight (>2 – 5 km/h) 3. Moderate (>5 – 13 km/h) 4. Severe (>13 km/h)
V25	Wind Direction	6	1. North 2. Northeast 3. East 4. Southeast 5. West 6. Northwest
V26	Rock Cover	6	1. None 2. 1-30% 3. >30%
V27	Total grass height	3	1. 0-50 mm 2. >50-500 mm 3. >500-800 mm
V28	Grass leaf height	4	1. 0-50 mm 2. >50- 100 mm 3. >100-400 mm 4. >400 mm

APPENDIX 2 Continued.

Variable	Description	Number of categories in group	Categories and abbreviations used
V29	Plant utilisation	4	1. Low 2. Moderate 3. High 4. Excessive
V30	Visibility	4	1. 0-50 m 2. >50-100 m 3. >100-200 m 4. >200 m
V31	Distance to shade	4	1. 0-5 m 2. >5-100 m 3. >100-600 m 4. >600 m
V34	Erosion	3	1. Low 2. Moderate 3. High
V35	Altitude		1. ≤1340 m 2. >1340-1360 m 3. >1360-1380 m 4. >1380
V36	Date of last burn	5	1. 2001 or earlier 2. 2002 3. 2003 4. 2004 5. 2005
V39	Exposure	3	1. Shade 2. Partial shade 3. Full sun
V40	Geomorphology	3	1. Flat 2. Concave 3. Convex
V41	Forb : grass ratio	4	1. 0:100 2. 10:90 3. 30:70 4. 50:50
V43	Social structure	3	1. Bachelor herds 2. Female herds 3. Territorial bulls