CHAPTER 1

Introduction

General aims

The aims of the study were:

a. To establish the annual pattern of movement of zebra and wildebeest in northern Botswana,

b. to establish the annual and seasonal ranges of the zebra and wildebeest populations,

c. to investigate the influence of surface water availability and rainfall on the annual distribution and movement of zebra and wildebeest, and

d. to investigate the influence of changing levels of available forage quantity and quality on the movements and distributions of zebra and wildebeest in the wet season range.

Background

There are few remaining migrations of large ungulates in southern African savannas. Documented studies of migratory populations include zebra (Smuts, 1972) and wildebeest (Whyte, 1985) in the Central district of the Kruger National Park and wildebeest in the Kalahari Gemsbok National Park (Mills & Retief, 1984a; van der

Walt *et al*, 1984). Less well documented cases, of what may be migratory populations, are the seasonal movements of wildebeest and red hartebeest in the Central Kalahari Game Reserve (Campbell, 1981; Williamson *et al*, 1988; Parry, 1987; K. Lindsay, pers. comm.) and zebra, wildebeest (Kgathi & Kalikawe, 1993) and springbok (R. Ritter, pers. comm.) in the Nxai - Makgadikgadi Pans National Park, both areas in Botswana. Former migrations, the movements having been curtailed by fence erection and water provision, were undertaken by wildebeest in Etosha National Park, Namibia (Berry, 1980) and a western sub-population of wildebeest in the Kruger National Park (Whyte, 1985; Whyte & Joubert, 1988).

Studies conducted on the wildebeest and zebra migrations in the Serengeti region in East Africa (Pennycuick, 1975; Maddock, 1979), elucidate the relationships between animal movements and different environmental factors in detail. While this information might be translated to wildlife management systems in southern Africa, there are a number of differences between the Serengeti region and southern African savannah ecosystems (Table 1.1).

Table 1.1: Some differences in environmental factors between the Serengeti region and two southern African savannah ecosystems.

	Southern Africa		
Factor	*Central district*, Kruger National Park, S. Africa[1, 2]	Chobe National Park, Botswana[3]	Serengeti region, Tanzania[4]
Rainfall	N-S gradient; 500 mm - 600 mm	S-N gradient; 500 mm – 600 mm	SE-NW gradient; 250 mm - 1000 mm
Soils	Granitic soils in west; shallow, rocky basaltic soils in east	Deep Kalahari sands interspersed with shallow fluvial *sediments in north*; lacustrine clays in south	*Shallow volcanic* derived soils becoming deeper granitic soils to the west
Relative soil Fertility	Moderately good	*Poor (sands) to* medium (clays)	*Rich (volcanic* derived soils) becoming moderate to the west.
Grassland structure	Tall, coarse grasslands in east; *short, fine* grasslands in west	Tall, coarse perennials on sands; *short, fine* perennials & abundant annuals on clays	Short grass on southern plains; taller coarse grass in north-west *woodlands*
Migratory Herbivores	W'beest,~*10 000* *Zebra, ~12 000*	*W'beest, 800 – 1 000* *Zebra*, 8 000 – 10 000	W'beest, +1 500 000 Zebra, ~250 000

[1]Gertenbach, 1983.

[3]Joos-Vandewalle, 1984; 1988; present study.

[4]Sinclair & Norton-Griffiths, 1979; McNaughton, 1983.

[2]Viljoen, 1993.

The Chobe district wildlife area in northern Botswana is a largely unrestricted ecosystem and in southern Africa is possibly the only such ecosystem in existence. Several aspects distinguish northern Botswana from other migratory ecosystems studied in Africa. Firstly, there are no fences and wildlife can move freely throughout the region. The erection of fences elsewhere in southern Africa in the past has had a major influence on the migrations of ungulates, inevitably resulting in large declines in the affected populations. The erection of a veterinary cordon fence between the Kruger National Park (KNP) in South Africa and neighbouring privately owned farms along the western boundary of the park in 1961, excluded wildebeest from their dry season range near the Sand River (Whyte & Joubert, 1988). The physical barrier directly caused an unknown number of deaths but the restriction of the annual range, and subsequent overgrazing, appears to have been the main cause of mortality. To alleviate the effects of overgrazing, a large number of wildebeest were also culled over a seven year period starting in 1965. In all, by 1979 the population had declined by an estimated 66% (Whyte & Joubert, 1988).

A second documented case was in the Central Kalahari Game Reserve in Botswana where the Khuke veterinary cordon fence, aimed to control the spread of foot-and-mouth disease, was erected along the northern border of the reserve in the late 1950's. As in the KNP example, the geographical location of the fence was decided on socio-political rather than on ecological grounds. The fence prevented access of the Kalahari migratory wildebeest population to the Boteti River in the dry season during years of poor rainfall (Williamson, Williamson & Ngwamotsoko, 1988). Lake Xau in the east, a populated settlement with domestic stock, was the only alternative area with available fresh water which attracted many of the surviving but

emaciated wildebeest (Parry, 1987; Williamson *et al.*, 1988). Since the erection of the fence, more than 100 000 wildebeest have died of starvation and a lack of fresh water while persecution by cattle owners and the fence itself also contributed to mortality (Owens & Owens, 1980; Williamson & Williamson, 1981; Parry, 1987; Williamson & Mbano, 1988). Estimates of mortality were made in 1964, 1970 and 1979-1983 and Williamson & Mbano (1988) suggest that mortality was certain to have occurred during below average rainfall years when estimates of deaths were not recorded and that the total number of wildebeest that have died more realistically exceeds 200 000.

The second distinguishing characteristic of the Chobe wildlife ecosystem is the distinct lack of management activity such as water provision, culling and controlled burning, all or some being common management practices in wildlife sanctuaries elsewhere in southern Africa. Although some water has recently been provided to animals in Chobe, the pumps and engines have operated intermittently. Poor maintenance, lack of finances and damage to equipment by large concentrations of elephants at the water points has contributed to the failure of a consistent and widespread provision of water (personal observation). As a result, water provision does not appear to have had an affect on the behaviour pattern, especially the movements, of zebra and wildebeest in the region. Badly maintained bore-holes intended for the provision of water to animals in the Makgadikgadi Pans National Park have also had minimal influence on the movement patterns of zebra and wildebeest in the region (Kgathi & Kalikawe, 1993). The supplying of water to animals in dry regions or manipulation by closure of such artificially supplied watering points however can influence, and have markedly affected, the seasonal movements and

distributions of water dependent ungulates in semi-arid savannas elsewhere (Child, 1972; Joubert, 1974; Western, 1975; Mills & Retief, 1984a & b; Knight, 1991, 1993). In the Kalahari Gemsbok National Park (KGNP) in South Africa, a total of 88 artificial waterholes exist in the Auob and Nossob dry riverbeds (Van Wyk & Le Riche, 1984; Knight, 1991, 1993). Wildebeest have been shown to use these waterholes extensively, even in the wet season (Mills & Retief, 1984a), and experimental closure of watering points in the Auob river resulted in the redistribution of the associated wildebeest away from previous areas of concentration around water points (Mills & Retief, 1984b; Knight, 1993). In the KNP, widespread water is supplied for animals throughout the park in more than 300 manmade structures such as dams, weirs and troughs pumped from bore-holes (Pienaar, 1970; Joubert, 1974; Thrash, Theron & Bothma, 1993). Although some dispersal of animals occurs in the wet season and migrations of wildebeest and zebra are still evident (Smuts, 1972; Whyte, 1985), the dry season distribution of water dependent animals tends to be closely associated with the water points (Thrash *et al.*, 1993; Whyte & Joubert, 1988). Furthermore, the policy of water provision to redistribute water dependent herbivores throughout the park (Joubert, 1974) appears to have been successful in that large numbers of zebra and wildebeest now reside in previously unoccupied areas where seasonal supplies of water have over time been replaced by permanent supplies. Large increases in elephant, buffalo and hippopotamus numbers, species allegedly capable of inflicting extensive impact on the vegetation, were regularly controlled by culling while zebra, wildebeest and impala numbers have also been reduced on occasion (Pienaar, 1969; Joubert, 1974; Smuts, 1974). The cropping of large predators has also been implemented as a management strategy in KNP in the past to manipulate

predator-prey relations (Smuts, 1975, 1978).

Perennial water availability in Chobe is limited to the large rivers, the Linyanti, Chobe and Kwando, in the north and north-west (Child, 1968; Joos-Vandewalle, 1988). The vast interior region is devoid of water for most of the winter months but seasonal pans fill during the summer rains. Hence, the pattern of surface water availability changes markedly from season to season. The cropping of animals for management purposes is not practised in Chobe but professional and subsistence hunting is conducted in the Controlled Hunting Areas (CHA) bordering CNP to the north and west. Numbers of animals shot are controlled by a quota system although poaching (or illegal hunting) appears to contribute to an additional number of animals shot each year. The exact number of animals shot annually is not known and may or may not have an effect on the population dynamics of the hunted species. It is unlikely, however, that the hunting is affecting the annual movement patterns of zebra and wildebeest because the main concentrations of animals in the dry season range were in a limited area, and close to the villages (Parakarunga and Satau), which is where the most disturbance can be expected.

Finally, other than the possible influence of hunting on animal populations in the Chobe district, the encroachment of humans and associated activities of people in the ecosystem is limited. Human settlement and development, pastoral and agricultural activities associated with settlement inevitably impact on wildlife especially when the encroachment of humans impinges on wildlife range. The lifestyle of humans increasingly conflicts with wildlife as localised human populations multiply and the wild animals are hunted, displaced or seasonal range is lost to

grazing by domestic stock or ploughing (Sinclair & Fryxell, 1985, Bell, 1987). The most commonly used management strategy to resolve human-wildlife conflicts is the separation of the two by fences and the situation along the western boundary of the Central District in KNP and the resultant effects on the wildebeest population there has already been discussed. Human encroachment and rising potential conflict with migratory zebra and wildebeest has recently been reported around the Makgadikgadi Pans National Park in Botswana (Kgathi & Kalikawe, 1993). The annual ranges of the zebra and wildebeest extend beyond the park boundaries when pans are used in the wet season and the Boteti river in the dry season, thereby bringing the animals in contact with villagers and their stock. As the local human population increases and demands for water, forage and space increase, the outcome is likely to mirror that of the conflict between villagers and wildebeest at Lake Xau in the Central Kalahari in Botswana as described above.

The absence of fences and management strategies that restrict animal behaviour and movement in the Chobe district make it an attractive migratory ecosystem to study. The influence of seasonally variable water supplies and various factors of forage availability on the movement patterns of zebra and wildebeest can be investigated without the presence of confounding management and human activities. The study would allow comparisons to be made with other ecosystems in the southern African sub-region where human intervention is present. The rate of human population increase in Africa is the highest (3.5 % p.a.) of any continent and exceeds 4 % in Botswana (Myers, 1980 in Bell, 1987). Future human encroachment on the extensive wildlife ecosystems in the north of the country is an inevitable likelihood. Hence, a further advantage to studying the migrations means the gathering of

information to prevent conflicts arising and would greatly assist with the development of an appropriate management policy (if required) to ensure the persistence of the migrations and the resource in the region.

Literature review

i. Annual movement patterns of large African grazing ungulates

Animal movement tends to be linked to the distribution and nature of available resources and such movement, in evolutionary terms, is thought to improve the long-term fitness of individuals (Baker, 1978; Swingland & Greenwood, 1983). Grazing ungulates in African ecosystems are surrounded by an apparent abundance of forage but plant foliage is of generally low nutritional value so that bulky food intakes by herbivores are required to meet nutritive requirements. Furthermore, the quantity and quality of food resources and surface water availability, in the absence of provision by management staff, in semi-arid areas varies both spatially and temporally. Hence, large herbivores interact with forage and water resources at several levels of ecological resolution and are confronted by a series of interrelated foraging problems (water requirements included) at different temporal and spatial scales (Senft *et al.*, 1987).

Small scale movements, usually less than 10 km a year, of large herbivores generally involve changes in habitat and grass communities in relation to food resources (Senft *et al.*, 1987), breeding (Sinclair, 1983a), anti-predator behaviour (Sinclair, 1985) or daily extremes of weather. Such movements are exhibited by resident species. Large scale movements of 30 km or more occur in response to seasonal fluctuations in

environmental conditions. Such movements involve changes in the use of landscape units within regions (Senft *et al.*, 1987) and the annual range of individuals is large, often equal in extent to that of the population (Duncan, 1975). Three types of large scale movement patterns of wildlife have been described. These are i) wet season dispersal, ii) nomadic movement and iii) migration. Each type of movement relates to the particular water and food requirements of animals and the specific nature of the spatial and temporal availability of water and food within the ecosystem.

ii. Rainfall and water availability

Large grazing ungulates in Africa, with few exceptions, are dependent on accessibility to a consistent supply of surface water (Western, 1975). Water supplies can be seasonally limited, thereby restricting the dry season range and distribution of grazing ungulates to feeding areas within ranging distance from surface water. In dry areas with a reasonably uniform distribution of permanent water, animals will tend to converge around water sources in the dry season (Sinclair, 1983b). In the wet season the animals then disperse from the dry season range as described for Amboseli in Kenya (Western, 1975), Tarangire in Tanzania (Talbot & Talbot, 1963; Lamprey, 1963), the Zambezi Valley in Zimbabwe (Jarman, 1971) and the Kalahari Gemsbok National Park in South Africa (Knight, 1991). Movement patterns such as these are described as wet season dispersion but take on at least two forms. The degree to which the wet and dry season ranges overlap distinguishes the two forms. Firstly, in the Kalahari Gemsbok National Park, individual animals in the population essentially expanded home ranges in the wet season. The wet and dry season home ranges of individual animals and those of the population, however, overlapped

markedly (Mills & Retief, 1984b; Knight, 1991). Although centred around permanent water sources, the seasonal ranges varied in size between years depending on the amount and distribution of rainfall. The second form of wet season dispersal tends to be more predictable as in Amboseli, for example, where water dependent populations used a wet season range that was discrete from the dry season range (Western, 1975).

In regions where rainfall is highly variable in time and space, and water availability is related to the pattern of rainfall, ungulate concentrations may shift from year to year (Sinclair, 1983b). Grazing ungulates then roam in a nomadic fashion in search of the best forage and the distinction between wet and dry season ranges tends to be less clear. Buffalo in East Africa typically exhibit such nomadic movements tracking green grass growth following rainfall events within a fixed although large home range (Sinclair, 1974a).

Some movements are determined by the distribution of rainfall during the drier months of the year rather than by the distribution of permanent and seasonal water supplies (Sinclair, 1983a). For example, the migration of grazing ungulates in the Serengeti region (Pennycuick, 1975; Maddock, 1979) where zebra and wildebeest move to areas with a high annual rainfall in the dry months of the year and to areas with a low annual rainfall in the wetter months. The zebra and wildebeest populations used discrete wet and dry season ranges which were separate from each other although the time of arrival and departure of animals to and from the seasonal ranges differed according to the timing of the rains (Maddock, 1979). The general area of high rainfall is predictable as there is a steep rainfall gradient in the region

(McNaughton, 1983) so the overall pattern of migration is also predictable. Although the annual pattern of movement is governed by the timing and distribution pattern of rainfall, various factors of forage availability determine the specific nature of the migration and will be discussed in the next section.

Wet season dispersal movements appear to be intermediate between nomadic movements and migrations. Wet season dispersal movements differ from migrations in the more limited scale of distance moved between seasons in the former type. During migratory movements, such as the wildebeest in the Serengeti region, the seasonal and annual ranges of all individual animals are similar in location and extent as the ranges of the population (Pennycuick, 1975; Inglis, 1976; Maddock, 1979). Though this has not been demonstrated, I expect that in contrast to migratory species, in those which show wet season dispersal and nomadic movements, the individual seasonal ranges tend to be smaller than the population range and the wet season ranges unpredictable and variable between years. Although the overall annual pattern of migrations are largely, but not entirely, predictable both in time and space (Western, 1975; Sinclair, 1983a), movements at the smaller seasonal scale are unpredictable and nomadic because of the unpredictability of rainstorms and hence green food.

iii. *Forage and other factors*

Grazing ungulates can be separated into two categories according to digestive physiology, namely the ruminants and the non-ruminants (hind-gut fermenters). The nutrient requirements and digestive anatomical and physiological differences between ruminants and non-ruminants have been suggested in detail (Bell, 1969,

1971; Owen-Smith, 1982; Demment & Van Soest, 1985; McNaughton & Georgiadis, 1986; Duncan, 1992). The most relevant difference in the context of this work is the tolerance levels of low food quality and quantity exhibited by ruminants and non-ruminants. The digestive system of ruminants enables them to achieve high levels of digestibility of nutrients from ingested food, but they cannot survive on low quality forage. They select vegetation parts with high protein/fibre ratios such as leaves and shoots. Non-ruminants have simple stomachs and overall digestion of food is less complete than in ruminants but, with more fibrous food, a higher gut passage rate in non-ruminants more than compensates for the poorer digestive efficiency and protein absorption (Duncan *et al.*, 1990). As a result, non-ruminants require a greater daily food intake rate than ruminants of the same body size and can tolerate higher fibre contents in their diet.

In grazing, ungulates effect change in the grass layer by decreasing forage availability. Theory states that animals move because the resources gained more than offsets the expense of movement so that reproductive output is enhanced (see Swingland & Greenwood, 1983). When resources in a patch used by an animal decrease with time as a result of depletion by consumption and the rate of energy gain declines with increasing residence time in a patch, then at some point the animal should move (Pennycuick, 1979). The point in time when an animal should move is described by the marginal value theorem which predicts that an animal should move when its net rate of energy gain declines to the average rate it can expect from the habitat (Charnov, 1976; Stephens & Krebs, 1986).

According to optimal foraging theory, animals need to decide, firstly, when to move

and, secondly, where to move to (Pyke *et al.*, 1977). The decision when to move should be prompted by a decreased rate of food intake as a result of the local consumption and subsequent depletion of resources, while the decision where to move to is determined by the sampling of feeding conditions in areas close by (Pyke, 1983). Both decisions might be influenced by past experience of grazing conditions in areas used enabling the animal to anticipate the net difference in food gain among habitats (Pyke, 1983).

Nutrients play an important role in the foraging behaviour and movement patterns of herbivores. It has been suggested by Westoby (1974) that large generalist herbivores, such as zebra and wildebeest (Jarman, 1974; Demment & Van Soest, 1983), should include the best mix of food in their diet such that the total intake of nutrients satisfies the daily minimum requirement of the animal. The model for foraging behaviour developed by Owen-Smith & Novellie (1982) suggest an ungulate would select a diet that maximises rate of intake of the most limiting nutrients over time. In general, foraging models and feeding pattern theories underscore the principle that an ungulate should increase the nutritional value of its diet by selecting plant parts of highest nutritional quality from species of high nutrient quality in communities with a high proportion of these nutritious plants. Tests of the theory for herbivorous animals show that their decisions sometimes fit theory, but not always (Belovsky, 1984).

Important forage related factors that influence the wildebeest and zebra migration in Serengeti are grassland physiognomy and grass phenology in terms of growth stage, greenness and increment of green biomass (productivity) (Maddock, 1979;

McNaughton, 1979, 1985; Sinclair & Fryxell, 1985). The distribution of forage minerals also influences the seasonal movements and distributions of these migratory ungulates, especially at the time of parturition (McNaughton, 1990). Predator avoidance, breeding synchronisation and avoidance of saturated muddy soils have been proposed as added advantages of the migration (Talbot & Talbot, 1963; Maddock, 1979; Sinclair, 1983a).

Movements of the northern, or Satara, non-migratory sub-population of wildebeest in the Kruger National Park can best be related to availability of suitable habitat in relation to fire, rainfall and utilisation (Whyte, 1985). The only true migratory zebra in the Kruger National Park are found in the Central District. Observations made on the movement and distribution patterns of these zebra imply that the most important factors affecting the seasonal choice of habitat were water and grazing conditions (Smuts, 1972). Other factors which may affect the movement patterns are hilly terrain, waterlogged and sticky soils, scrub thickets and presence of predators and potentially competing herbivores, all of which there was a tendency to avoid.

Two distinct populations of wildebeest occur in the southern Kalahari. A small sedentary population inhabits the riverbeds, where permanent water supplies have helped establish this population, and a highly nomadic population which appears to be independent of water but dependent on water storing plants (Mills & Retief, 1984b). The river population does not move far from the riverbeds although numbers along the rivers tend to increase in the wet season, indicating some dispersal in the dry season. Vegetation in the riverbeds is richer in minerals than the surrounding dune fields and some of the grasses are of the highest quality grasses in the area

and animals concentrate in the rivers in the wet season. In general, wildebeest distribution was positively correlated with available green foliage, particularly in the wet season following rainstorm events or on burned areas in the dry season (van der Walt *et al.* 1984).

Cape mountain zebra (*Equus zebra zebra*) in South Africa moved onto the plateau in summer and the hill slopes in winter in association with a relative change in dietary crude protein levels in the faeces and favoured grass species (Novellie, Fourie, Kok, & Van der Westhuizen, 1988).

In summary, various types of movement patterns are evident amongst large African ungulates. The nature of these movements in terms of range use, seasonal home range patterns and distances moved are determined by patterns of change in resource availability and other factors across time and space. Habitats, rainfall and its influence on water and forage availability as well as forage quantity and quality all play a role in determining movement patterns and are linked to the anatomical and physiological adaptations of the animals involved.

Very little is known about the feeding ecology of zebra and wildebeest. It is widely held that wildebeest and zebra use areas and feed on grasses of different heights, wildebeest preferring shorter grasslands than zebra (Bell, 1969, 1971). There have been many studies of comparative diets (e.g. Gwynne & Bell, 1968; Ben-Shahar & Coe, 1992) which show that the animals use different grass species and plant parts. However, the overlap in diets is extensive. In spite of the key place that zebra and wildebeest occupy in African grazing ecosystems, very little is known about the nutritional causes and consequences of choice of food items by these animals (e.g.

plant species, plant parts). But we do know that analyses of habitat choice and migration indicate that zebra and wildebeest use seasonal ranges with grasses of high nutrient factors (Novellie *et al.*, 1988; McNaughton, 1990; Ben-Shahar & Coe, 1992).

The data for this study are presented in three chapters. Each chapter has been written as a stand-alone paper although none of these have been submitted for publication yet. The first data chapter (Chapter 2) describes the individual wet season ranges of zebra and wildebeest, the seasonal and annual ranges of the two populations and then investigates the relationship of seasonal movement patterns with rainfall and water availability. The second chapter (Chapter 3) describes the selection of feeding areas in the wet season range in relation to grassland species composition, phenology and height. The third chapter (Chapter 4) describes the possible influence of differences in grass nutrient factors on the choice between two areas of concentrated use by zebra within the wet season range. The final chapter of the thesis is a discussion chapter summarising the study.

CHAPTER 2

Movements of zebra and wildebeest in relation to rainfall and surface water availability in north-eastern Botswana

Introduction

Regular movement of large ungulates between distinct seasonal ranges, better known as migrations, has gained much ecological attention. In Southern Africa alone, a number of studies have documented migratory movements of wildlife populations. These include the migrations of zebra and wildebeest in the Central District of the Kruger National Park (Smuts, 1972; 1975; Whyte, 1985), wildebeest in the Kalahari Gemsbok National Park (Mills & Retief, 1984a, 1984b; van der Walt, Retief, le Riche, Mills & de Graaf, 1984), wildebeest in the Central Kalahari (Williamson, Williamson & Ngwamotsoko, 1988) and zebra and wildebeest in the Nxai-Makgadikgadi Pans National Park (Kgathi & Kalikawe, 1993). There are presently also a number of ongoing studies on animal movements throughout Botswana. Despite numerous investigations (cf. Chapter 1), there is no body of theory that allows prediction of the patterns of movement by large mammalian herbivores. Furthermore, most wildlife populations in southern Africa are exposed to some level of human management such as water provision, culling, controlled burning and/or fencing. The ability to define seasonal ranges and assess factors affecting migratory behaviour of large African herbivores independent of any management practices is, therefore, limited.

Studies have attempted to relate observed movement patterns and various factors of

interest. In the Amboseli region of Kenya, movements by zebra and wildebeest appeared primarily related to water (Western, 1975). Annual movements were between dry season concentration areas near perennial water sources and dispersal in the wet season to areas lacking permanent water. Seasonal movements by some sub-populations of wildebeest and zebra in Kruger National Park (KNP), South Africa, also followed this pattern (Smuts, 1972; Whyte, 1985). However, the effect of fencing, water provision, culling and controlled burning practices on these movements is difficult to determine (Pienaar, 1970; Joubert, 1974; Whyte & Joubert, 1988; Thrash, Theron & Bothma, 1993). In the central Kalahari region of southern Botswana, wildebeest remain in ranges lacking surface water year-round in most years, but are forced to trek to permanent water in very dry years (Campbell, 1981; Williamson *et al.*, 1988). New fences restricting these movements resulted in a population crash in 1982-83 from approximately 100 000 animals to 10 000 (Owen & Owen, 1980; Williamson & Williamson, 1981; Parry, 1987; Williamson & Mbano, 1988) illustrating the essential nature of these movements and the sometimes dramatic effects of management intervention.

The spectacular migration of wildebeest and zebra in the Serengeti region of Tanzania and adjoining Kenya appears to be influenced by the lack of surface water on the plains and rainfall effects on green grass growth (Maddock, 1979). However, these movements appear not to be solely related to water but include selection for areas offering high concentrations of mineral nutrients, particularly phosphorus, around the time of parturition (McNaughton, Oesterheld, Frank & Williams, 1989; McNaughton, 1990; Murray, 1993).

In the Makgadikgadi Pans region of central Botswana, surface water, food supplies and mineral nutrients were potential influences on the seasonal movements of zebra and wildebeest, but no clear causal relationship could be established (Kgathi and Kalikawe, 1993).

Although seasonal changes in the numbers of the zebra and wildebeest populations in the Savuti region of Chobe National Park (CNP) in north-eastern Botswana suggested the existence of long distance movements (Joos-Vandewalle, 1988), seasonal movement patterns and factors influencing these movements have never been studied. Prior to 1995, wildlife populations in and around CNP were largely unaffected by human interference. Restricted hunting occurred in areas adjacent to the park and one borehole-reticulated pan was in existence near the camps in Savuti. However, movement was unrestricted by fences, human settlement or artificial water sources. Study of the zebra and wildebeest populations, therefore, provided a good opportunity to evaluate the effects of environmental factors on the movement patterns of large herbivores in an African ecosystem.

In this chapter, the population and seasonal ranges of zebra and wildebeest and the detailed timing and pattern of movement between their seasonal ranges are described. The influence of rainfall and surface water availability on the observed movement patterns was investigated.

Study area

i. Location

The study was conducted in north-eastern Botswana (Fig. 2.1a & b). The distribution

of zebra and wildebeest during the study determined the spatial limits of the study area. For the most part, this included the north-western part of the unfenced Chobe National Park and adjacent Wildlife Management Areas along the Linyanti River, the Savuti region centrally and the Mababe region in the south. The Linyanti River was the only perennial water source in the area. In the wet season water in rain filled pans occurred throughout the study area.

ii. Climate

The climate is sub-tropical with distinct wet and dry seasons. Rains occur during the summer months from October to March while rainfall during the winter months from April to September is negligible (Fig. 2.2). There is a rainfall gradient from Kasane[1] in the north-east (annual average of 579 mm; N=13 years) through Savuti[2] (525 mm; N=10 years) towards Maun[1] in the south-west (415 mm; N=11 years).

iii. Soils and vegetation

Except for deposits of fluvial and lacustrine clays and sediments (Cooke, 1980), the flat expanses of northern Botswana are covered mostly by deep Kalahari sands (Blair-Rains & McKay, 1968). The central and southern parts of the study area lay within an ancient lakebed known as the Mababe Depression. Within this depression, the soils exhibited distinct patterns of sediments and clays and this pattern was reflected in a similarly distinct mosaic of vegetation types (Joos-Vandewalle, 1988).

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[1] Data from Meteorological Services, Gaborone

[2] Data from Savuti Research Camp; only possible source of accurate data in the region

The Savuti Marsh lies in the north-central part of the Mababe Depression and was seasonally flooded prior to 1983. During the period of this study, the marsh was never inundated and was a dry, short to medium height grassland comprising predominantly *Cynodon dactylon* and *Sporobolus ioclados*. Other than a narrow strip of *Acacia* woodlands along the western side of the plains, the wooded vegetation to the west, north and east comprised *Colophospermum mopane*, interspersed with patches of *Terminalia* and *Combretum* woodlands and scrublands. Grass biomass in the *C. mopane* vegetation was generally low, even in the wet season (Joos-Vandewalle, 1984). The heavy clays in the southern parts of the Mababe depression supported medium to tall grasslands of *Bothriochloa insculpta*, *Aristida congesta* and *Cenchrus ciliaris* with patches of short *C. dactylon*. *Echinichloa crus-galli* was common around the edges of seasonal pans. It is not clear when this southern Mababe grassland last flooded but it was not as recent as the Savuti grassland. As a result, trees and shrubs have established and patches of *Acacia mellifera* thickets occurred in varying densities throughout the southern grassland while *A. tortilis* woodlands occurred in the south-west.

The vegetation in the northern parts of the study area outside the Mababe depression comprised a mixture of tall *Burkea africana, Terminalia sericea* and *Baikaea plurijuga* woodlands on deep sands. Ancient floodplains, historically flooded from the Linyanti River, occurred in the extreme north. The more clay soils and sediments of these ancient floodplains supported woodlands and scrublands dominated by *Combretum* spp. and *C. mopane* along the edges, while short grasslands of predominantly *C. dactylon* and *Brachiaria nigropedata* occurred within the ancient channel network.

Throughout the study area, annuals formed an important component of the grass layer and *Urochloa trichopus* was particularly common especially on the Savuti grassland.

iv. Zebra and wildebeest populations

Between 8 000 and 10 000 zebra and between 800 and 1 000 wildebeest occurred in the Savuti region of CNP in the 1985/6 wet season (Joos-Vandewalle, 1988). These estimates were made during times of peak concentration of herds in the area from December to May. In the dry season, no zebra and few wildebeest occurred in or around the Savuti grassland and Mababe Depression due to the movement of the animals to a dry season range away from these areas. Accurate estimates for the zebra and wildebeest populations prior to 1985 were not available but the populations have both declined substantially since the Savuti Channel dried up in 1983. Prior to the channel drying, approximately 40 000 zebra and 5 000 wildebeest were estimated to occur in the Savuti region (P. Viljoen & R. Fuhr, Chobe Lion Research Camp, data unavailable).

Methods

i. Rainfall

The study was initiated during the 1990/91 wet season and was concluded at the end of the dry season in 1993. Daily rainfall was measured at the Savuti research camp, situated in the centre of the study area, which was the only possible source of accurate data for the region.

ii. Surface water availability

Surface water availability was measured as the percentage of seasonal pans in the wet season range that contained drinking water for animals (a layer at least 5 - 10 cm above the mud substrate). During the course of the 1991 dry season, twenty-nine large seasonal pans were mapped. Small pans dried quickly and therefore were not monitored (Joos-Vandewalle, 1988). The rate at which pans dried up after the last rains of the season was determined as the proportion of pans still containing available drinking water each consecutive fortnight. The rate at which pans dried in 1992 was similar to that in 1985 (Joos-Vandewalle, 1988) despite different rainfall amounts in the two years. Therefore, pans were not monitored in 1993 and the 1992 data were used as a general pattern for the annual drying of pans in the region.

iii. Radio tracking

Radio-collars were fitted on a total of 20 zebra and 8 wildebeest during the study (see Appendix I). At the start of the project, 9 zebra and 7 wildebeest were collared. Dry season mortality of zebra due to hunting and predation was high and a number of radio-collared animals died each year. Therefore, collars were fitted to an additional 5 mares during the 1991/92 wet season and 6 mares during the 1992/93 wet season. In order to reduce variability in the data due to age and sex differences, the majority of animals collared were adult females. However, two zebra stallions and two wildebeest bulls were collared to investigate any differences between the behaviour of sexes. When selecting target animals for collaring, individuals far removed from previously collared animals were chosen in order to distribute collars as widely as possible in the population. The high mortality rate of collared zebra posed a problem

for obtaining sequential data that were required for analysis of animal movements between the seasonal ranges. Each newly marked animal was, therefore, considered a new sample during these analyses. Therefore, those animals that were collared, or collared animals that died, during the migration, did not satisfy requirements for the analysis of sequential data and were excluded from movement analyses for that particular season.

Standard aerial radio-tracking techniques were used to investigate the patterns of annual movement and the extent of seasonal ranges of the zebra and wildebeest populations (White & Garrott, 1990). Generally all collars were located every fortnight in the wet season although adverse weather conditions occasionally precluded a set flying schedule. In such cases, tracking was conducted at the soonest possible time after the fortnightly set date. During migrations (October to December and April to May), locations were made weekly. No tracking was done in January 1992 (due to unavailability of an aircraft) and during the dry season from June to September except for one tracking in June and one in July of 1993 because of the late rains in April. Independence of observations was ensured by tracking individual collared animals at the most every two or three days (White & Garrott, 1990). In total, 544 locations on zebra and 263 on wildebeest were made from April 1991 to July 1993 during 19 aerial tracking months.

Because visual observation of collared animals during tracking flights was not always possible, the level of error (distance between actual and estimated locations) was tested under field conditions. Three radio collars were placed at different locations by an independent observer. The location of these collars was then determined during

an aerial tracking flight. In addition, nine mortality collars were retrieved from the field after their estimated positions had been determined during aerial tracking. The mean (±sd) distance between the actual and estimated locations was 123 m (±72.3 m) with a range of 25 m - 260 m. Given the large distances that zebra and wildebeest moved and the objectives of the study, the level of error measured was considered to be insignificant.

iv. Home range analysis

The individual home ranges of collared animals were estimated by the Minimum Convex Polygon algorithm of the MCPAAL computer package (National Zoological Park, Smithsonian Institute, USA). The delineated ranges were not obviously concave and therefore the assumption of convex shape was not considered to be an important limitation (White & Garrott, 1990). When estimating the seasonal population ranges, all the points for all radio-collared individuals were used as there were roughly an equal number of locations per individual. The 90% contour of the seasonal ranges of the zebra and wildebeest populations was determined by ranking locations by distance from the mean X and Y co-ordinates. Those points furthest from the mean that made up 10% of all the locations were then excluded from analysis (Kenward, 1987 in White & Garrott, 1990). Overlap of the population seasonal ranges between years was compared graphically (Tierson, Mattfeld, Sage & Behrend, 1985) as a measure of seasonal fidelity or the tendency for zebra and wildebeest to use the same areas each year (White & Garrott, 1990). Seasonal range fidelity was tested statistically at the 95% significance level using Hotelling's T^2 test with the H_0 that the different year's seasonal mean X and Y co-ordinates were equal.

The wet season was recorded as that period between the first and the last rains each year. The dry season was recorded as that period when no rains occurred. There was a period of transition when animals moved between the seasonal ranges immediately after the first and last rains. The transition period from the dry to the wet season was defined as the period 30 days after the first rainfall event of the season (some time in October). The transition from the wet to the dry season was defined as the period 30 days after the last rainfall event of the season (some time in March or April). When determining the extents of the seasonal ranges of animals, these periods of transition were excluded from analysis.

v. Analysis of animal movements

The weekly displacement, or cumulative distance moved from the dry to the wet season ranges by the zebra and wildebeest populations, was calculated following the first rains of the 1991/92 and 1992/93 wet seasons. The weekly distance moved was calculated as the difference between the average of the latitude and longitude points for all radio-collared animals located each week. The point of origin used for displacement calculations was the average location in the dry season range the week prior to the first rainfall event for each season. The relationship between displacement and cumulative rainfall was represented graphically.

The rate at which the radio-collared zebra and wildebeest left the 1991/92 and the 1992/93 wet season ranges was calculated as the proportion of collared animals remaining in these ranges each week after the first rains of the season. The rate at which they left the 1991, 1992 and 1993 dry season ranges was calculated as that proportion that remained in these ranges after the last rainstorm at the end of the dry

season.

Results

i. Rainfall and surface water availability

The amount and pattern of rainfall during the three years of the study was highly variable (Fig. 2.2). The total annual rainfall (July to June) was the lowest in the 1990-91 season, when only 447 mm of rain fell. Most of this rain fell late in the season. The 1991/92 and 1992/93 wet seasons comprised early, heavy rains with a drier period in the middle of the season with recorded totals of 519 mm and 648 mm, respectively The majority of pans in the wet season range dried up in the first four months after the last rains (Fig. 2.3). Five particularly large pans dried at a slower rate and held water up until mid-August. From this time onward until the first rains of the following season no surface water occurred in the wet season range in all study years.

ii. *Migration from the dry to the wet season range*

Zebra

The first rains of the wet season, irrespective of the amount, caused an initial movement of zebra away from the Linyanti River. The first rains of the 1991/92 wet season occurred on the 18th October as a single storm when 9 mm fell. Within the first week after this rain, the zebra moved 30 km southward (Fig. 2.4). In the 1992/93 wet season the rains started on the 1st November when 104 mm fell over 5 days and the zebra moved between 10 km and 25 km southward (Fig. 2.4). Only once the rains continued and more than 80 mm had fallen in the 1991/92 season and 150 mm in the

1992/93 season, did all the collared zebra move out of their dry season range to the wet season range (Fig. 2.5). The radio-collared zebra left the dry season range progressively over time during the low rainfall of the 1991/92 season compared to the quicker and more unified movement during the high rainfall 1992/93 season. In both study years, a segment of the population, which comprised approximately one-third of the collared zebra, remained within a 20 km distance of the Linyanti River and did not comprise the same zebra from one study year to the next. This portion of the population remained close to the Linyanti River for 10 weeks in 1991 and 7 weeks in 1992 before following, and eventually joining, the rest of the population on the southward migration. Zebra comprising the first segment of the migration tended to move 20 km or more southward following a weeks rainfall of 20 mm or more and, either remained in place or, reversed their movement if less rain fell (Fig. 2.4 & Table 2.1). The relationship between displacement and cumulative rainfall in both years was linear.

Wildebeest

Initially, wildebeest followed the zebra and began leaving the dry season range approximately one week later than the zebra but then, once the migration was initiated, the wildebeest left the dry season range sooner than the zebra did (Fig. 2.5). Only in the 1991/92 season did the wildebeest migration move southward in two groupings when one-third of the collared wildebeest remained within 20 km of the Linyanti River for a short time (Fig. 2.6). The displacement of the first segment of wildebeest was linearly related to cumulative rainfall during the low rainfall 1991/92 season compared to the high rainfall 1992/93 season when they moved about 50 km

to Savuti after the first rains. This 'pulse' of movement occurred following only 40 mm of rain after the initial 100 mm of rain at the start of the season and, despite continued rains, further movement south was minimal (Fig. 2.6). Unlike the zebra did during the eighth week of 1992/93 season, wildebeest never reversed the southward movement once the migration had been initiated even if little rain fell within a week or two (Table 2.1). However, like the zebra, the weekly distance moved by wildebeest indicated a distinct response to rainfall of the preceding week.

iii. Migration from the wet to the dry season range

Zebra

In 1992 the rains stopped abruptly in late March. In 1993 the last significant rains occurred at the end of March but some small showers occurred late in April. Approximately two weeks after the last rains in both study years, the zebra began moving northward to the dry season range (Table 2.2). Any rainfall event that occurred after the initiation of the migration to the dry season range such as the storms in April of 1993, either slowed down, halted or, even in some cases, reversed the northward movement of zebra. The longest period that any collared zebra remained in the wet season range after the last rains was 9 weeks. Almost 50% of the pans still contained water at this time (Fig. 2.7), indicating that surface water availability was not the key factor initiating migration to the dry season range.

Table 2.1: Average weekly distance moved to the wet season range by radio-collared zebra and wildebeest in relation to the rainfall for the same week. A negative distance represents a movement in the direction of the dry season range.

Time since 1st rain (weeks)	1991 – 92			1992– 93		
	Weekly rainfall (mm)	Weekly distance moved (km)		Weekly rainfall (mm)	Weekly distance moved (km)	
		Zebra (N=7)	W'beest (N=6)		Zebra (N=7)	W'beest (N=4)
0	0	0	0	0	0	0
1	9.5	22	-	3	-	-
2	0	12.8	27.2	103.5	27.8	24.1
3	15	-0.6	-	2	-2.3	6.3
4	6.5	-	2.0	24	12.1	17.1
5	1	20.2	6.8	9	2.7	25.6
6	20.5	-2.9	3.4	12.5	5.6	-4.1
7	0	18.1	15	21	14.7	6.0
8	17.5	8.5	0.9	0	-17.4	-6.7
9	6	4.1	12.7	17.5	8.3	9.6
10	56	1.2	7.6	26	13.0	5.2
11				124	15.5	0.5
12				100	10.8	8.2
13				4	7.7	
14				30	3.7	

The greatest linear distance between the most northerly extreme of the zebra population dry season range and the most southerly extreme of their wet season range was 170 km. In any one year, the average point-to-point distance moved by all the radio-collared zebra from a location in the wet season range of one year to within the vicinity of the same location in the wet season the following year was 377 km (±56.8). The greatest point-to-point distance moved by one zebra in a year was 488 km from a location in the 1992 dry season range back to within the vicinity of the same location in the 1993 dry season.

Table 2.2: Average weekly distance moved by radio-collared zebra (N=11 in 1992 & N=14 in 1993) to the dry season range in relation to the time since the last significant rains of the wet season. A negative distance represents a movement in the direction of the wet season range.

	1992		1993	
Time (weeks)	Weekly rainfall (mm)	Weekly distance moved (km)	Weekly rainfall (mm)	Weekly distance moved (km)
1	40.5	0	24.0	4.6
2	0	0	1.0	3.6
3	0	30.1	2.0	25.6
4	0	20.1	0	0.3
5	0	35.2	4.0	-8.0
6			0	9.4
7			0	30.7
8			0	17.3
9			0	10.3

Wildebeest

The northward migration of wildebeest from the wet to the dry season range was not investigated. However, wildebeest stayed longer in the wet season range than the zebra. All collared wildebeest were still present in the wet season range at the end of May on the last tracking date of each year, i.e. the 9th week after the last rains (Fig. 2.7). In 1993, one collared wildebeest still occurred in the wet season range as late as July.

The greatest linear distance between the most northerly extreme of the wildebeest population dry season range and the most southerly extreme of their wet season range was 100 km. In any one year, the average point-to-point distance moved by all the radio-collared wildebeest from a location in the wet season range of one year to within the vicinity of the same location in the wet season the following year was 300 km (±39.5). The greatest point-to-point distance moved by one wildebeest in a year was 355 km from a location in the 1992 dry season range back to within the vicinity of the same location in the 1993 dry season.

iv. Population ranges

Zebra

The total extent of the zebra population range in the Savuti – Linyanti region in northern Botswana was 7 285 km^2 during the three years of study. The range was bounded by the Linyanti River in the north and north-west and the Kwaai River in the south (Fig. 2.8). In the northern parts of the range (i.e. the dry season range), any movement to the west was restricted by the Linyanti River that formed the western

limit of the range. In the southern parts of the range (i.e. the wet season range), tall *C. mopane* woodlands bound the entire eastern and southern limits of the range. The zebra preferred open and savanna grasslands (Joos-Vandewalle, unpubl. data) and the boundaries of their wet season range coincided closely with boundaries of the Savuti and Mababe grasslands.

The sizes of the individual home ranges of some of the collared zebra were larger, by more than 1 000 km^2, than those of others (Table 2.3). These differences were evident because the former zebra tended to move in a westerly direction at the end of the wet season compared to those that moved directly northward to the dry season range. Despite this difference in movement pattern, the means of the individual home range sizes did not differ much between the two years studied.

Wildebeest

The wildebeest population range extended from the Linyanti river in the north to the Savuti region in the south and covered a total area of 3 556 km^2 (Fig. 2.9). Although the wildebeest followed the zebra during the seasonal migrations, they never moved as far south in the wet season nor as far west in the dry season as the zebra did. Hence, the home ranges of individual wildebeest were much smaller than the home range sizes recorded for zebra (Table 2.4). The wildebeest did not tend to wander as much as the zebra herds and as a result there was also a lot less variation amongst the individual home range sizes of the wildebeest.

Table 2.3: Individual wet season and annual range sizes of radio-collared zebra in northern Botswana during the two years of study. Rows are arranged in order of decreasing annual range size for 1993.

	Wet season range size (km^2)		Annual range size (km^2)	
Zebra	1991/2	1992/3	1992	1993
280	279	1214		3338
180	833	709	2982	3251
380		611		2877
340	586	658		2767
160	835	866	1709	2714
300	701	554	2737	2507
320	834	1098		2437
240		614	2233	2369
140	721	446	1976	2198
200		548		2032
220		597	2486	2010
100	877	677	1602	1870
360		446		1825
260		534		1003
Mean	708	684	2246	2371
s.d.	198.3	228.0	519.1	617.6

v. Seasonal home ranges

Zebra

Discrete temporal (start and end of the rains) rather than more imperious spatial criteria were used to define the seasonal ranges. Therefore, because one and sometimes two collared zebra occasionally remained behind the rest of the migration longer than the 30 days expected for animals to move between the ranges, some

locations during seasonal home range analyses occurred far outside the core area determined by the 90% home range contour. While these points were excluded as trivial outliers during home range analysis, the biological significance of these points were assessed in terms of the timing of the movements between the seasonal ranges.

Table 2.4: Individual wet season and annual range sizes for radio-collared wildebeest in northern Botswana during the two years of study. Rows are arranged in order of decreasing annual range size for 1992.

	Wet season range size (km^2)		Annual range size (km^2)	
Wildebeest	1991/92	1992/93	1992	1993
460	284	128	1907	1567
440	248	63	1597	1634
480	240		1395	
580	276	80	1342	1411
500	131		1093	
540	282	97	982	1587
Mean	243	92	1386	1550
s.d.	58.1	27.7	336.8	96.7

The 1991/92 and 1992/93 wet season ranges of all radio-collared zebra were similar in extent, overlapped by 87% and jointly encompassed an area of 1 577 km^2 in the Savuti / Mababe region (Fig. 2.8). However, these ranges differed significantly in their mean location (Table 2.5). These differences can best be explained by the low and

erratic rainfall midway in the 1991/92 season, which caused zebra herds to wander more widely, especially to the east, than the following season. Also, no tracking was done during January 1992 when zebra were expected to mostly occur in the southern extreme of the range. The individual home ranges of each radio-collared zebra overlapped closely with one another (Fig. 2.10) and, therefore, no distinct sub-populations were evident. One zebra ranged over a smaller area than the rest of the zebra in 1991/2 while three ranged over substantially larger areas than the rest in 1992/93 (Table 2.3). Although it is not known why, it was not uncommon for individuals, and occasionally a herd, to stray some distance away from the rest of the herds in the migration. However, these 'outlying' points were not excluded by the 90% polygon and would explain some of the larger differences found amongst the home range sizes in both years.

The 1991, 1992 and 1993 dry season ranges of all radio-collared zebra extended over a joint area of 1 743 km^2 and included the only permanent water in the region, the Linyanti river. The zebra used a common area in all three dry season years in the extreme north along the Linyanti River (Fig. 2.8). However, the extent of the dry season ranges differed because, in 1991 and 1992, some zebra remained in the south longer than in 1993. The 1992 and 1993 dry season ranges did not differ significantly in each of the years' mean location (Table 2.5). Too few locations were made in the dry season to estimate individual home ranges of zebra.

Except for a marginal overlap (<1% due to the 1991 distribution), the wet and the dry season ranges were spatially distinct from each other (Fig. 2.8). The distance between the centres of the wet and dry season population ranges was 80 km.

Table 2.5: Seasonal longitude and latitude means of zebra and wildebeest locations and the probability of a significant difference between these mean locations, tested by Hotelling's T^2-test. Also shown is the percentage overlap of the 90% contour estimates for the population seasonal ranges between years.

	Season	Mean longitude	Mean latitude	T^2-test and % overlap
Zebra	Wet 1992	24.12	18.79	P<<0.01; 86.4%
	Wet 1993	24.08	18.91	
	Dry 1991	24.07	18.53	P<<0.01; 13.5%
	Dry 1992	24.17	18.16	P=0.08; 38.9%
	Dry 1993	24.19	18.12	P<<0.01; 2.0%
Wildebeest	Wet 1992	24.12	18.78	P=0.30; 43.4%
	Wet 1993	24.12	18.80	
	Dry 1991	24.09	18.57	P=0.13; 31.3%
	Dry 1992	24.07	18.56	P<<0.01; 51.9%
	Dry 1993	24.10	18.56	P=0.62; 42.9%

Wildebeest

The wet season ranges of wildebeest for the 1991/2 and 1992/3 seasons overlapped by 43% and jointly covered an area of 354 km^2 on and south of the Savuti grasslands. Although the extent of the two wet season ranges differed, there was no significant difference in the mean location of these ranges (Table 2.5). Individual home ranges in the wet season overlapped closely with each other (Fig. 2.11), were of a similar size (Table 2.4) and no sub-populations were evident.

The dry season ranges extended from Savuti in the south to the Linyanti River in the north and jointly encompassed an area of 1 070 km^2. The 1991 dry season range differed in extent and location from those in 1992 and 1993 (Fig. 2.9 & Table 2.5). Too few locations were made in the dry season to estimate individual home ranges of wildebeest.

The seasonal ranges overlapped marginally by 2% in the northern part of the Savuti region. Apart from this overlap, the ranges were spatially distinct from each other and the distance between the centres of the seasonal ranges was 61 km.

Discussion

This study provided the first documentation of the occurrence of migratory zebra and wildebeest populations in northern Botswana. Furthermore, it has provided the first detailed analysis of individual home range sizes, seasonal ranges and movement patterns of migratory populations of zebra and wildebeest. Both species displayed a typical pattern of migratory movement (Pennycuick, 1975; Baker, 1978; Sinclair, 1979; Fryxell & Sinclair, 1988). They moved long distances annually, the size and extent of individual home ranges overlapped closely and each year they used the same seasonal ranges which did not overlap.

The home range of zebra was larger, by more than a factor of ten, than the home range of the migratory sub-population of zebra in the central district of Kruger National Park (Smuts, 1975). However, Smuts used non-telemetry collar re-sightings to establish home ranges that were estimated in only one year. The use of non-telemetry collars precludes systematic relocation of collars especially during

spontaneous, long-distance movements and it is not clear whether all collars were found during searches. It appears as though Smuts (1975) used opportunistic re-sightings and therefore home range size may have been underestimated. Although home range size has not been documented for the migratory zebra and wildebeest in Serengeti, it appears from observed monthly distributions during aerial surveys (Maddock, 1979), that the animals ranged over an area of similar size as the zebra in northern Botswana.

Two important features of this migration emerged. Firstly, the respective wet season ranges of individual zebra and wildebeest overlapped closely with each other as well as with the population seasonal range. The second feature was that all the animals moved and there were no resident animals that remained behind in either of the seasonal ranges (cf. Joos-Vandewalle, 1988). The only documented study that investigated individual home ranges of zebra was Smuts (1972, 1975) and, although overlap of individual home ranges was not analysed as such, the results of this work indicated that little overlap in home range of animals marked in the same population occurred. Smuts (1975) also found that some marked zebra used different seasonal ranges during successive years. In Serengeti (Maddock, 1979), Amboseli (Western, 1985), Makgadikgadi (Kgathi & Kalikawe, 1993) and the Central Kalahari (Williamson *et al.*, 1988) some zebra and wildebeest remained behind in their dry season ranges each year when the rest of the animals moved to the wet season range.

In northern Botswana, water availability in the dry season appeared to be the primary factor influencing the dry season distribution of zebra and wildebeest, which are dependent on the accessibility of drinking water (Smithers, 1983). Wildebeest in the

Kalahari Gemsbok National Park can go for long stretches without water but then seem to obtain their moisture requirements from melons and tubers (Mills & Retief, 1984a) although wildebeest in the Central Kalahari were never observed using this resource (Williamson, 1987). With the onset of the wet season, the water constraint was alleviated as pans filled up and the zebra and wildebeest moved away from the Linyanti River. Although the wet and the dry season population ranges were of similar size, in the height of the dry season the zebra and wildebeest concentrated in the northern parts of the range (≈500 km^2; cf. 1993 range) close to the Linyanti River. This general pattern of dry season concentration and wet season dispersal was therefore similar to that of the movement patterns of large water dependent herbivores, particularly zebra and wildebeest, in Makgadikgadi (Kgathi & Kalikawe, 1993), Amboseli (Western, 1985) and the KNP (Whyte, 1985; Smuts, 1972, 1974, 1975). The pattern of migration of zebra and wildebeest in Chobe in terms of the distance moved between seasonal ranges, the repeated use of the same route of the migration and the repeated use of the same wet and dry season ranges each year was, however, similar only to the migration of the wildebeest and zebra migration in Serengeti (Maddock, 1979).

Zebra and wildebeest initiated movement out of their dry season range in response to rainfall. Continued movement to the dry season range appeared to be in response to the amount as well as the time since the first significant rain of the wet season. Zebra took two months in each year to move to the wet season range. Wildebeest responded later but moved faster than the zebra.

Zebra and wildebeest started the migration to the dry season range approximately

two weeks after the last significant rainfall event of the wet season. Zebra left the wet season range despite substantial water still available in seasonal pans. In contrast, wildebeest remained longer in the area and their departure appeared to coincide with the disappearance of water in seasonal pans although this was not confirmed because early dry season monitoring of collars was not done. The underlying mechanisms determining the timing of departure between zebra and wildebeest remains an important area for further study.

Seasonal fidelity of range use by zebra and wildebeest was an important feature of this study. In contrast, migratory zebra in the Kruger National Park did not utilise the same seasonal ranges each year (Smuts 1972). In Northern Botswana, open grasslands cover a small area in proportion to wooded vegetation (Joos-Vandewalle, 1985) and occurred predominantly on old sediments deposited by floodwaters. The Savuti grassland was seasonally inundated in the 1970's and early 1980's and remains the predominant open grassland in the wet season range. Other than the open wooded savanna in the Mababe to the south of the Savuti grassland, the surrounding vegetation comprised dense woodlands and scrublands. In the dry season range, open grasslands are restricted to the seasonally flooded flatlands around Lake Liambizi and the meandering channels of old river systems in the north. The preference of zebra and wildebeest for lightly wooded and open grasslands and avoidance of more densely wooded vegetation in the study area (Joos-Vandewalle, 1988), appears to have had a strong influence on their seasonal distribution. The influence of historical hydrological patterns on the soils (Cooke, 1980; Shaw, 1985) and related influence of the soils on the vegetation has resulted in distinct boundaries between habitats that also formed natural boundaries for the wet season distribution

of zebra and wildebeest. The wet season range of the zebra overlapped very closely and encompassed the whole of the area covered by their preferred habitats in the region and probably explains the fidelity and hence spatial predictability of the migration. In Kruger National Park, the distribution of vegetation types is less distinct (Gertenbach, 1983). Where zebra had a wide choice of preferred habitats, or in regions with sub-optimal habitats, their seasonal movements were probably less predictable than in Chobe because they moved about in apparent search of preferred conditions which varied spatially depending on rainfall, water availability, burning patterns or predation (Smuts, 1972; 1975). The Serengeti ecosystem extends over an area of 25 000 km^2 and includes the vast Serengeti plains, the wet season range of zebra and wildebeest (Sinclair, 1979). Even though there are over one-and-a-half million wildebeest and 800 000 zebra, the nutrient rich grasslands are expansive enough to accommodate them and they tend to wander around following local rains in search of green grass of nutrient quality (Maddock, 1979; McNaughton, 1990; Georgiadis & McNaughton, 1990). Although fidelity of use of the wet season range in Serengeti has not been measured, it would be expected that it would be lower than that of the Chobe wet season range of zebra and wildebeest where the extent of preferred wet season habitat limited their potential range. The extent of the wildebeest range in the Kalahari differed every year depending on long-term rainfall patterns and during drought years they moved great distances extending their dry season range (Williamson & Williamson, 1988). In the Makgadikgadi – Nxai Pan NP, seasonal distributions of zebra and wildebeest also differed each year apparently in relation to rainfall and water availability (Kgathi & Kalikawe, 1993).

In the dry season range, few expanses of open grasslands were interspersed

amongst mopane woodlands and scrublands. This may explain the larger ranges and decreased home range fidelity in the dry season range. Both zebra and wildebeest seemed to spend some time during the early stages of the dry season wandering about in search of suitable grazing whilst water still remained in large pans. Once pans dried up they were compelled to move closer to the Linyanti River and regular access to the permanent water. However, this water was distributed widely enough to allow herds to move around in search of food supplies that were also being shared with large numbers of other water dependent grazing herbivores in the area.

Although rainfall did not have a noticeable effect on the intra-seasonal movements as noted in other studies, the influence on the inter-seasonal movements was marked. The arrival of the first rains of the wet season was a cue, indicating that water in rain filled pans and green grass became available in areas away from the Linyanti River. However, the zebra and wildebeest did not noticeably track individual rainstorms. The initial movement away from the river was quick but the continuation of rains and probably the guarantee of drinking water *en route* dictated any long distance movement. The amount and pattern of rainfall during the three years of the study was highly variable, especially at the start of the wet season, but despite this, a clear relationship between rainfall and the movement of zebra and wildebeest to the wet season range emerged. No evidence of a similar relationship between migratory animals in Africa and rainfall could be found probably because it has not been investigated at this level. Maddock (1979) showed that the seasonal distribution of migratory zebra and wildebeest in the Serengeti was related to the amounts and distributions of rainfall at different times of the year but did not investigate the progress of these movements to rainfall amounts.

In contrast, at the end of the wet season it was the lack of rains, or rather the elapsed time following the last rainfall event, that initiated zebra and wildebeest to begin the movement back to the dry season range. They both concentrated on the Savuti grassland despite adequate drinking water availability further south. They then spent some time in Savuti but zebra then left before water supplies here had dried. Interestingly, the wildebeest stayed until there was very little water remaining. Zebra in the KNP also left the wet season range before water in seasonal pans was depleted (Smuts, 1972) but no explanation for this behaviour was offered. A possible reason for this difference in behaviour in Savuti was related to the availability of forage. Wildebeest prefer short grasslands and seldom graze grass that is more than 15 cm – 20 cm high (McNaughton, 1976, 1979; Skinner & Smithers, 1990). Zebra on the other hand, tend to be a lot less selective for the height of grasslands but tend not to graze lower than 10 cm – 15 cm from ground level (Smuts, 1972). The high concentration of zebra, wildebeest and occasionally other grazers on the Savuti grassland, results in the rapid removal of grass biomass. In the five to six weeks that the zebra spend in Savuti, the height of these grasslands could conceivably be reduced to a height that would force the zebra to move out. Yet, the grassland would still be suitable for wildebeest that prefer shorter grasslands and only once water in the pans is depleted do they then leave the area. The depletion of grass abundance as a possible factor influencing the movement of zebra and wildebeest within the wet season range was investigated and is discussed in Chapter 3.

The zebra at all times ranged over much larger areas than wildebeest did in this study. The reason for this is not immediately apparent but again might be a result of the difference in habitat requirements between the two species, especially in terms of

grass height or food abundance. Zebra, being a non-ruminant, require a greater daily intake of food than wildebeest, a ruminant (Bell, 1969, 1971; Owen-Smith, 1982; McNaughton & Georgiadis, 1986). Zebra may range over larger areas in order to obtain sufficient quantities of food while the wildebeest can satisfy their needs on short grasslands without having to expend the energy in search of areas with a greater abundance of grass. The influence of 10 000 zebra grazing together compared to only 1 000 wildebeest would also have a marked difference on the rate at which food resources become depleted in any one grazing area. Except in the dry season when animals were forced to remain close to water, the zebra never remained in one area longer than 5 – 6 weeks before moving on. This might be the amount of time it takes for this number of animals to deplete food resources in that feeding area to a point where energy gain drops below the animals' requirements. Whether it is simply the amount of food available or the quality of food, or perhaps a relationship of both, is not clear. The influence of food quantity and quality on the movements of zebra and wildebeest in the wet season is investigated in the next two chapters.

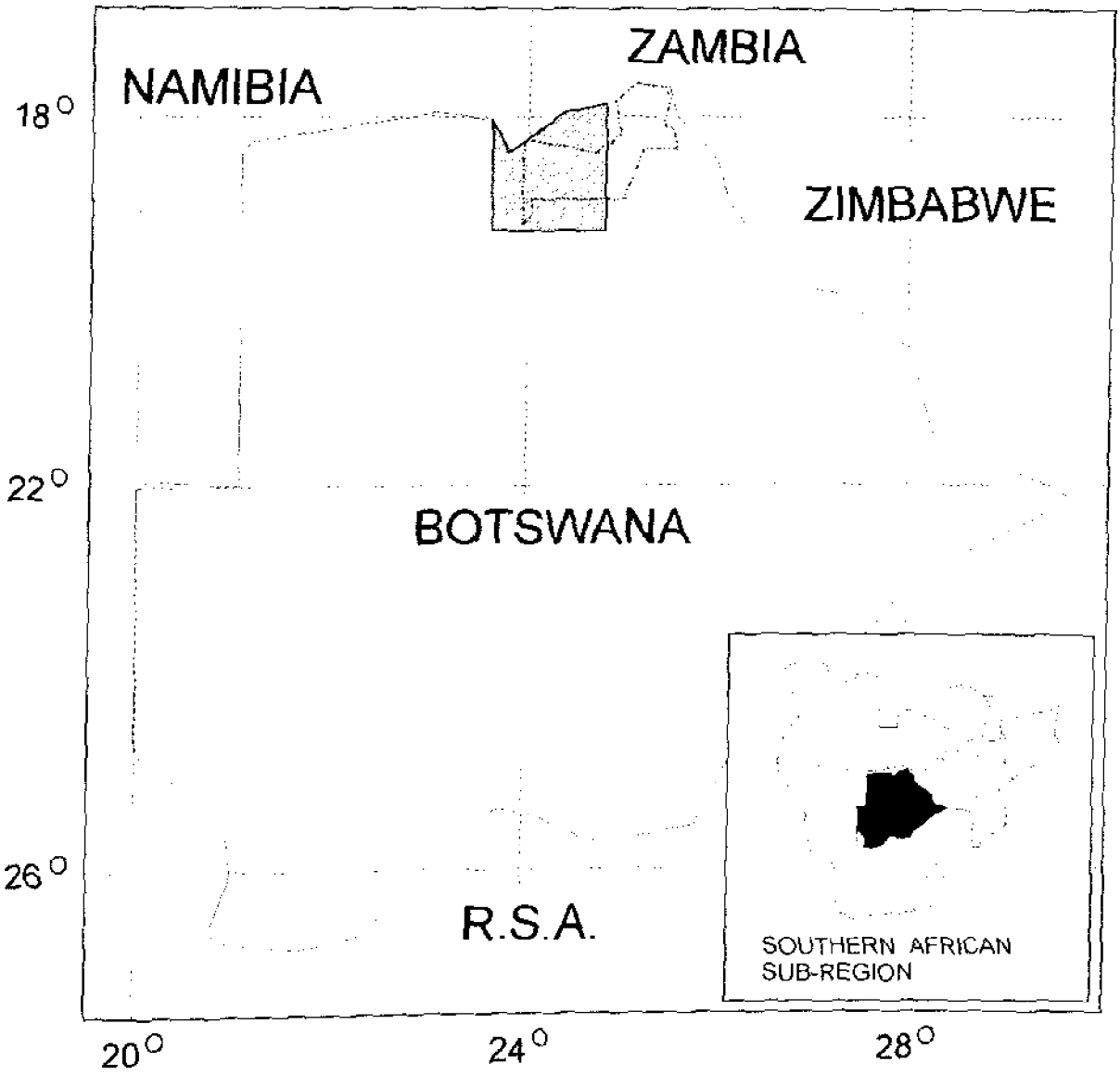

Figure 2.1a: Location of the study area (shaded) in northern Botswana and its position in relation to Chobe National Park (dotted boundary). Inset shows the position of Botswana in the southern African sub-region.

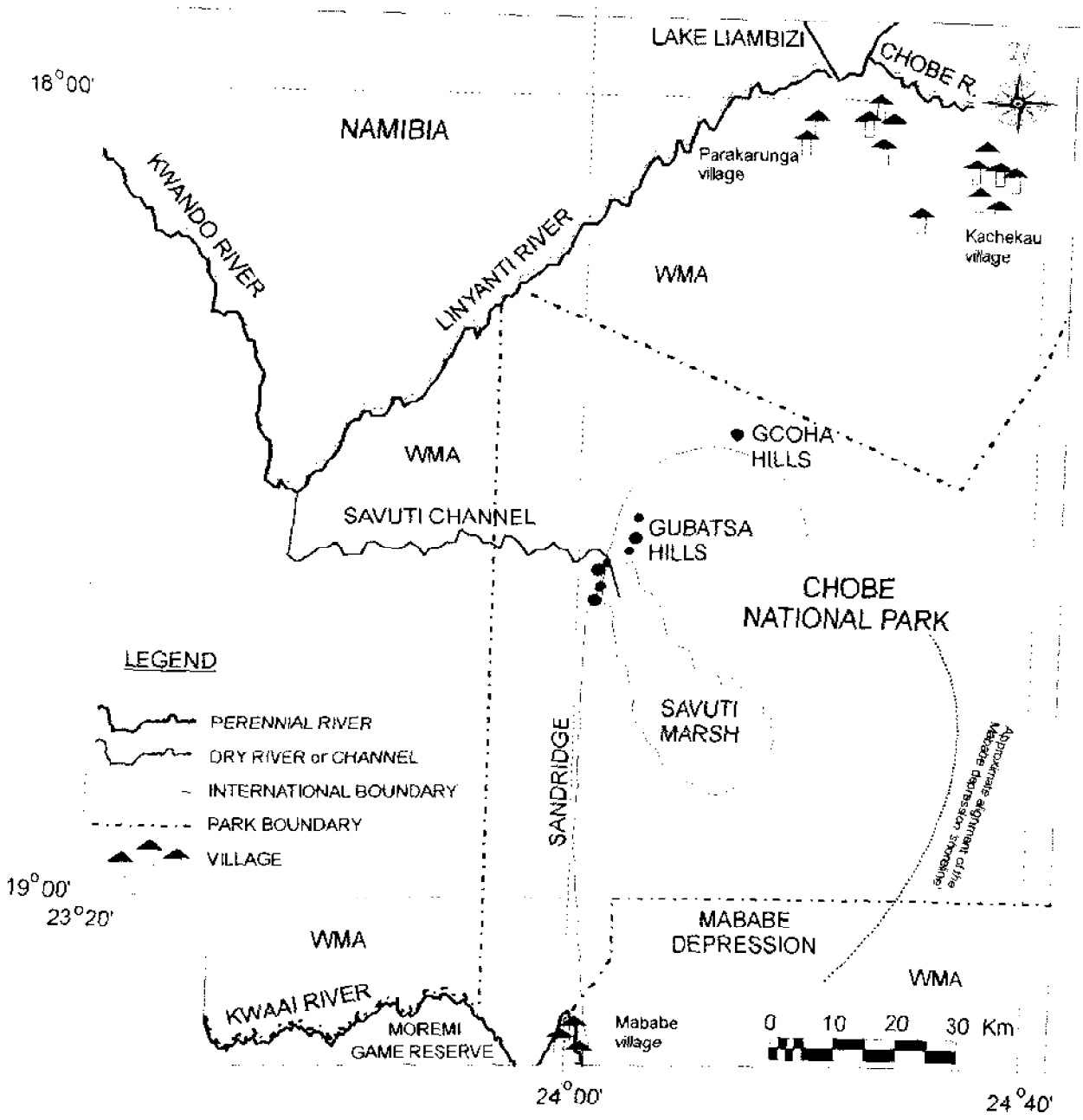

Figure 2.1b: Western Chobe National Park showing relevant topographical features, the Savuti and Mababe regions as well as the Wildlife Management Areas and villages outside the park.

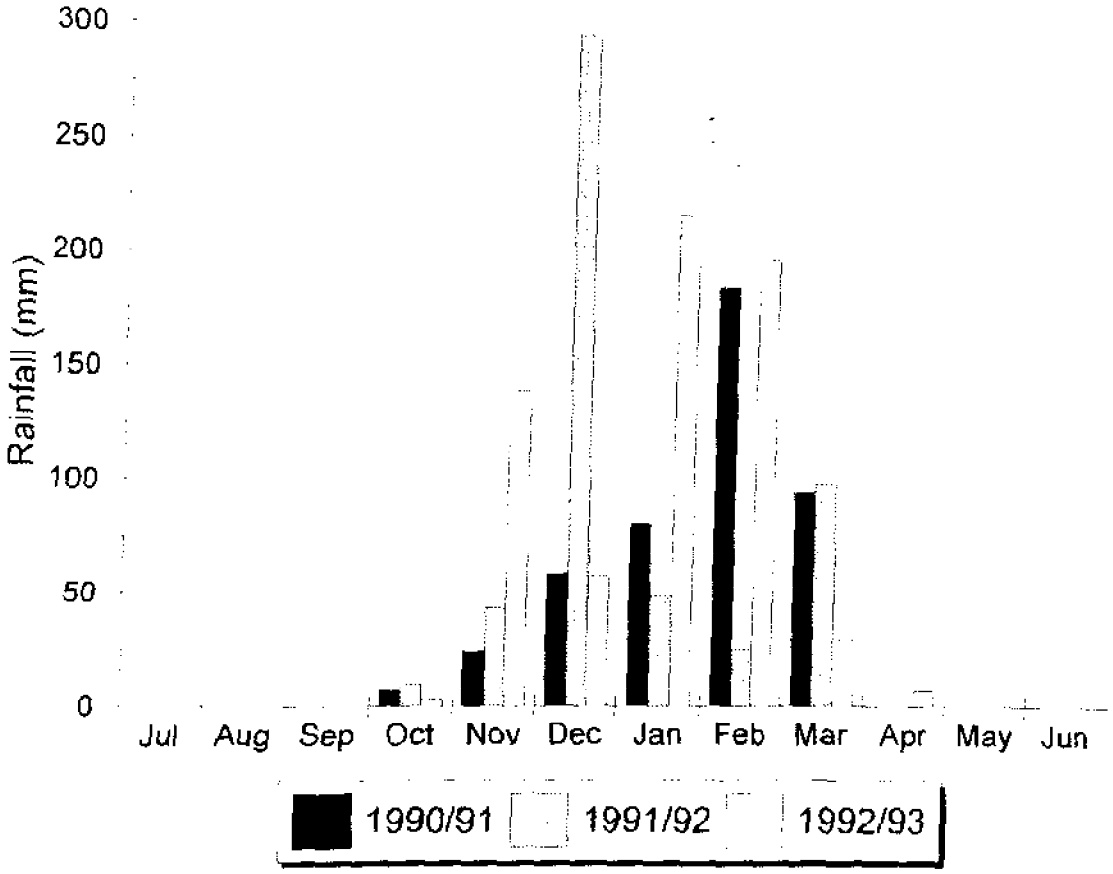

Figure 2.2: Monthly rainfall at the Savuti Research Camp during the three years of study. Total rainfall for the seasons were 447 mm in 1990/91, 519 mm in 1991/92 and 648 mm in 1992/93.

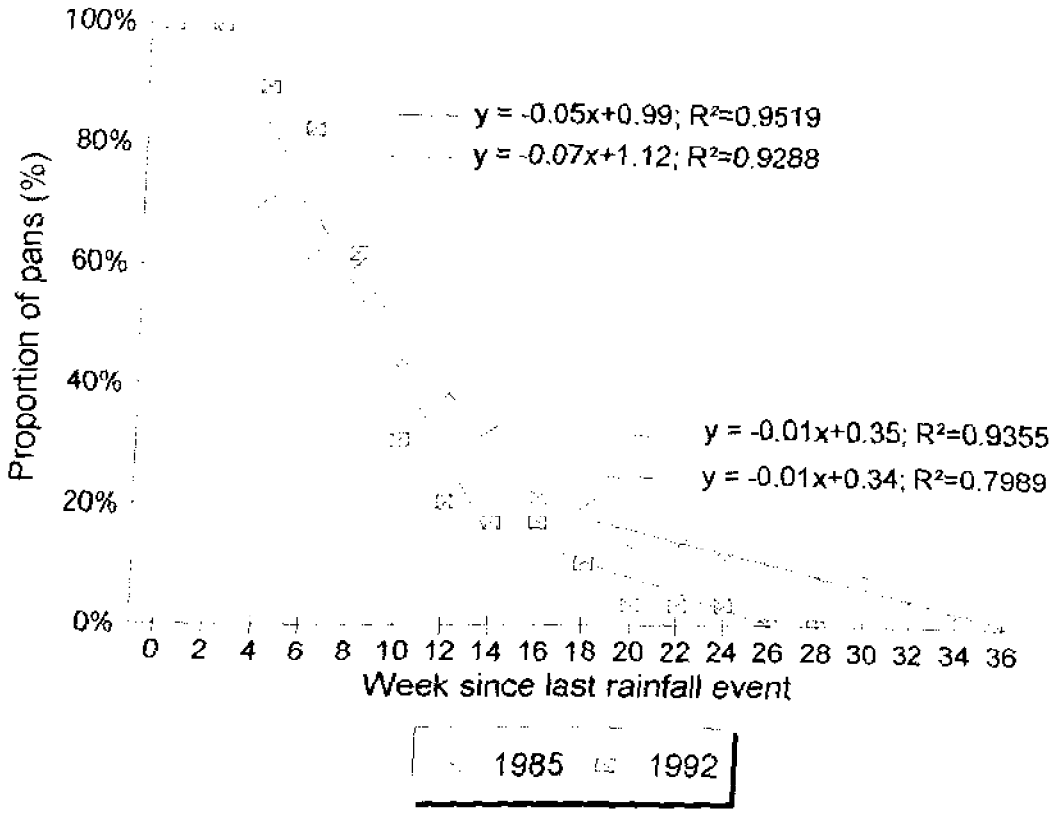

Figure 2.3: The proportion of pans retaining water in the Savuti region in the dry season of 1985 (after Joos-Vandewalle, 1988) and 1992. Also shown are the best fit lines, their equations and R values.

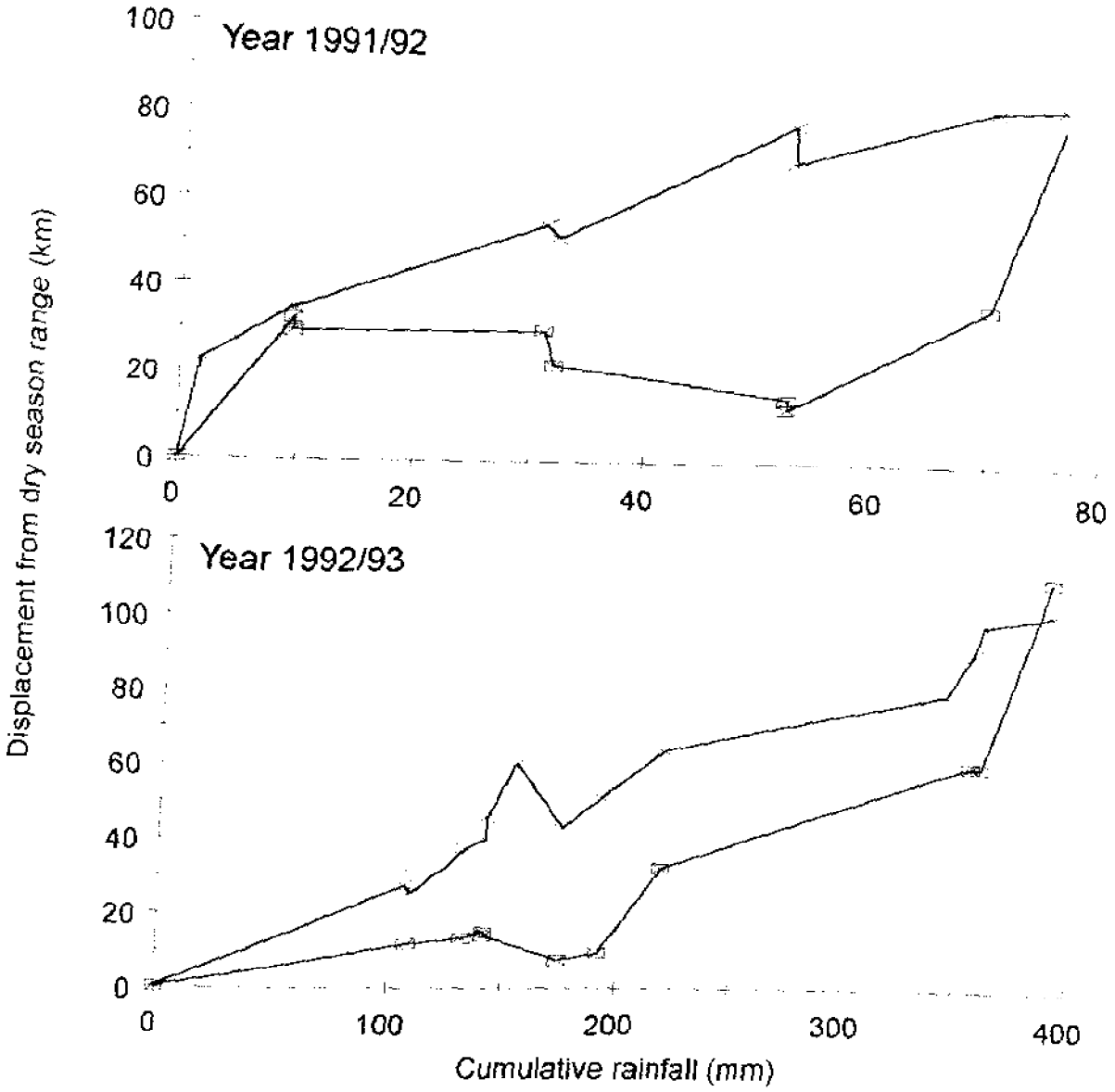

Figure 2.4: The mean weekly displacement of collared zebra in relation to cumulative rainfall during the migration from the dry to the wet season range. In both seasons, one segment of the zebra population moved in advance (n = 5 collared zebra) while a smaller segment (n = 2 collared zebra) lagged behind.

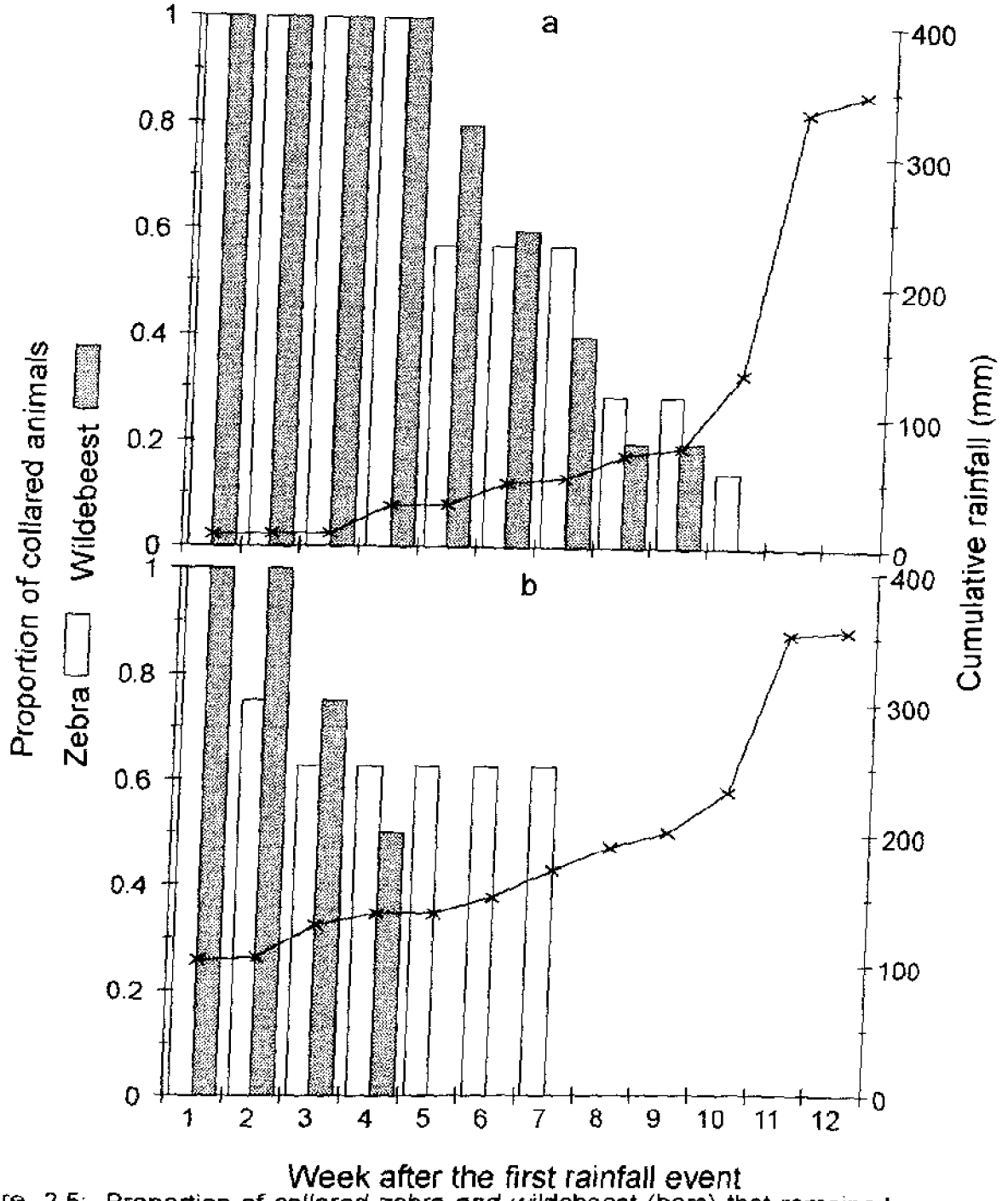

Figure 2.5: Proportion of collared zebra and wildebeest (bars) that remained in the dry season range after the first rainfall event of a) the 1991/92 wet season (n=7 zebra & n=6 wildebeest) and b) the 1992/93 wet season (n=8 zebra & n=4 wildebeest). Lines are cumulative rainfall.

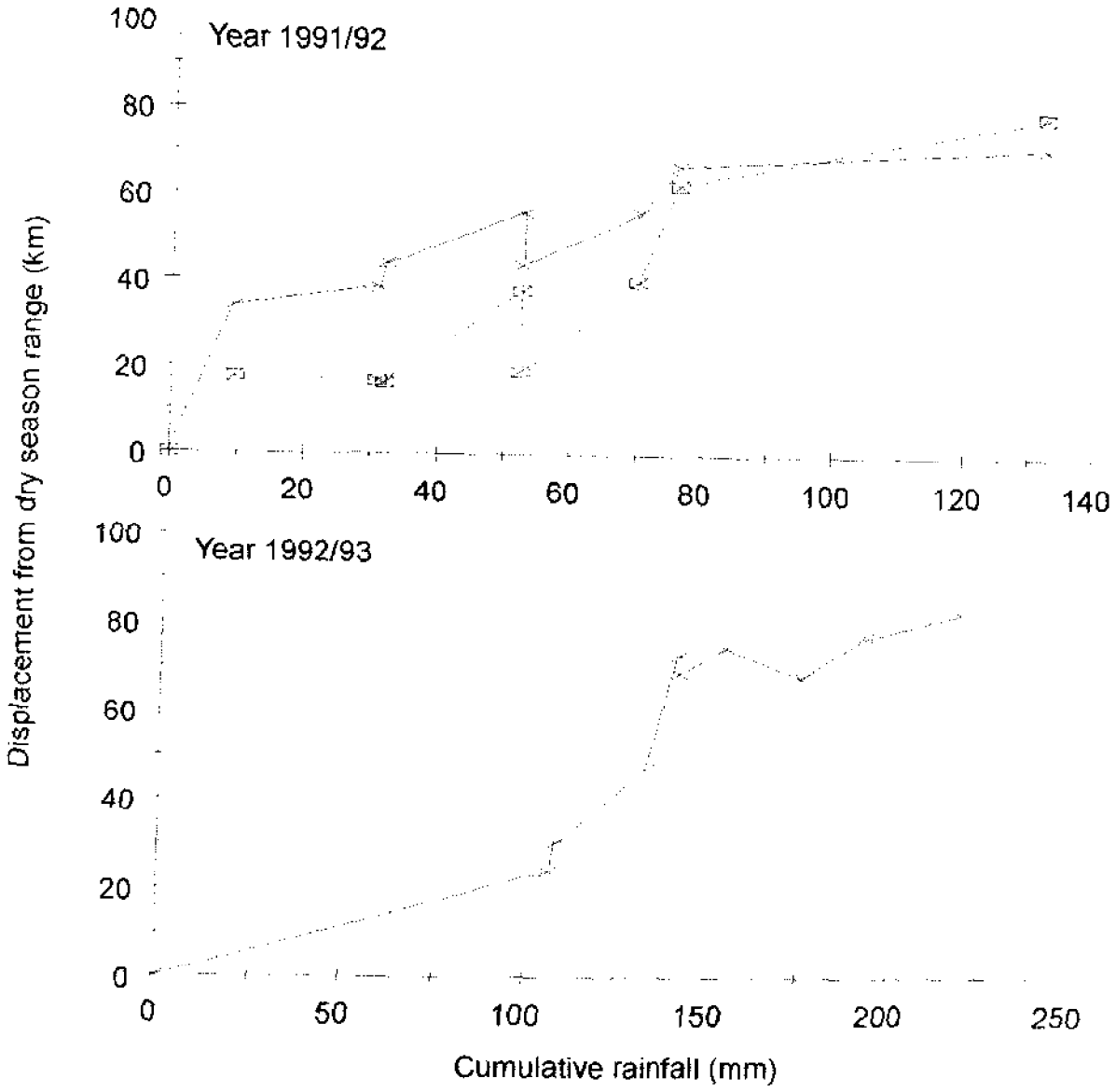

Figure 2.6: The mean weekly displacement of collared wildebeest in relation to cumulative rainfall during the migration from the dry to the wet season range. In the 1991/92 year, one segment of the wildebeest population moved in advance (*n*=4 collared wildebeest) while a smaller segment (*n*=2 collared wildebeest) lagged behind. All collared wildebeest (*n*=4) moved together in the 1992/93 year.

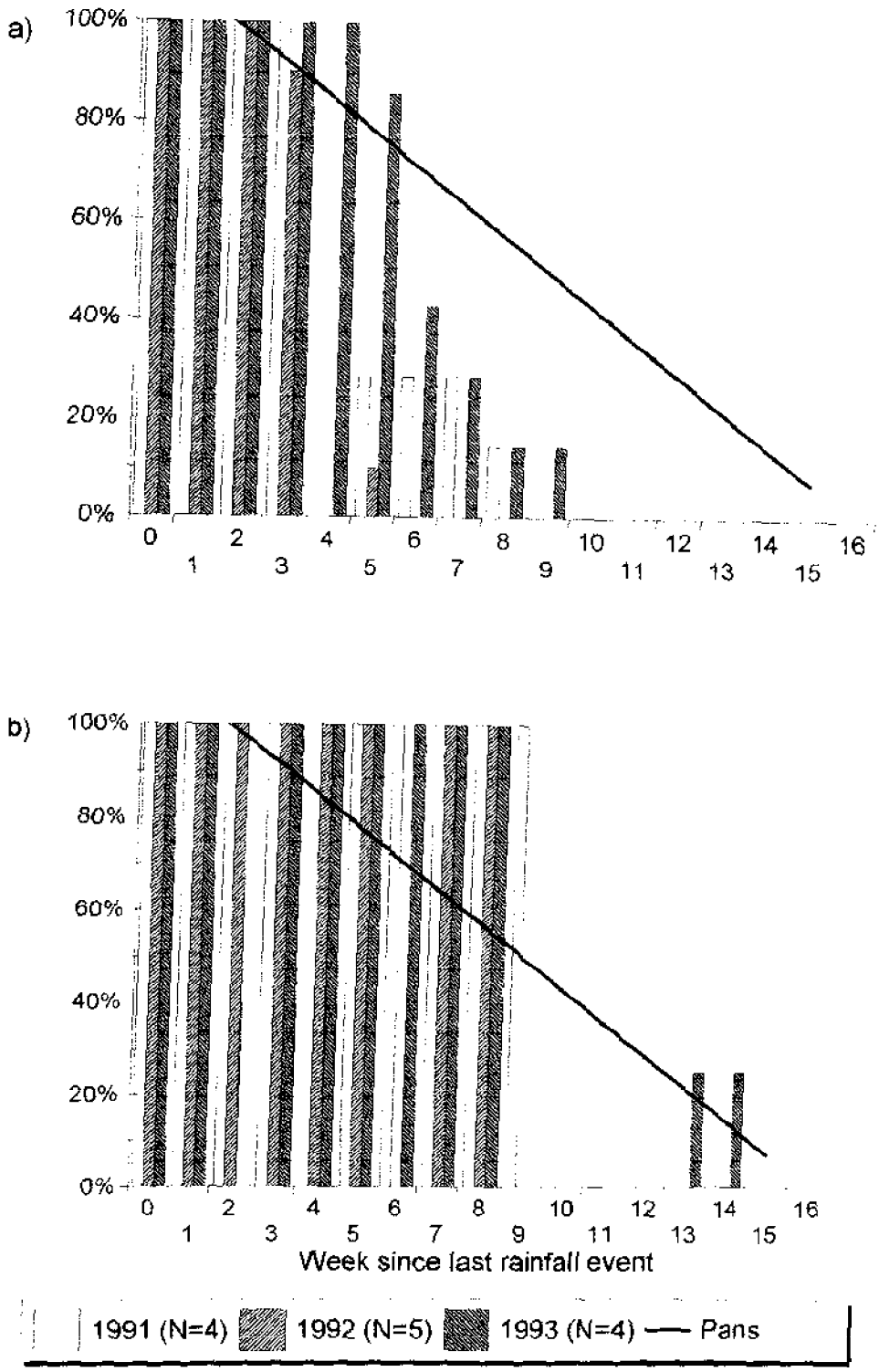

Figure 2.7: Percentage of collared a) zebra and b) wildebeest that remained in the wet season range after the last rains (bars) in relation to the percentage of pans still retaining water (line) in the same period.

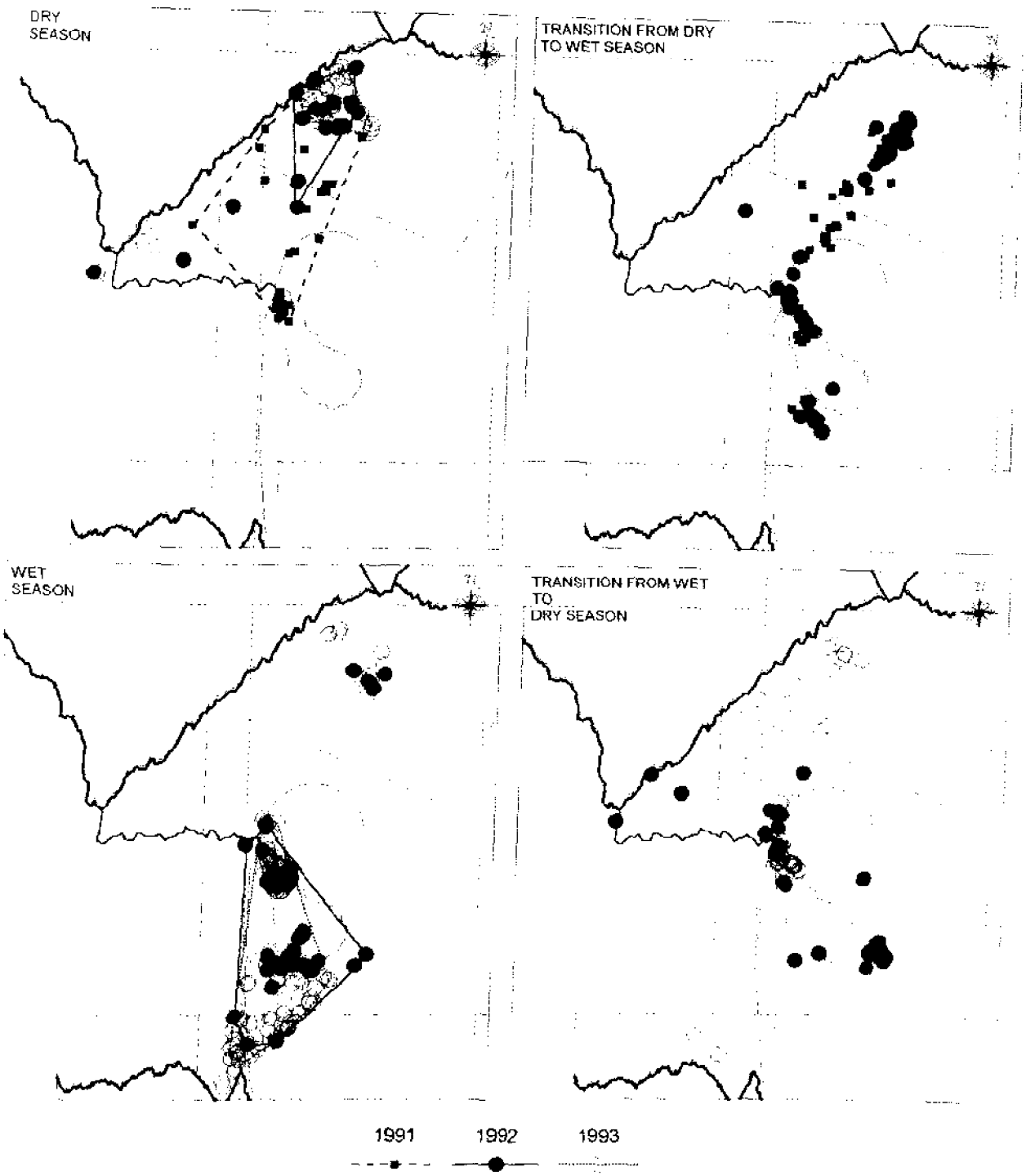

Figure 2.8: Seasonal distribution of radio-collared zebra located by aerial tracking. Polygons are the wet and dry season 90% range probability boundaries. (See text for explanation of seasonal range estimation.)

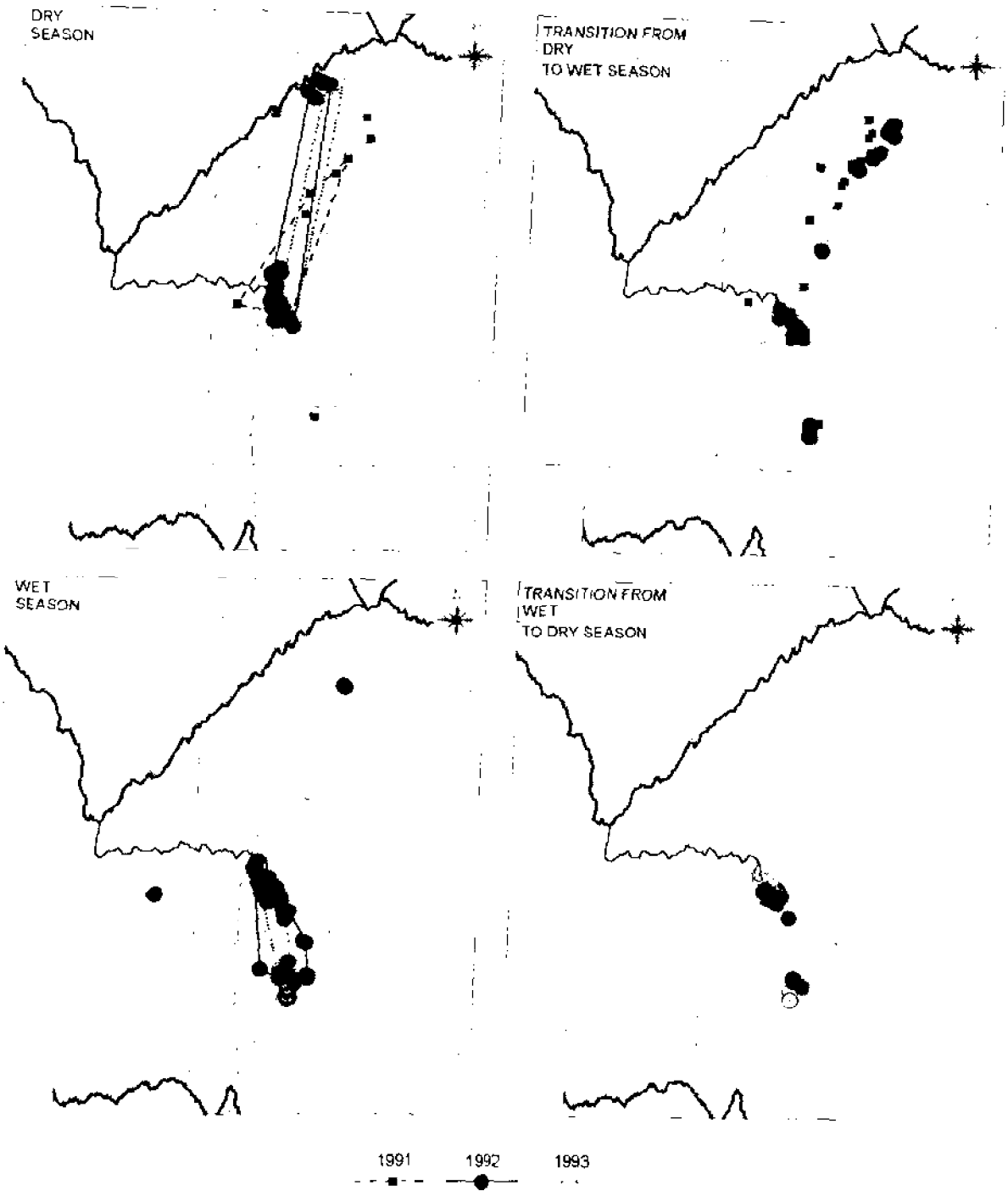

Figure 2.9: Seasonal distribution of radio-collared wildebeest located by aerial tracking. Polygons are the wet and dry season 90% range probability boundaries. (See text for explanation of seasonal range estimation)

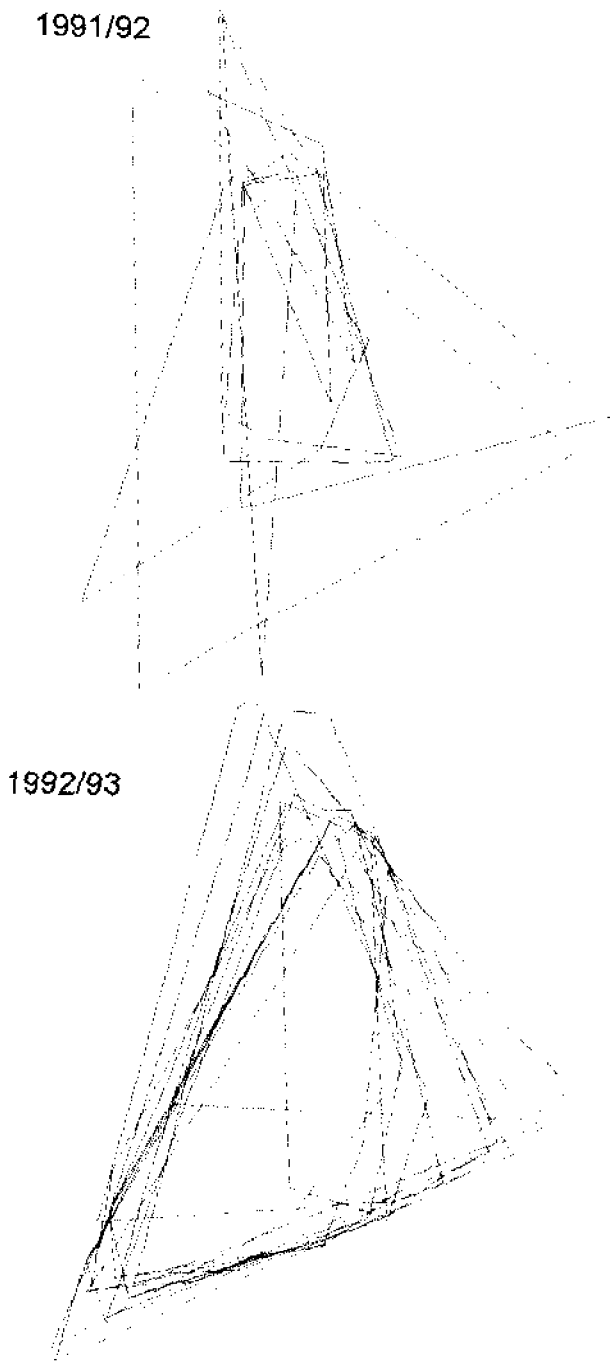

Figure 2.10: The 90% home range probability boundaries of radio collared zebra in their 1991/92 (n=8) and 1992/93 (n=14) wet season ranges.

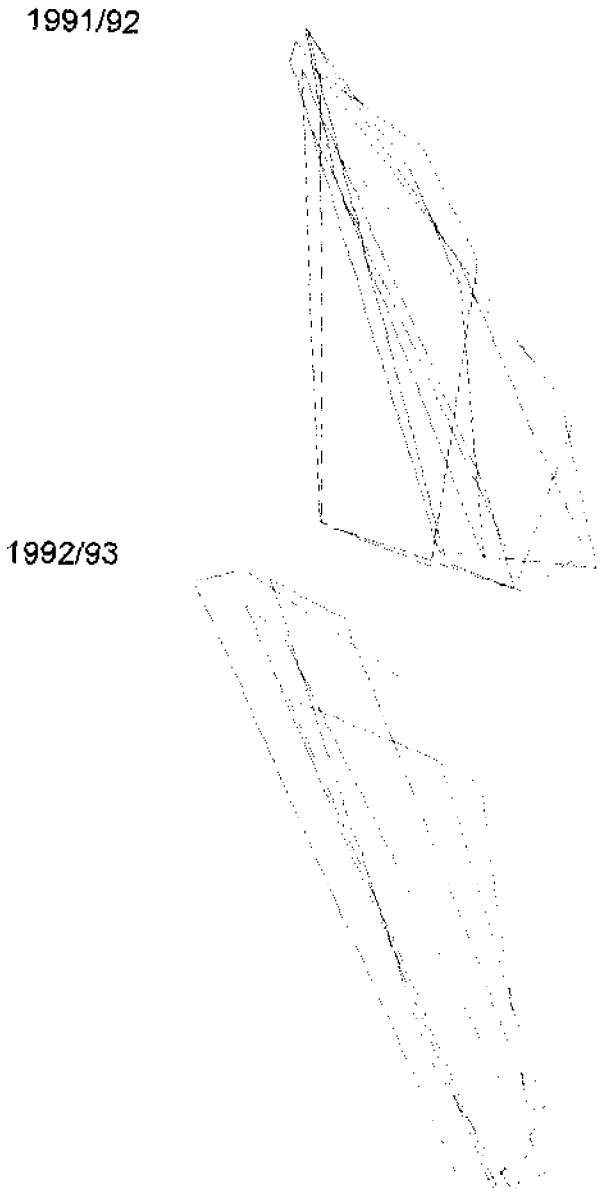

Figure 2.11: The 90% *home range* probability boundaries of radio-collared wildebeest in their 1991/92 (n=6) and 1992/93 (n=4) wet season ranges.

CHAPTER 3

Feeding area selection by zebra and wildebeest in relation to grassland composition, phenology and height

Introduction

In African ecosystems, the quantity and quality of food resources available to grazing ungulates varies spatially and temporally. Spatially, the abundance and quality of grasses varies at several different scales or levels of ecological resolution (Senft *et al*, 1987). Within a region, the largest of these scales can extend over hundreds of square kilometres, such as landscapes, which are made up of several grassland communities. A landscape, therefore, can be defined as an aggregation of communities as determined by geomorphic features (Forman & Godran, 1981) such that grassland species composition varies according to differences in soil type, soil moisture availability and soil nutrient status. Grass abundance and quality within each community will largely be determined by the balance between soil nutrient and soil water availability (Bell, 1971, 1982, 1984). Within a feeding area, morphological characteristics of grasses such as grass height, leaf size and texture, tuft shape and size, and leaf to stem ratio differ among species. Such a patch then presents the herbivore with plants of different growth form, each varying in available forage biomass. The quality of forage available to ungulates at the plant level also differs. Mineral element concentrations, crude protein and carbohydrate contents are highest in grasses in the early growth stages and decline as the plant matures and structural

fibre is laid down (Jarman & Sinclair, 1979; Ben-Shahar, 1993). In order of decreasing nutritional quality, therefore, a grass plant can be separated into emergent leaf, green mature leaf, leaf sheath, dry leaf and stem.

In northern Botswana, the variability of rainfall, both in time and space, and its influence on grass growth further enhances the temporal and spatial variability in forage resources available to herbivores. After five to six months of the dry season with no rainfall, showers of varying intensity fall in scattered locations at the start of the wet season (Joos-Vandewalle, 1988; Chapter 2). These rains induce local green biomass production in grasses (McNaughton, 1985; Rutherford, 1978, 1980). The amount of growth in patches where rain has fallen is related to the amount and timing of each rainfall. Later in the wet season, rains tend to be more widespread but can still vary in amount and distribution (Joos-Vandewalle, 1988).

Hence, a grazing ungulate is faced by a number of choices regarding food availability that differs both in quantity and quality at different spatial scales while also changing temporally. It has been suggested by Westoby (1974) that large generalist herbivores, such as zebra and wildebeest (Jarman, 1974; Demment & Van Soest, 1983), should include the best mix of food in their diet such that the net intake of nutrients is maximised given the digestive constraints of the animal. The model for foraging behaviour developed by Owen-Smith & Novellie (1982) suggest an ungulate would select a diet that maximises rate of intake of the most limiting nutrients over time. The optimal foraging theory predicts that, when animals deplete their resources, they should leave a patch when intake rate declines below the average for the habitat (Charnov, 1976; Stephens & Krebs, 1986). Most of this work has been done at small

scales (100 m^2 or a burn) but the principles should apply at all scales.

In Chapter 2 it was established that the wet season range of zebra and wildebeest in northern Botswana was largely restricted to the open grasslands of Savuti and the open savanna of the Mababe depression. In both these areas, herds grazed together in small patches or feeding areas, moving about within the grassland and then at some point moved *en masse* to the next area or, toward the end of the wet season, to the dry season range. Exactly why they moved to Mababe is not known. Also, zebra left the Savuti grassland for the dry season range in Linyanti before water in the area was depleted whilst the wildebeest stayed longer. The reason for this is not known either but I suggest that aspects of forage quantity and quality may influence both the southward and the northward movements (Chapter 2).

The aims of this study, therefore, were twofold. The first was to investigate the influence of forage quality by means of inferred indices relating to plant and grassland community structure and plant phenology on the selection of feeding areas by zebra and wildebeest in the wet season range. The second was to investigate the influence of grass abundance on the movements of zebra and wildebeest within the wet season range and movement to the dry season range.

Study area

The study was conducted in the wet season range of zebra and wildebeest which covered the Savuti and Mababe regions of northern Botswana (Chapter 2). The study area was described in detail in Chapter 2 as well as by Joos-Vandewalle (1988). Six vegetation types were described by Joos-Vandewalle (1988) according to woody

species composition and physiognomy, which in turn were closely associated with soil texture. Open grasslands in Savuti (the Savuti grassland) and *Acacia* scrubland interspersed with hydromorphic grassland in Mababe were the preferred habitats used by zebra. Open grasslands and *Acacia* woodlands in Savuti were the preferred habitats used by wildebeest. It was also shown and described in detail by correspondence analysis (Joos-Vandewalle, 1988), that a particular grass species composition was associated with each vegetation type (see Chapter 2 for more detailed description).

Methods

i. Identification of feeding sites

Every third day while zebra and wildebeest were in the wet season range, three collared zebra and three wildebeest were located by telemetry from a vehicle in the early morning or late afternoon. All zebra within a radius of 100 m of the collared individual were observed for 10 minutes to ensure that at least two-thirds of the animals were grazing. Wildebeest occurred in discrete herds and the herd was observed to establish that they were feeding. When these criteria were met, the locus of the feeding site was then defined as the point where the collared animal was observed grazing. From each locus, 25 points, one metre apart, along each of four transects were paced out. Transects were orientated at right angles to each other along the four main compass bearings. The grass plant nearest to each point along transects was assessed, yielding 100 plants per feeding site.

ii. Species composition of feeding sites

The species composition of feeding sites was calculated as the proportion of each species recorded among all species recorded along the four transects. To assess the influence of species composition on feeding site selection by zebra and wildebeest, the proportion of species occurrence in all sites was ordinated by Correspondence Analysis (CA) using the CANOCO computer package (Greenacre, 1984; ter Braak, 1985, 1986, 1987). Both species-environment relationships and specific responses of species to environmental variables can be assessed by this programme (ter Braak, 1987). Two options for gradient analysis are available. The first, Canonical Correspondence Analysis (CCA), constructs linear combinations of environmental variables directly along the species axes. The second, CA, first extracts the ordination axes, which explains the variance in the weighted averages of the species. After extraction, the environmental variables are correlated with the axes without influencing the ordination of samples and species scores (ter Braak, 1985) and, hence, is an indirect gradient analysis. To investigate the temporal and spatial influences of grass species composition on feeding site selection by animals, the indirect canonical relationship of the month of assessment and the location of sites in either Savuti or Mababe was determined after extraction of the ordination axes (ter Braak, 1987). CA and not CCA was used for ordination, because the 'environmental' variables in the data set were categorical rather than continuous (Greenacre & Hastie, 1987), and linear combination of the variables was considered to be inappropriate. Arch distortion was not evident and, therefore, detrending was not included in the analysis (Hill, 1979; Hill & Gauch, 1980; Gauch, 1982).

iii. Selection of grass species and plant part

Recent grazing of green leaves and seed heads was identified by the presence of darker green plant tissue and sap at the place of incision. Old grazing was identified by the presence of an edge of brown, dead or dried plant tissue at the place of incision. Recent versus old grazing on dry leaves and seed heads was identified by close observation for the presence of saliva. Tufts that had evidence of old grazing were excluded so as to limit the analysis to grazing done by zebra or wildebeest just prior to sampling.

Grass species

Although widely used as an index of food preference, the forage ratio was not used in this study as it can vary asymmetrically between zero and infinity. While this particular problem can be avoided by log transformation, conclusions about the selection of food species by animals depends on the set of food types categorised as available, and confidence limits are difficult to estimate (Owen-Smith & Cooper, 1987). Therefore, the method developed by Owen-Smith and Cooper (1987) was used to evaluate the selection of grass species within and between animal feeding patches.

The site-based acceptance value developed by Owen-Smith & Cooper (1987) was modified and calculated as the proportion of feeding sites in which a species, when present, was grazed. Availability was calculated as the proportion of feeding sites in which the species occurred. Sites assessed on the same day were more than one kilometre apart and were focussed around different sample animals. Each day of site

assessment was also separated from the next by a minimum of 3 days. Hence, feeding sites were independent of each other (Brown & Hollander, 1977) and the 95% confidence limits were calculated according to binomial statistics (after Owen-Smith & Cooper, 1987).

The chance of any one tuft of a species in a feeding site being grazed, and hence giving that species a site-based acceptance score, was good because of the high concentration of animals within feeding sites shortly before assessment. Therefore, to establish the importance of each grass species in the diet of zebra and wildebeest relative to the availability of tufts compared to all other species, the proportion of tufts of a species that were grazed over all feeding sites was calculated. The availability of that species was calculated as the proportion of tufts of each species recorded over all feeding sites (i.e. the species composition across all feeding sites).

Annual grasses were a major component of the grasslands in the study area. The availability of annual relative to perennial grasses changed over time, as the former had a shorter life span and zebra were observed to graze them in preference to perennials. Therefore, the weekly proportions of tufts of an abundant annual species (*U. trichopus*), relative to two abundant perennial species (*C. dactylon* and *S. ioclados*), grazed by zebra in feeding sites were assessed as the wet season progressed.

Plant parts

For each grass species, the proportion of leaves and inflorescences grazed over all feeding sites was calculated. The availability of inflorescences was calculated as the

proportion of tufts with inflorescences of a species over all feeding sites.

iv. Selection of green leaf

Green leaf material is more digestible, contains higher levels of crude protein, higher concentrations of nutrients and mineral elements but lower levels of indigestible structural components than brown leaves in grasses (Pratchett, 1976; Georgiadis & McNaughton, 1990). The proportion of green versus brown leaf on tufts was used as an index of the quality of available forage to herbivores.

The greenness of tufts in feeding sites was recorded using the following numerical grading:

1 = whole tuft brown,

2 = tuft more brown than green,

3 = tuft more green than brown, and

4 = whole tuft green.

Only feeding sites where 10 % or more comprised brown tufts were used in analysis for selection of greenness. The feeding site greenness index was calculated by averaging the greenness index for all tufts within a feeding site. The selection by zebra and wildebeest of grass in relation to the greenness of tufts was calculated as the proportion of 'green' (graded 3 & 4) tufts grazed over all tufts grazed in a feeding site. The selection for greenness by species was calculated as the proportion of 'green' (graded 3 & 4) tufts grazed of a species over all tufts grazed of that species for all feeding sites. Availability was recorded as the proportion of green and brown tufts of each species present in feeding sites. A paired samples Student t-test was

used to test for a significant difference between the means in the proportions of green and brown tufts grazed in feeding sites.

v. Influence of sward height on animal movements

Estimating biomass of grasses by clipping, sorting, drying and weighing is a labour intensive and time consuming process. Although visual estimates of grassland yields are possible (Campbell & Arnold, 1973; Haydock & Shaw, 1975; Jones & Hargreaves, 1979), the method requires observer practice. Furthermore, due to differences in the morphometric structure of pastures, for example tall sparse grasslands versus short dense grasslands, large errors in dry weight or yield estimates between grassland types tend to be unavoidable. However, shoot height in grasses, irrespective of tuft structural differences, is positively and exponentially related to shoot weight (Coughenour, McNaughton & Wallace, 1985) and can easily and quickly be accurately measured in the field. Grass height was, therefore, used as an index of the availability of forage abundance to herbivores. The weekly change in the height of the sward (calculated as the mean maximum leaf height) in feeding sites during the wet season was recorded. Grazing by a large number of zebra and wildebeest concentrated in feeding sites would be expected to have a major influence on the height of the sward. Selective grazing would, however, effect only some grass species but not others and the height of ungrazed species would skew the results. Therefore, changes in mean maximum leaf height of tufts was assessed by recording the weekly change in the frequency distribution of leaves in different height classes. Mean maximum leaf heights of tufts between 0 cm and 70 cm were recorded in classes of even intervals 5 cm apart.

Results

i. Species composition of feeding sites

Zebra and wildebeest largely selected feeding sites (n=102) of similar grass species composition, of predominantly *Urochloa trichopus* (Hochst.) Stapf and *Cynodon dactylon* (L.) Pers., in both Savuti and Mababe (Fig. 3.1). However, wildebeest occasionally used feeding sites (n=6) in the Savuti area with a high contribution of *Brachiaria nigropedata* (Fical. & Hiern) Stapf which accounted for 61% of the observed variation in site species composition (Axis 1 of the ordination). The remaining 39% variation (along Axis 2) was due to the presence of uncommon species.

Ordination of grass species composition separated zebra feeding sites into open grasslands in Savuti and thorn savanna in Mababe (Fig. 3.2). Although both areas had a high proportion of *U. trichopus*, Mababe feeding sites differed largely due to the absence of *C. dactylon* and a lower species richness (Table 3.1). Among feeding sites in Savuti, the species composition differed mainly in the differing contributions of *Sporobolus ioclados* (Trin.) Nees and *C. dactylon* (Fig. 3.2). The area in which sites were assessed (Area variable) described most of the variation and was highly correlated with both axis 1 and axis 2 (R^2 = 0.9635 and R^2 = 0.9989, respectively). The month in which zebra feeding sites were assessed had little influence on the described variation in species composition. One site in Savuti (#7) and another in Mababe (#19) were excluded from the ordination analysis as outliers. Both were located close to the edge of seasonal pans and had unusually high contributions of

Digitaria species (36.9% and 76.4%, respectively) and *Dactyloctenium giganteum* Fisher & Schweick. (#19, 14.7%).

Table 3.1: Species composition (%) of grasses in zebra feeding sites in the Savuti and Mababe areas (n= number of sites).

Species	Site location	
	Savuti grassland (n=46)	Mababe savanna (n=18)
Echinochloa crus-galli (L.) Beauv.		3.1
Eustachys paspaloides (Vahl) Lanza & Mattei	1.1	6.1
Tragus berteronianus Schult.	0.5	0.9
Sporobolus ioclados (Trin.) Nees	9.3	0.6
Urochloa trichopus (Hochst.) Stapf	48.5	89.3
Cynodon dactylon (L.) Pers.	33.1	
Digitaria spp.	1.3	
Eragrostis rotifer Rendle	0.3	
Eragrostis rigidior Pilg.	0.1	
Chloris virgata Swartz	3.6	
Brachiaria nigropedata (Fical. & Hiern) Stapf	1.1	
Panicum repens L.	0.7	
Bothriochloa insculpta (A. Rich.) A. Camus	0.4	
Eragrostis superba Peyr.	0.1	

Ordination of grass species composition clustered wildebeest feeding sites into open grassland, woodlands on the edge of the open grassland in Savuti and hydromorphic pan grassland in Mababe (Fig. 3.3). *Cynodon dactylon* was abundant in all feeding sites (Table 3.2). The edge woodlands differed primarily from the open grasslands in the predominance of *B. nigropedata* and lower species richness. Feeding sites in the

plains were characterised by a high percentage of U. *trichopus*. Other than *C. dactylon*, the feeding sites in Mababe were quite different from those in Savuti. The month in which wildebeest feeding sites were assessed had little influence on the species composition.

Table 3.2: Species composition (%) of grasses in wildebeest feeding sites clustered by correspondence analysis (n= number of feeding sites).

	Site location		
Species	Savuti savanna (n=6)	Savuti grassland (n=22)	Hydromorphic pans in Mababe (n = 8)
Brachiaria nigropedata	82.3		
Cynodon dactylon	17.2	75.1	34.1
Urochloa trichopus	0.5	21.2	0.1
Sporobolus ioclados		0.9	28.4
Eragrostis rotifer		0.5	12.1
Chloris virgata		0.2	8.1
Eragrostis viscosa		0.1	4.3
Aristida meridionalis		0.1	2.6
Dactyloctenium giganteum		0.1	1.9
Digitaria spp.		1.6	
Eustachys paspaloides		0.1	

ii. Selection of grass species and plant part

Grass species

Most grass species, irrespective of their availability in feeding sites, were grazed by zebra and had high site-based acceptance values (Fig. 3.4). A few uncommon

species were not utilised (e.g. T. *berteronianus*, Mababe and *E. superba*, Savuti) or had low acceptance values (e.g. *E. rotifer*, Savuti).

Only three species, namely *U. trichopus, C. dactylon* and *S. ioclados*, were important in zebra feeding sites when assessed at the plant level rather than the site level (i.e. site-based availability) and made up 91% of the total availability (Table 3.3). Although high proportions of tufts of some species were grazed, the overall availability of these grasses was very low. As much as half the tufts of the abundant grasses were grazed and therefore contributed to the bulk of the zebra's diet. In Mababe, fewer species were available and all were heavily grazed, except *T. berteronianus*. The most predominant grass, as in Savuti, was *U. trichopus*, which contributed to the bulk of the zebras' diet (Table 3.3).

The annual grass, *U. trichopus*, was the single most abundant species on the Savuti grasslands while the two perennial grasses, *C. dactylon* and *S. ioclados*, jointly were the next most abundant and almost equal in contribution as *U. trichopus* (see Table 3.1). When zebra first arrived on the plains, they selectively grazed a higher proportion of the annual grass than the perennial grasses (Fig. 3.5). However, as zebra grazed on the open grasslands, the annuals decreased in abundance due to this selective grazing pressure, and zebra then switched to grazing the two more abundant perennial species. The zebra moved to Mababe after the tenth week of assessment but returned to Savuti again after 4 weeks. There were so few perennial species in feeding sites in Mababe that a meaningful ratio of annual versus perennial species grazed could not be calculated. There was substantial re-growth of the annuals in Savuti due to the lack of grazing pressure during the absence of zebra.

On their return from Mababe, the zebra exhibited a similar selection for the annuals over the perennials when they first arrived in Savuti. However, they soon switched to grazing more perennials again. The switch in the diet of zebra from primarily annuals to an increasing percentage of perennials was gradual over time and curvilinear ($F = 40.35$, $P<<0.001$ with 2 DF; Fig. 3.6).

Table 3.3: Availability of grass species and the proportion of tufts grazed in zebra feeding sites.

	Feeding site location			
	Savuti		Mababe	
Species	Proportion grazed	Availability	Proportion grazed	Availability
Eragrostis rigidior	1.0	0.1%		
Bothriochloa insculpta	0.7	0.4%		
Digitaria species	0.6	1.3%		
Panicum repens	0.5	0.8%		
Sporobolus ioclados	0.5	9.3%	0.6	0.6%
Chloris virgata	0.5	3.6%		
Brachiaria nigropedata	0.5	1.0%		
Cynodon dactylon	0.5	33.1%		
Urochloa trichopus	0.4	48.5%	0.5	88.7%
Eustachys paspaloides	0.4	1.1%	0.7	6.1%
Eragrostis rotifer	0.4	0.3%		
Tragus berteronianus	0.3	0.5%	0.0	0.9%
Eragrostis superba	0.0	0.1%		
Echinochloa crus-galli			1.0	3.7%

Irrespective of whether analysed at the site (Fig. 3.7) or the plant level (Table 3.4), all grass species except *Aristida meridionalis* and *Eragrostis viscosa* in wildebeest feeding sites were heavily grazed.

Table 3.4: Availability of grass species and the proportion of tufts grazed in wildebeest feeding sites.

Species	Proportion grazed	Availability
Digitaria species	1.0	1.1%
Dactyloctenium aegyptium	1.0	0.3%
Eustachys paspaloides	1.0	0.1%
Eragrostis rotifer	1.0	1.6%
Chloris gayana	0.9	1.8%
Brachiaria nigropedata	0.8	8.9%
Eragrostis rigidior	0.7	3.6%
Urochloa trichopus	0.7	13.0%
Cynodon dactylon	0.6	58.4%
Sporobolus ioclados	0.6	9.5%
Eragrostis viscosa	0.4	1.0%
Aristida meridionalis	0.2	0.7%

Plant part

Except in the very early growing stage, neither zebra nor wildebeest grazed inflorescences of species with awned seeds. More than 85% of the 15 grass species that occurred in zebra feeding sites produced round, awnless seeds. The more common of these included *B. nigropedata, C. dactylon*, *Digitaria* species, *E. crus-galli*, *E. paspaloides*, *S. ioclados*, and *U. trichopus*. Both zebra and wildebeest grazed high proportions of inflorescences, when present, of all grass species in feeding sites (Table 3.5). It might be expected that inflorescences on a grass like *C. dactylon* were grazed by chance because of the short inflorescence stalk. The

inflorescence does not protrude much higher than the leaves and might have been grazed with the leaves in one bite. However, all the other species in the grass layer had inflorescences that protruded well above the leaves and were heavily grazed. Greater proportions of inflorescences were grazed than leaves on tufts of all grass species in both zebra and wildebeest feeding sites.

Table 3.5: Proportions of inflorescences and leaves grazed in zebra and wildebeest feeding sites.

	ZEBRA					WILDEBEEST				
	Inflorescence		Leaf		Species prevalence	Inflorescence		Leaf		Species prevalence
Species	Grazed	Present	Grazed	Present		Grazed	Present	Grazed	Present	
B. nigropedata	-	-	-	-	-	0.97	0.04	0.78	1.0	0.09
C. dactylon	0.54	0.02	0.50	1.0	0.26	0.93	0.20	0.6	1.0	0.58
S. ioclados	0.67	0.03	0.52	1.0	0.07	0.64	0.08	0.58	1.0	0.10
U. trichopus	0.70	0.26	0.45	1.0	0.58	1.0	0.12	0.68	1.0	0.13
Other species	0.71	0.03	0.56	1.0	0.09	0.85	0.08	0.78	1.0	0.10
Total		0.34			1.00		0.52			1.00

iii. Selection of green leaf

Grasses remained green from 5 weeks into the wet season until the 11th week. By the 19th week, many grasses, especially the annual species, had begun drying out following maturation and seed ripening. The grasslands were mostly green when zebra occurred in Savuti and Mababe and they left the wet season range before

grasses dried out completely. However, when grasses started to turn brown, the zebra tended to feed mostly in the greener areas (Fig. 3.8). Although zebra grazed significantly more green tufts than brown ($t_{\alpha=0.5}$ = 6.314; P < 0.10) of the two most common species, *U. trichopus* and *C. dactylon*, they grazed more brown tufts of *S. ioclados* and other uncommon species (Table 3.6). Over all species in feeding sites, however, there was no significant difference between the mean proportion of green (μ = 0.47) and brown (μ = 0.49) tufts grazed ($t_{\alpha=0.5}$ = 2.353; P = 0.36).

Wildebeest remained in the wet season range longer than zebra and were present as the grasslands progressively dried up toward the end of the wet season. Unlike the zebra, wildebeest often grazed on the short grasslands on compact soils around pans and the edge of the Savuti grassland where grasses dried out quickly in the absence of rain. Hence, a large proportion of brown grass occurred in wildebeest feeding sites and they never grazed in completely green areas (Fig. 3.9). Wildebeest were highly selective for green tufts in feeding sites and the mean proportion of green tufts grazed (μ = 0.70) was significantly ($t_{\alpha=0.05}$ = 2.132; P < 0.05) greater than brown (μ = 0.60) tufts of all species grazed (Table 3.6).

iv. Influence of sward height on animal movement

The average sward height (mean maximum leaf height) in zebra feeding sites was largely influenced by the sward height of *U. trichopus* because of the predominance of this species in the grass layer. The common perennials, *C. dactylon* and *S. ioclados*, were shorter than *U. trichopus*, especially later in the growing season. These three species also contributed to more than 80% of the species composition

and, therefore, were used to investigate the influence of grass height on zebra movements.

Table 3.6: *Proportions of green and brown tufts grazed in zebra and* wildebeest feeding sites in relation to the presence of tufts and species prevalence.

	ZEBRA					WILDEBEEST				
	Brown tufts		Green tufts		Species prevalence	Brown tufts		Green tufts		Species prevalence
Species	Grazed	Present	Grazed	Present		Grazed	Present	Grazed	Present	
B. nigropedata	-	-	-	-	-	0.67	0.58	0.93	0.42	0.09
C. dactylon	0.41	0.07	0.50	0.93	0.26	0.49	0.38	0.67	0.62	0.58
S. ioclados	0.63	0.10	0.51	0.90	0.07	0.57	0.70	0.58	0.30	0.10
U. trichopus	0.29	0.08	0.46	0.92	0.58	0.66	0.88	0.81	0.12	0.13
Other species	0.61	0.34	0.57	0.66	0.09	0.77	0.83	0.62	0.17	0.10
All species	0.47	0.11	0.49	0.89	1.00	0.60	0.54	0.70	0.46	1.00

In the first 10 weeks of the wet season, grasses were in an active growth stage. The sward height increased during this period despite heavy grazing pressure by zebra (Fig. 3.10). Later in the wet season when *U. trichopus* stopped growing, the sward height decreased as a result of grazing. However, grazing appeared to have little influence on the height of perennial grasses. Later in the wet season between the 16th and 18th weeks, the sward height appeared to decrease but the data were insufficient to support this. Zebra movements between Savuti and Mababe occurred in the 10th and the 14th week of the wet season. In the 18th week they left Savuti for

the dry season range. During all three these stages of movement, the zebra consistently moved from grasslands with a average sward height of approximately 17 cm to an area with a much taller sward. In the last week before the zebra moved, the majority of *U. trichopus* tufts in zebra feeding sites were shorter than 20 cm and *C. dactylon* and *S. ioclados* tufts were shorter than 15 cm (Table 3.7).

Table 3.7: Proportion of tufts below different heights in zebra feeding sites in the wet season range. *Bold figures highlight the height threshold at which the* proportion of tufts exceeds 50%.

	Urochloa trichopus			*Cynodon dactylon* & *Sporobolus ioclados*		
Height (cm)	9th week	15th week	19th week	9th week	15th week	19th week
<6	0.01	0.02	0.00	0.02	0.00	0.00
<9	0.14	0.06	0.10	0.17	0.00	0.03
<12	0.31	0.19	0.17	0.34	0.25	0.18
<15	**0.56**	0.33	0.35	**0.56**	**0.75**	**0.51**
<18	**0.75**	0.45	0.43	**0.70**	**1.00**	**0.64**
<21	**0.84**	**0.53**	**0.57**	**0.80**	**1.00**	**0.81**
<24	**0.95**	**0.67**	**0.68**	**0.94**	**1.00**	**0.95**
<27	**0.99**	**0.69**	**0.73**	**0.98**	**1.00**	**0.99**
<30	**0.99**	**0.74**	**0.84**	**0.99**	**1.00**	**0.99**
<33	**1.00**	**0.81**	**0.91**	**1.00**	**1.00**	**1.00**
<36	**1.00**	**0.81**	**0.91**	**1.00**	**1.00**	**1.00**
<39	**1.00**	**0.86**	**0.95**	**1.00**	**1.00**	**1.00**

When the zebra first arrived in Savuti in the wet season, much of the sward of the

annual, *U. trichopus*, was less than 10 cm in height while the sward of perennial grasses was less than 15 cm (Fig. 3.11). From the sixth week onward grass showed rapid growth and the height and variation in the height of tufts within the sward increased. However, grazing pressure by the zebra later reduced grass height and, by the 9th week when they moved to Mababe from Savuti, both annuals and perennials had been grazed to the same height as when the zebra first arrived in the wet season range. When the zebra arrived in Mababe, *U. trichopus* ranged from about 5 cm tall to over 60 cm tall. After four weeks in Mababe (i.e. the 13th week of the wet season) grazing by zebra had some effect on the height of tufts but this was not as marked as in Savuti. When the zebra returned to Savuti from Mababe in the 15th week, the grasslands had re-grown in the absence of grazing. In the five weeks the zebra spent at the end of the wet season in Savuti before leaving for the dry season range, the effect of grazing on grass height was marked. The medium height grassland of annuals and perennials was essentially reduced to a short grassland.

Wildebeest used feeding sites of variable sward height in the wet season and no clear pattern of height change over time was evident (Fig. 3. 12). The sward height in many of the sites was similar to that in sites used by zebra but the wildebeest remained longer in the wet season range than zebra. Toward the end of the wet season, the sward was very short (down to 10 cm) in some sites. Although wildebeest grazed in sites of variable sward height, they most often tended to use areas of predominantly short grass where most tufts were less than 20 cm in height (Fig. 3.13).

Discussion

Zebra and wildebeest were specific in their choice of grass communities in the wet season range. Wildebeest particularly grazed in grasslands that varied little in species composition, except for differences in the presence of uncommon species, throughout the region. Zebra ranged over a larger area than wildebeest and therefore there were distinct differences in species composition between the Savuti grassland and Mababe wooded grasslands probably due to edaphic characteristics. Despite these differences, *U. trichopus*, *C. dactylon* and *S. ioclados* were common and widespread and were principal grasses in the diets of both zebra and wildebeest.

Zebra have been classified as a generalist feeder, being relatively unselective for grass species (Hansen, Mugambi & Bauni, 1985; Skinner & Smithers, 1990; Smuts, 1972; Stewart & Stewart, 1970) and will even eat small amounts of non-graminous herbs and dicotyledons (Jarman, 1971; Novellie *et al.*, 1988). The feeding behaviour of zebra in northern Botswana showed consistency with these previous studies and almost all grass species were grazed to some degree in feeding sites. They also selected the inflorescences over leaves of most grasses but more especially the large round seeds of *U. trichopus*. This study did not investigate the proportions of stem and leaf sheath grazed but it can be assumed that a large proportion of stem (more specifically seed culm) must have been eaten with the seed heads. Analysis of the gut contents of zebra in Serengeti (Gwynne & Bell, 1968) revealed much higher proportions of sheath and stem compared to leaf while in Kruger National Park evidence indicates that zebra there did not show any preference for the structural components of grasses (Smuts, 1972).

Zebra showed a moderate preference for green grass but, because this study was only conducted in the wet season range, leaves did not start turning brown until late in the season when zebra started moving away. It was therefore difficult to assess whether zebra consistently grazed green tufts preferentially. They did appear to prefer grazing in greener areas though and in Kruger National Park (Smuts, 1972) and East Africa (Stewart & Stewart, 1970) zebra tracked areas of green grass flush following either fire or rain.

Grass quality was not measured empirically during this study but rather quality was inferred through the use of select indices. Hence, there are definite limitations to the data and the results and interpretations thereof should be seen in this light. Given this approach, it appeared that zebra were targeting forage of relatively high nutrient quality in feeding areas throughout the wet season range. They selected the green tufts of palatable species in green patches (Pratchett, 1976; Georgiadis & McNaughton, 1990). *Urochloa trichopus* formed an important part of the diets of zebra, particularly early in the wet season. Only later in the season did the perennial species become important largely because the annuals had either died off or been heavily grazed.

Zebra first arrived in Savuti from the dry season range when grasses were still in a stage of active growth and the average sward height was below 10 cm. The height of grasses would be expected to increase rapidly especially given the heavy rains that fell prior to, and following, the arrival of zebra. However, the net increase in height was low due to heavy grazing pressure exerted by the migrant animals and was particularly evident on *U. trichopus*, the preferred grass of zebra at this time of the

season. Grazing pressure on the perennials was low and these grasses grew to the maximum height they would attain in the season. Primary production clearly decreased as the season progressed and the grasses matured. Subsequently, the effects of grazing on the average height of the grasses became more evident and zebra consistently moved between Savuti and Mababe when the sward was reduced to between 15 cm and 20 cm. They also left the wet season range when grasses had been grazed down to these levels. Zebra avoided grazing grasses shorter than similar height levels in the Kruger National Park (≈10 cm – 15 cm; Smuts, 1972) and Serengeti (≈10 cm; McNaughton, 1976, 1979) while the Cape mountain zebra (*Equus zebra zebra*) preferred grasses taller than 5 cm (Grobler, 1983; Novellie *et al.*, 1988). The decrease in available food abundance in feeding areas within the wet season range appears, therefore, to be an important factor governing the decision for zebra to move long distances between areas (Bell, 1971; Sinclair, Dublin & Borner, 1985; Senft et al, 1987; Fryxell & Sinclair, 1988).

Wildebeest grazed in short to medium height grasslands with moderate to high levels of grazing. Although they grazed predominantly on tufts below 20 cm in height, they did graze taller grasses, unlike the Serengeti wildebeest that grazed to a low height of 7 cm in the plains (McNaughton, 1976, 1979). In general, wildebeest prefer short, lawn-like grasslands and seldom graze in grasslands taller than 15 cm (Skinner & Smithers, 1990). Characteristically, they were highly selective for green grass (Murray & Brown, 1993) although they did tend to graze in browner patches as conditions became drier toward the end of the wet season. This was most likely a function of opportunity for selection in relation to availability. Chobe wildebeest grazed a high proportion of inflorescences. Mostly, wildebeest tend to eat high

proportions of leaves and lower proportions of stem and sheath (Gwynne & Bell, 1968). This difference may be because wildebeest often grazed in close proximity to zebra, the latter having grazed the seed heads. Also, many of the grasses in wildebeest sites were tufted perennials that grew close to the ground with seed heads on short culms. Wildebeest have wide muzzles (Jarman, 1974; Skinner & Smithers, 1990) which makes it difficult for them to select leaf only when grazing plants of this structure and inflorescences were probably inadvertently removed with leaves during each bite.

There are several models that have been developed to explain the predominance of medium-sized ruminants, more specifically bovid artiodactyls, over co-existing hindgut fermenters, more specifically equid perissodactyls. The Demment and Van Soest (1985) model accounts for the absence of ruminants amongst the small and very large species. The Bell (1971), Janis (1976) and Foose (1982) model implies that ruminants have a greater ability to extract nutrients from medium quality forage compared to hindgut fermenters. The latter persist only because of the ability to consume more food in a day and thus extract more nutrients, particularly from high fibre, low quality forage. Duncan *et al.* (1990) tested this model using available data for nutrient extraction rates and they established that equids are capable of extracting more nutrients per day from forage than bovids, supporting part of the model. However, their data did not support the model in that ruminants did not achieve higher nutrition extraction rates than hindgut fermenters on middle fibre forages. Therefore neither of the nutritional models explained the greater success of ruminants over hindgut fermenters.

In contrast to Serengeti where 1.5 million wildebeest co-exist with a quarter of a million zebra (McNaughton, 1983; Sinclair & Norton-Griffiths, 1979), zebra in northern Botswana outnumbered wildebeest by a factor of eight (Joos-Vandewalle, 1988). Both these medium-sized ungulates more often than not are used as the test case for the nutritional models previously described. Results from this study suggest that zebra had access to and grazed taller, more nutritious grasses (predominantly annuals) than wildebeest (almost exclusively perennials). Tall annual grasses were predominant in the grass layer and as a result further enhanced the advantage of zebra over wildebeest because of this access to a greater bulk of forage. The zebra ranged over a large area and moved a long distance to Mababe where tall annuals, particularly *U. trichopus*, prevailed while the wildebeest remained in a much smaller range in the wet season. The zebra relocated when grasses were grazed short and they moved to areas of substantially taller (greater abundance) grass whilst the wildebeest essentially wandered about within the range grazing in short to medium height patches. This study suggests that zebra may be more successful than the wildebeest because they appeared to be eating greater quantities of forage and assimilating more nutrients daily, supporting the findings of Duncan *et al.* (1990) in refuting the Bell / Janis / Foose model.

Unable to propose or develop an alternative nutrient model, Duncan *et al.* (1990) merely proposed several hypotheses that might explain the predominance of medium-sized ruminants. Firstly, they suggest that the longer period of activity of equids might require greater energy costs than the less active wildebeest. Yet, the zebra in this study were not only more active (Joos-Vandewalle, unpubl. data) but they also moved substantially greater distances than the wildebeest thereby requiring

an even greater energy cost. Secondly, they suggest that the need to feed longer would also expose the equids to higher risks of predation whilst feeding, especially at night. This is indeed true in Savuti where lions and hyenas preyed more heavily on zebra than wildebeest (Viljoen, pers. comm.; Cooper, 1990). Hence, these two alternative hypotheses would still not adequately explain the differences in the predominance of ruminants over hindgut fermenters.

Zebra ate high quantities of food daily and quickly reduced the immediate availability of forage in feeding patches to low levels. They then relocated to areas of a greater abundance of forage, in principle supporting optimal foraging behaviour (Charnov, 1976; Stephens and Krebs, 1986). It seems therefore that the zebra have a competitive advantage over wildebeest due to foraging behaviour rather than digestive anatomical and physiological adaptations. What is not clear from this study though is whether the zebra are better at maximising the daily intake of nutrients by feeding on the 'best mix' of food (Westoby, 1974) or maximising the intake of the most limiting nutrient during short-term foraging periods (Owen-Smith & Novellie, 1982). The nutrient status of the grasses in Savuti and Mababe need to be established in order to assess the possible applicability of these theories in this ecosystem. On the Serengeti plains, food resources available to grazing ungulates differ from northern Botswana in that highly nutritious grasses on volcanic soils grow in short lawn-like grasslands (McNaughton, 1976, 1979, 1983). Only in the northern and western parts in the Masai-Mara do tall grasslands occur in the zebra and wildebeest ranges. It is perhaps this contrast in available food resources that gives the wildebeest an advantage over the zebra. In Kruger National Park, like northern Botswana, the zebra were more abundant than the wildebeest (Hall-Martin, Whyte &

Viljoen, 1987). However, there have been so many confounding management practices such as culling exercises (Smuts, 1978), provision of water (Joubert, 1974; Thrash, Theron & Bothma, 1993) and fencing activities (Whyte, 1985; Whyte & Joubert, 1988) that may well mask any inherent and comparative differences observed in the numbers of these two species here.

The nutrient and mineral concentrations of forage in Savuti and Mababe need to be established in order to further investigate the movements of zebra and wildebeest in relation to their foraging behaviour in northern Botswana. This was investigated and is discussed in the next chapter.

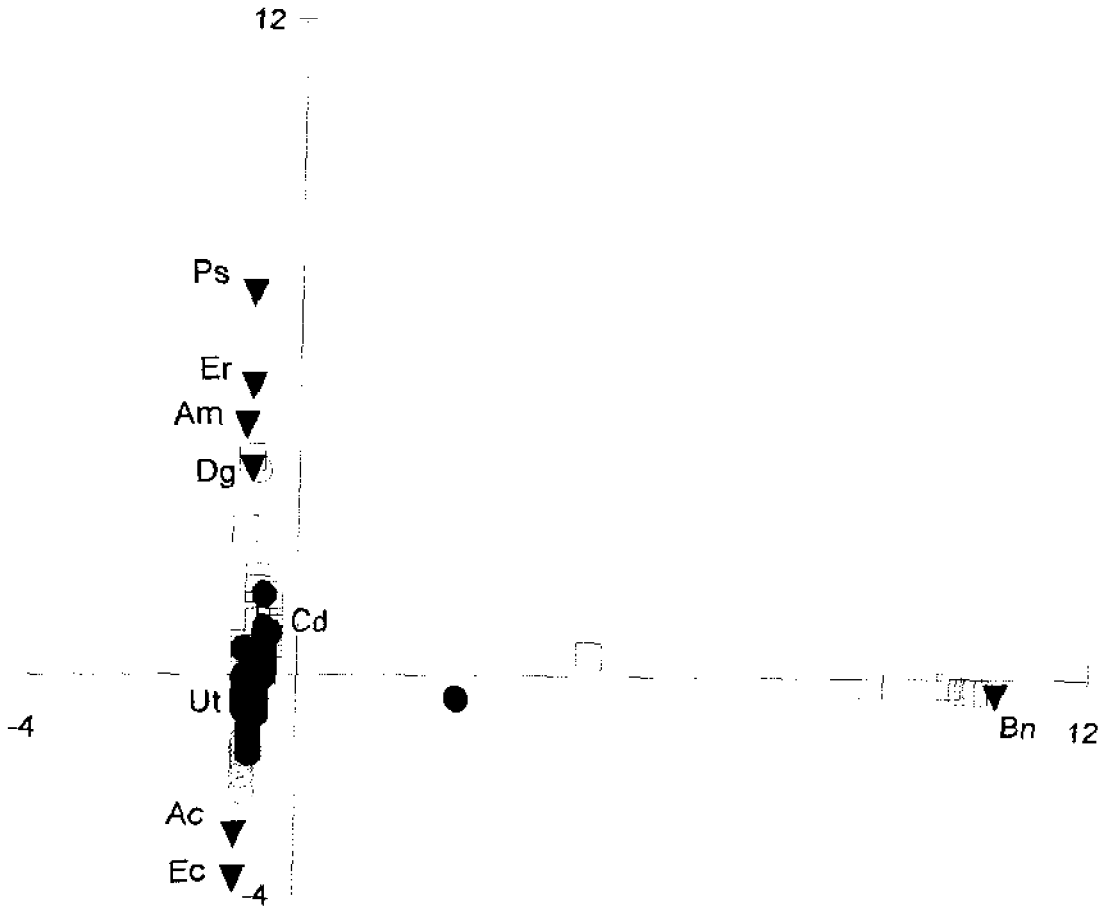

Figure 3.1: Ordination of grass species composition of both zebra and wildebeest feeding sites by correspondence analysis. Zebra sites were located in Savuti (open circles) and Mababe (solid circles). Wildebeest sites (open squares) were not separated into areas. For clarity, only the nine grass species (solid triangles) contributing most to the variation in the ordination were plotted. (See Fig. 3.2 for identification of acronyms).

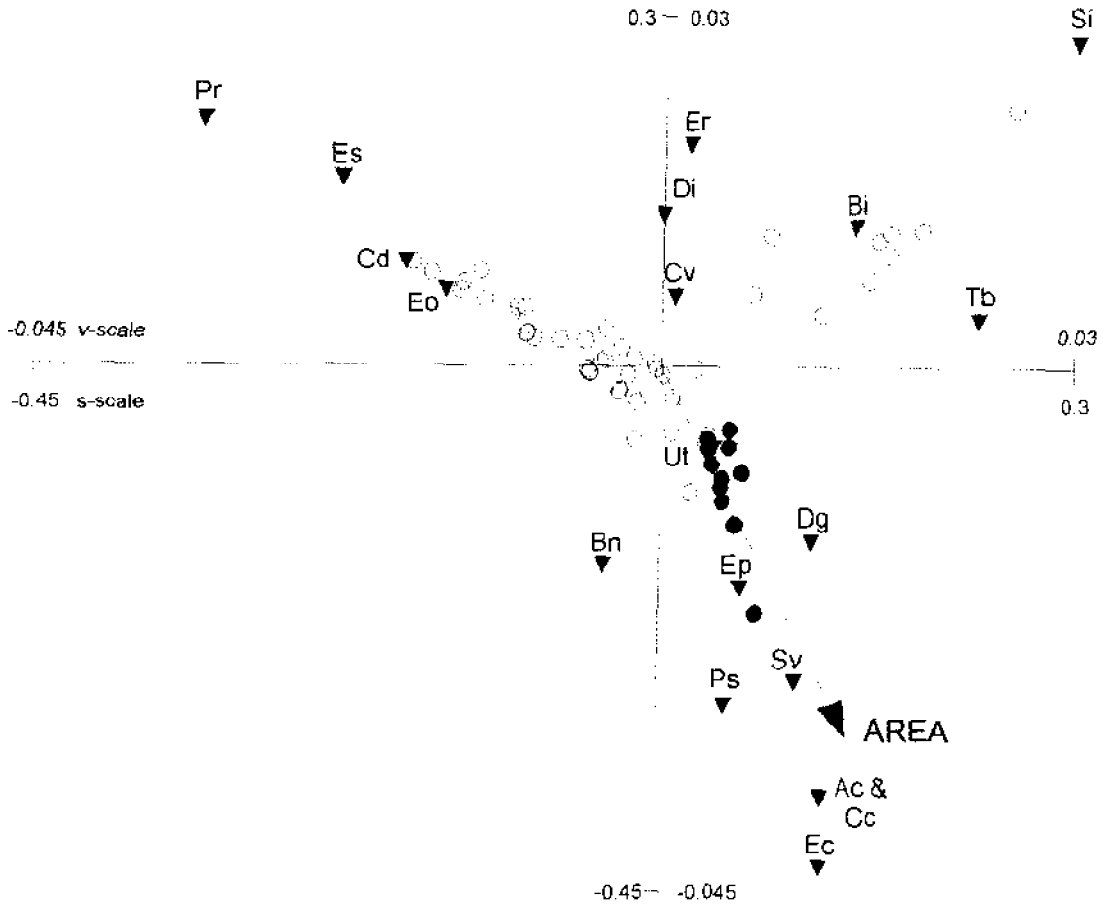

Figure 3.2: Ordination of grass species composition in zebra feeding sites in Savuti (open circles) and Mababe (solid circles) by correspondence analysis. The arrow indicates the influence of the location of feeding sites (AREA variable) relative to the axes on the variation described by the ordination. The v-scale applies to the variable arrow and the s-scale to the site and species points. Species (solid triangles) names are: Ac = *Aristida congesta*, Am = *A. meridionalis*, Bi = *Bothriochloa insculpta*, Bn = *Brachiaria nigropedata*, Cc = *Cenchrus ciliaris*, Cd = *Cynodon dactylon*, Cv = *Chloris virgata*, Di = *Digitaria* spp., Dg = *Dactyloctenium giganteum*, Ec = *Echinochloa crus-galli*, Eo = *Eragrostis rotifer*, Er = *E. rigidior*, Es = *E. superba*, Ep = *Eustachys paspaloides*, Ev = *E. viscosa*, Pr = *Panicum repens*, Ps = *Pogonarthria squarrosa*, Si = *Sporobolus ioclados*, Sv = *Setaria verticiliata*, Tb = *Tragus berteronianus*, Ut = *Urochloa trichopus*.

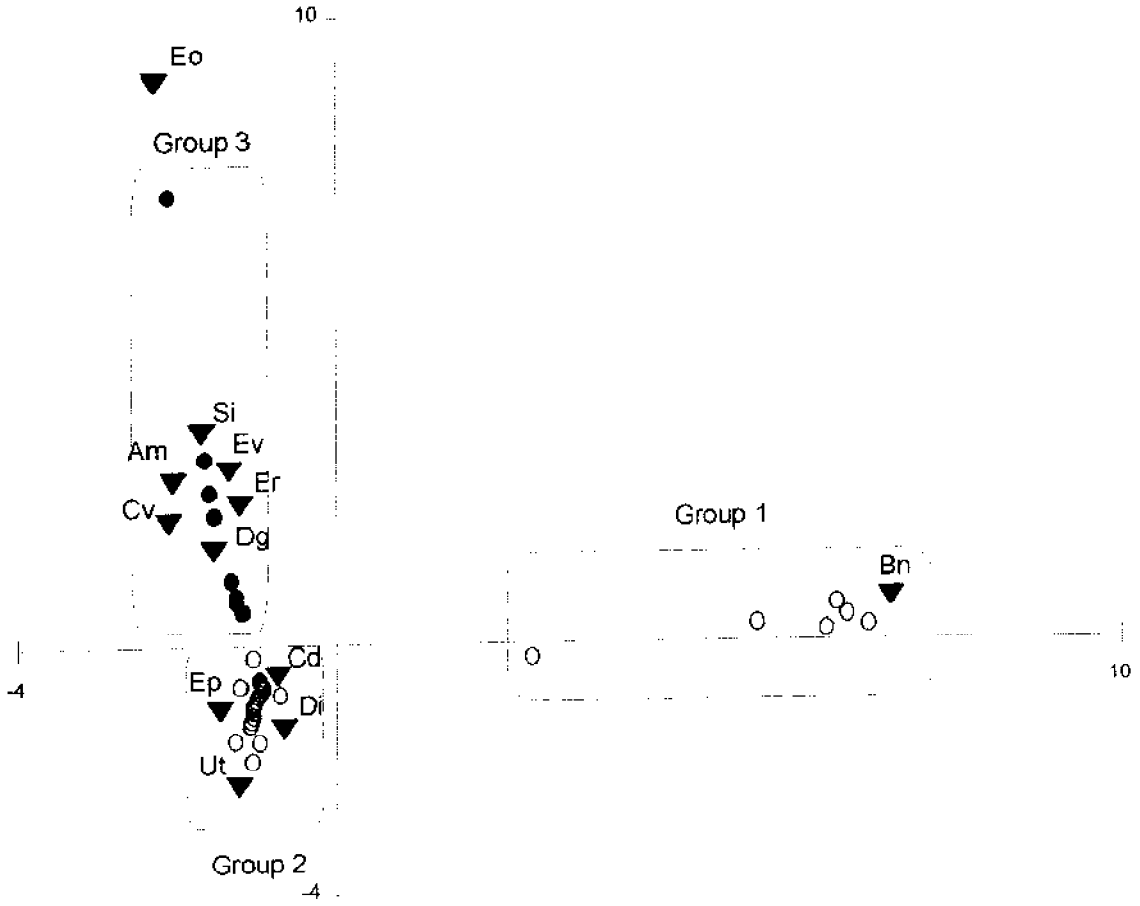

Figure 3.3: Ordination of grass species composition in wildebeest feeding sites in Savuti (open circles) and Mababe (closed circles) by correspondence analysis. See Fig. 3.2 for identification of species (solid triangles) acronyms.

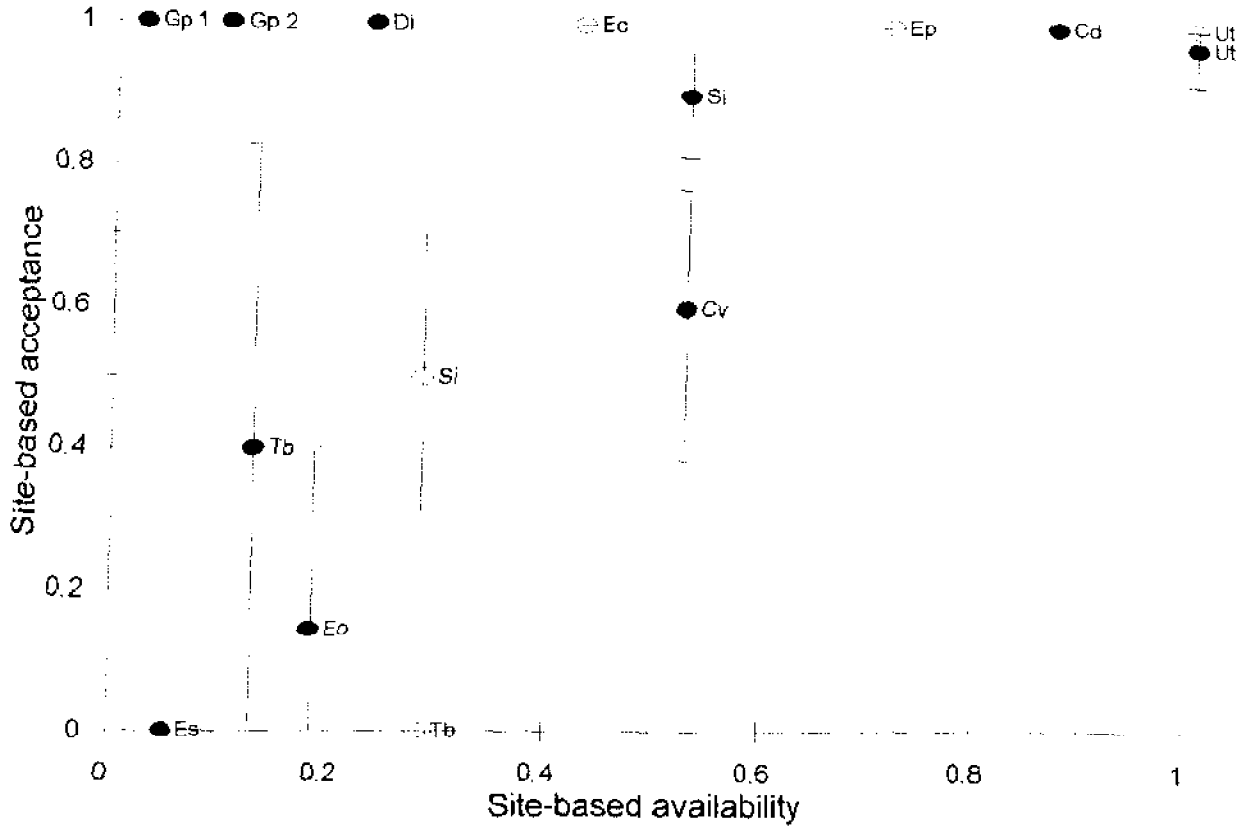

Figure 3.4: *Comparison* of site-based acceptance values in relation to the availability of grass species in zebra feeding sites in Savuti (solid circles) and Mababe (open circles). Lines indicate 95% CL. Gp. 1 comprises species Bn & Ec, and Gp. 2 comprises species Bi, Ep, Er & Pr. (see Fig. 3.2 for identification of acronyms).

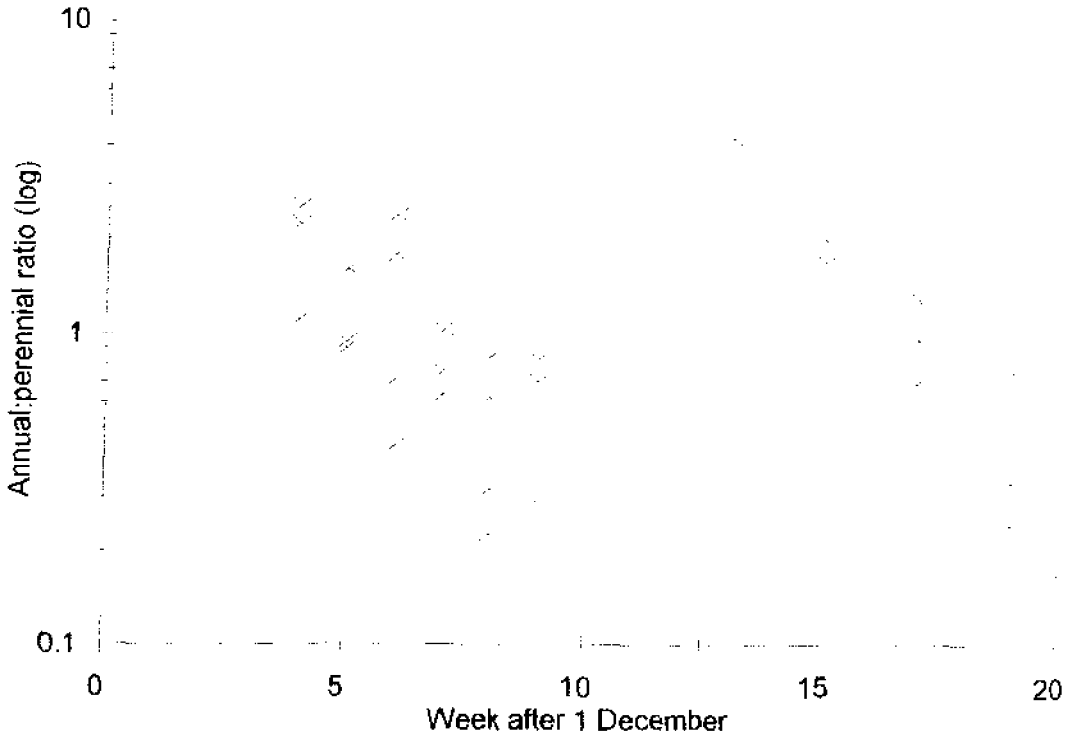

Figure 3.5: Weekly change in the ratio of the proportion of tufts of an annual grass species (*Urochloa trichopus*) grazed to the proportion of tufts of two perennial grass species (*Cynodon dactylon* and *Sporobolus ioclados*) grazed in zebra feeding sites in Savuti. Zebra were absent from Savuti from the 10th to the 14th weeks.

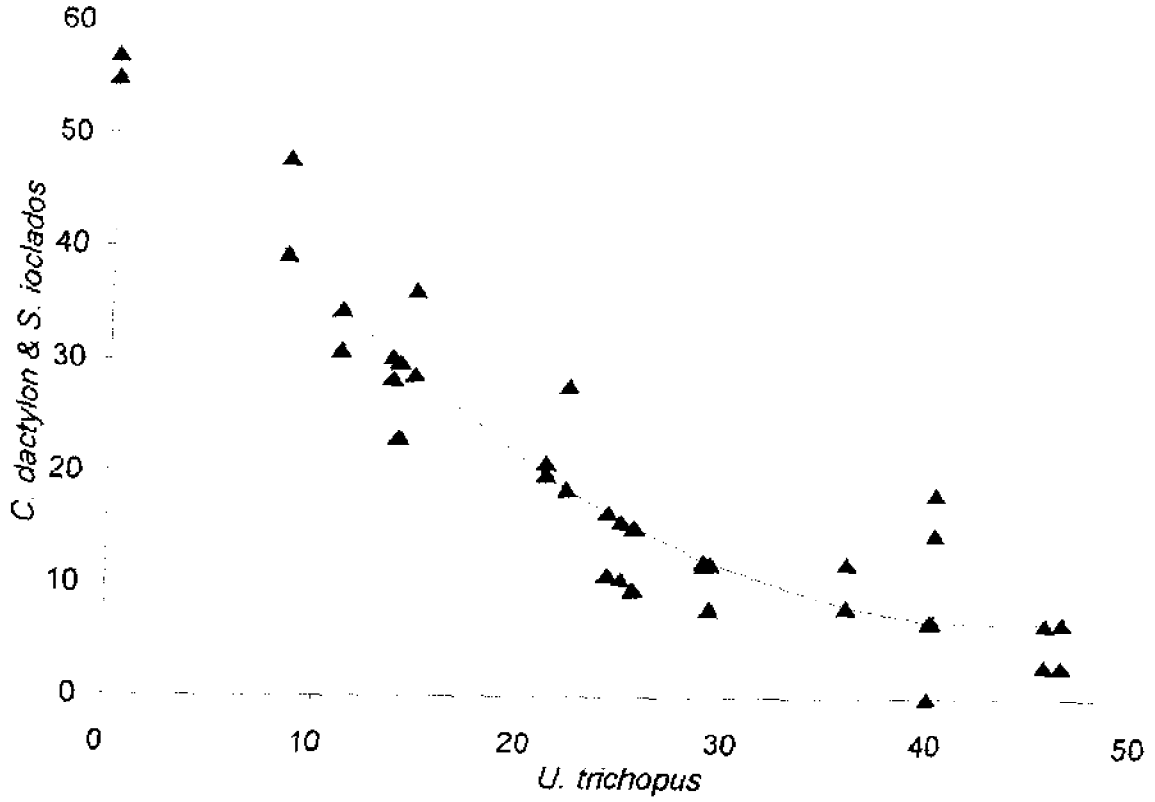

Figure 3.6: Percentage of tufts of a common annual (*Urochloa trichopus*) grass species grazed compared to two common perennial (*Cynodon dactylon* and *Sporobolus ioclados*) grass species in zebra feeding sites. Shown is the best-fit line with $R^2 = 0.8345$. The regression was highly significant with $F = 40.35$ and $P<<0.001$ at 2 DF.

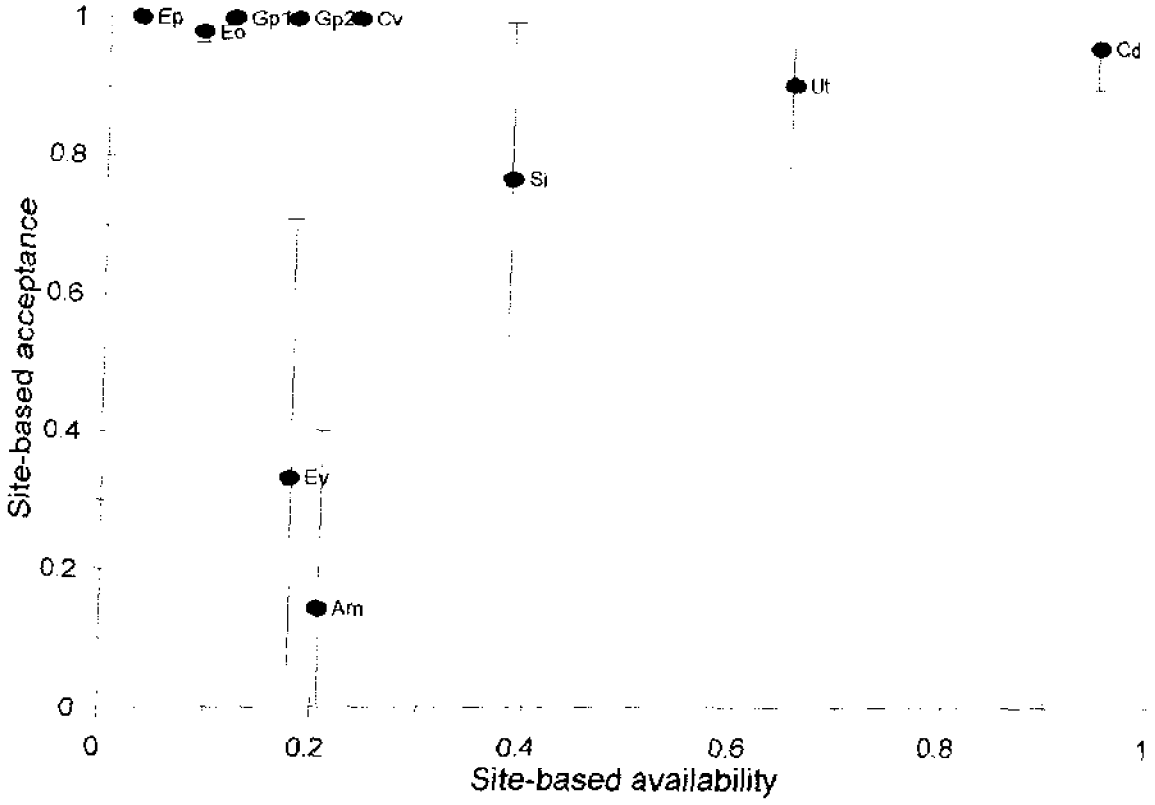

Figure 3.7: Comparison of site-based acceptance values in relation to the availability of grass species in wildebeest feeding sites in Savuti. Lines indicate 95% CL. Gp. 1 comprises species Bn & Dg, and Gp. 2 comprises species Di & Er. (see Fig. 3.2 for identification of acronyms).

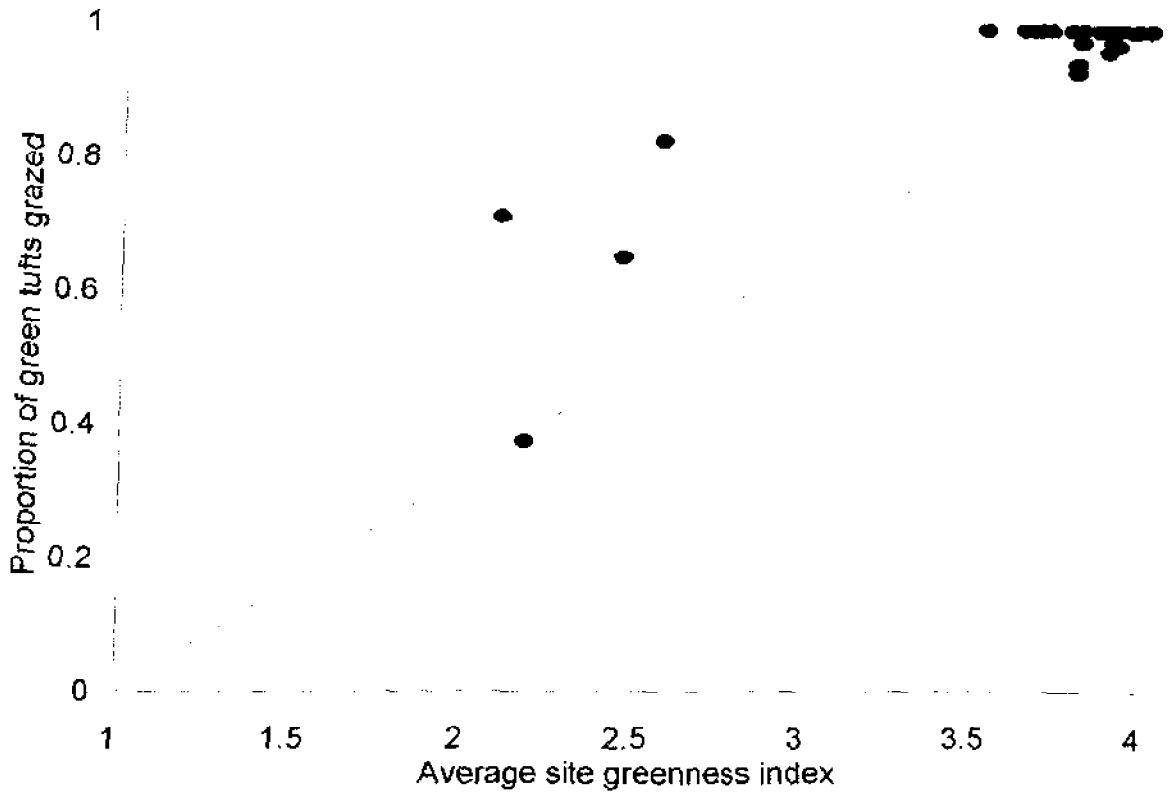

Figure 3.8: Green tufts grazed as a proportion of all tufts grazed in relation to the average greenness of zebra feeding sites. Greenness index of 2.5 for a site indicates equal presence of green and brown tufts. Line of equality indicates grazing of equal proportions of green and brown tufts.

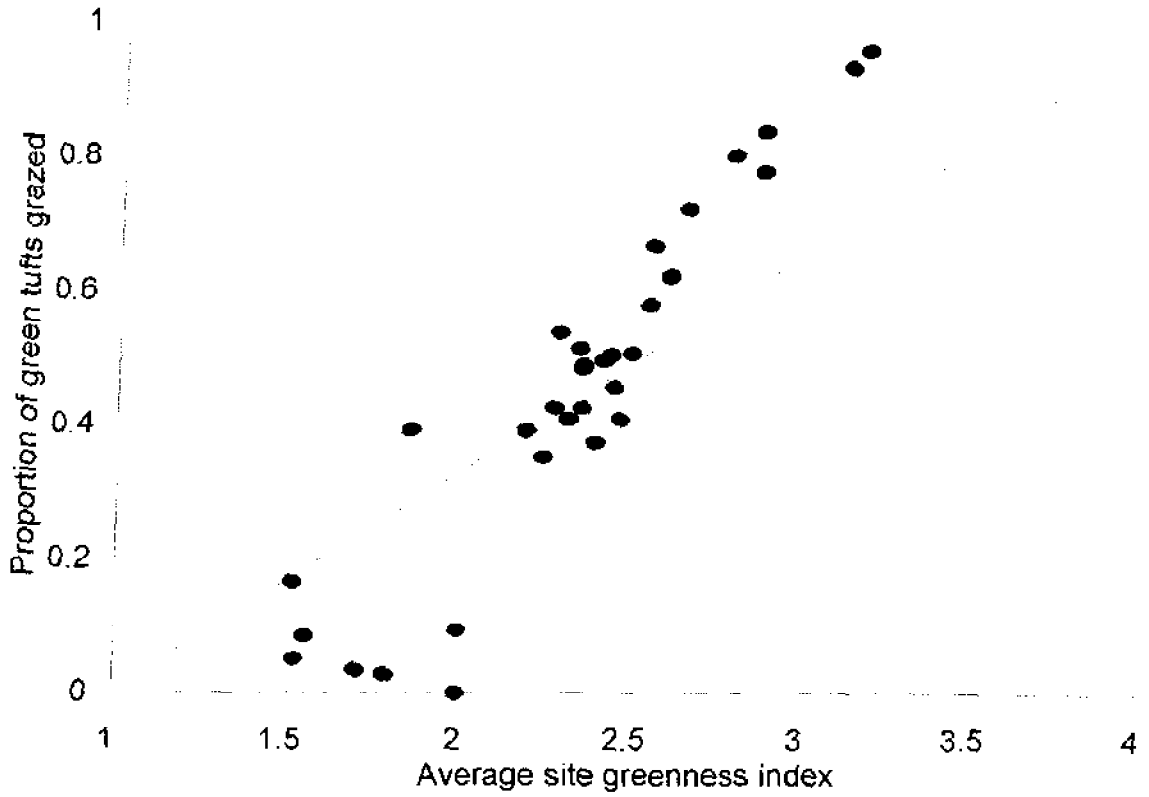

Figure 3.9: Green tufts grazed as a proportion of all tufts grazed in relation to the average greenness of wildebeest feeding sites. Greenness index of 2.5 for a site indicates equal presence of green and brown tufts. Line of equality indicates grazing of equal proportions of green and brown tufts.

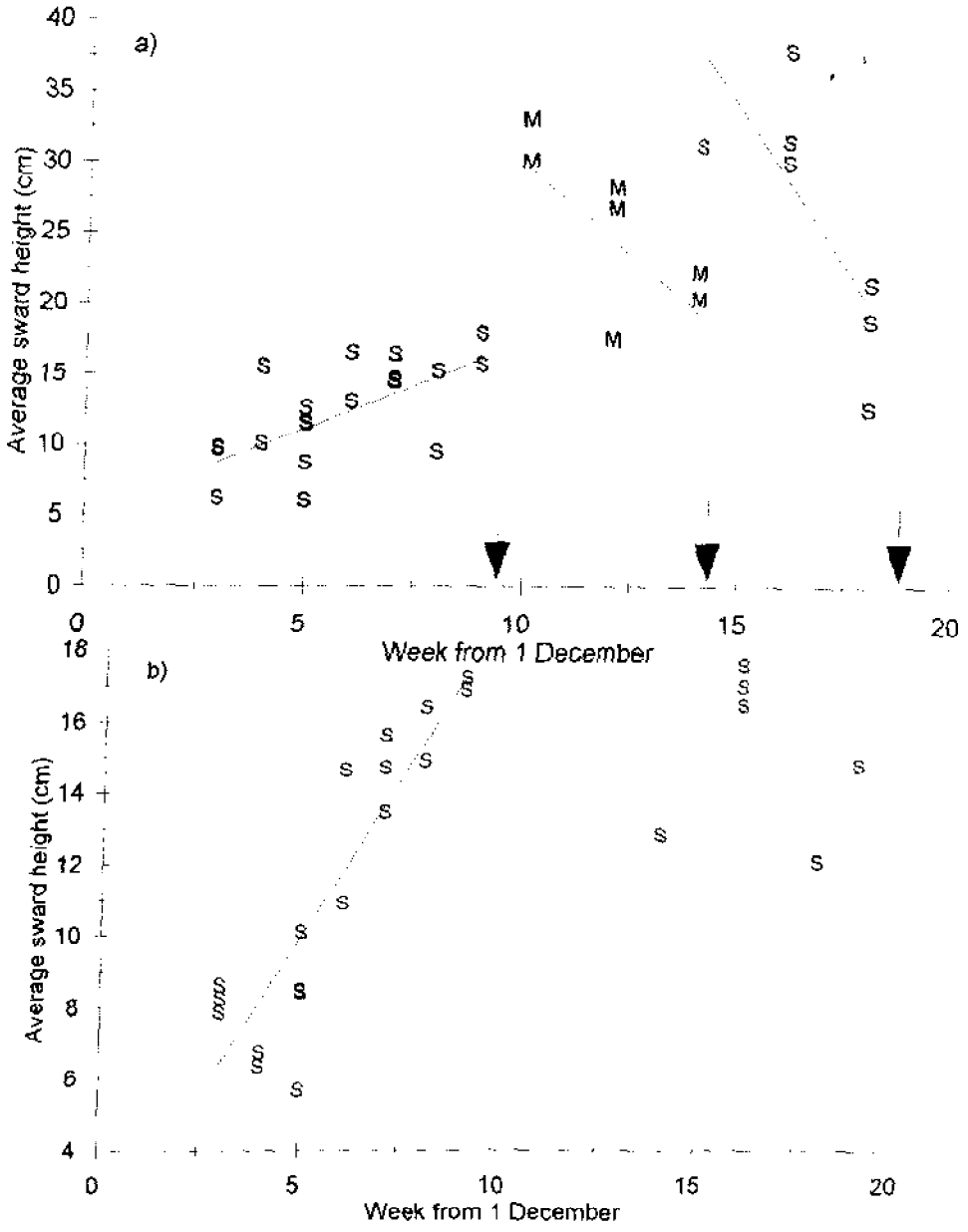

Figure 3.10: Average sward (mean maximum leaf) height of a) *Urochloa trichopus* (common annual) and b) *Cynodon dactylon* and *Sporobolus ioclados* (two common perennials) in feeding sites of zebra. Lines are best-fit lines for points in each of the respective areas; S = Savuti sites, M = Mababe sites. Arrows indicate week of zebra movements between the areas and in the 18th week, the movement to the dry season range.

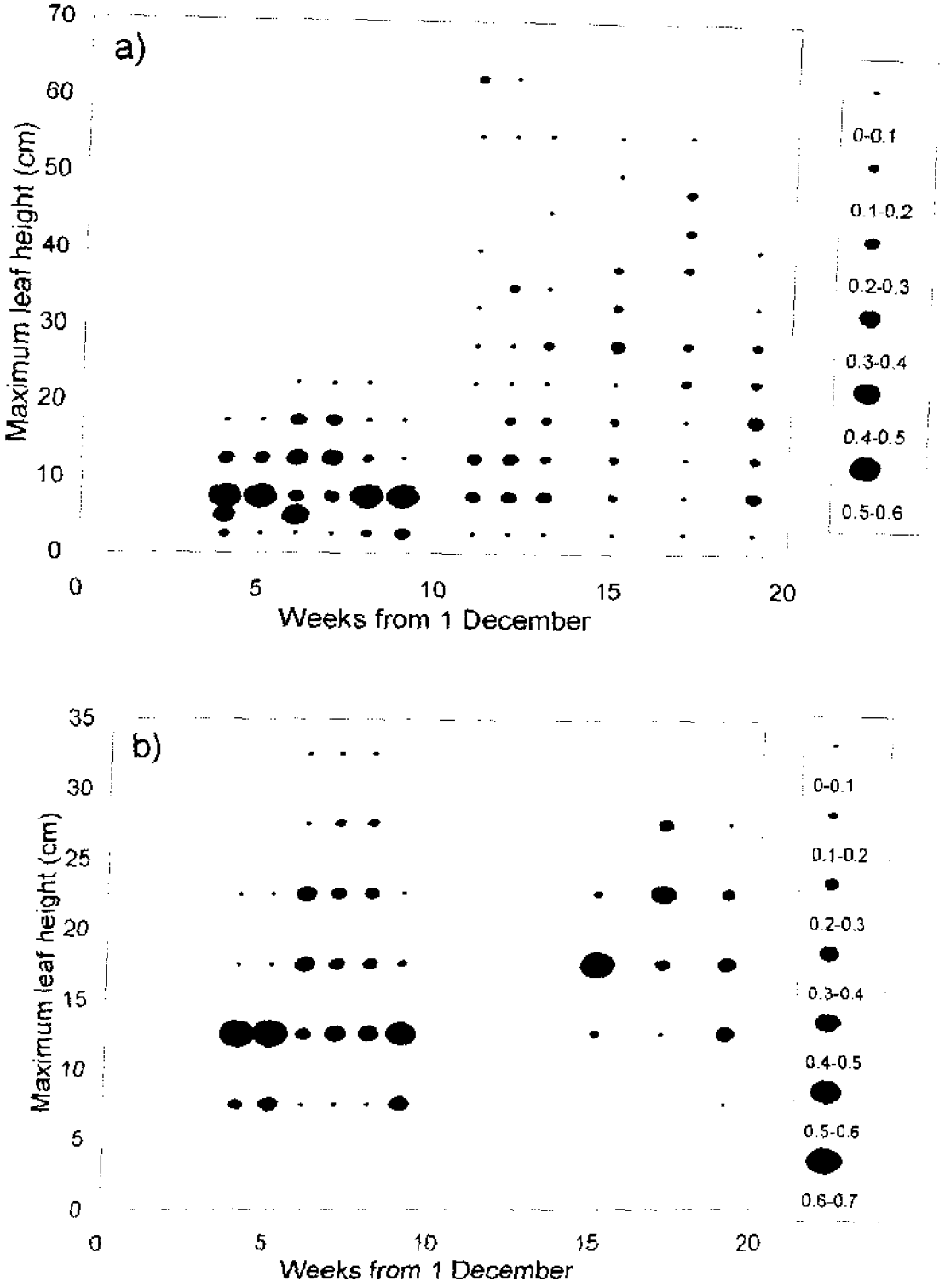

Figure 3.11: Change in the frequency distribution of the mean maximum leaf height of grass tufts of a) *U. trichopus* (a common annual) and b) *Cynodon dactylon* and *Sporobolus ioclados* (two common perennials) in feeding sites of zebra.

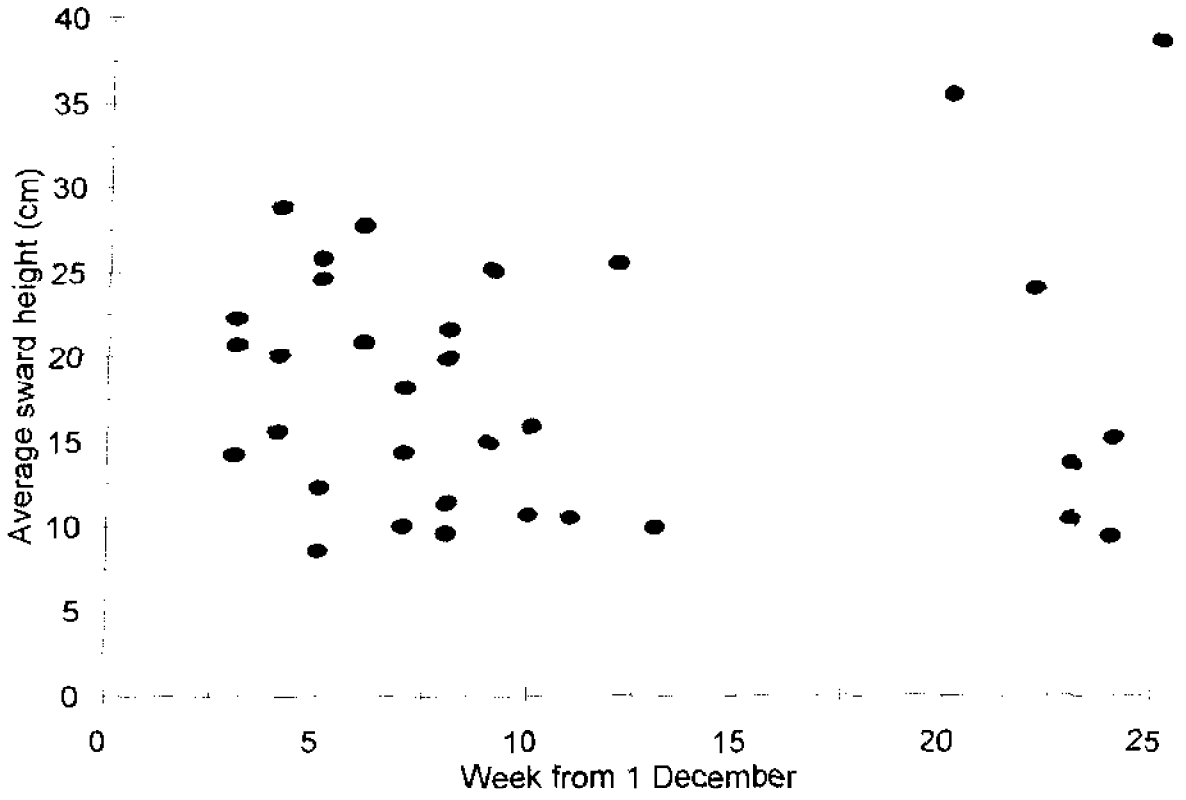

Figure 3.12: Average sward (mean maximum leaf) height in feeding sites of wildebeest. From the 15th to the 20th weeks, the wildebeest were in the southern extremes of Savuti and feeding sites were not assessed.

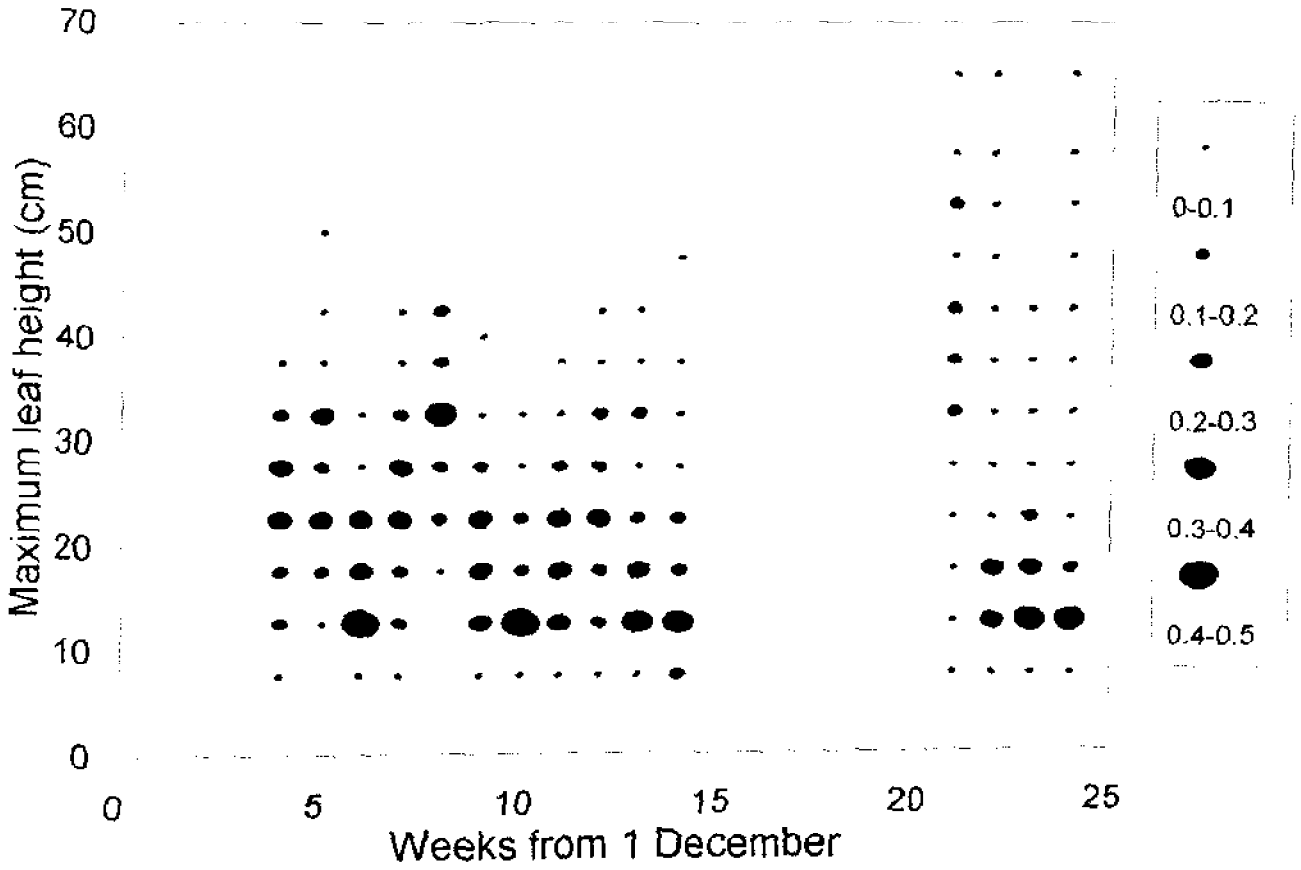

Figure 3.13: Change in the frequency distribution of the mean maximum leaf height of grass tufts in feeding sites of wildebeest. From the 15th to the 20th weeks, the wildebeest were in the southern extremes of Savuti and feeding sites were not assessed.

CHAPTER 4

Forage and faecal nitrogen and phosphorus concentrations and their relation to wet season movements of zebra

Introduction

Grass communities of varying species composition and nutrient contents offer large grazing herbivores a spectrum of different quality forage (White, 1978; Bell, 1982; Georgiadis & McNaughton, 1990; Ben-Shahar & Coe, 1992; Ben-Shahar; 1993). Despite an apparent abundance of vegetation biomass (Rutherford, 1978; McNaughton, 1985), it has been suggested by many ecologists that available nutrients to herbivores are low in African savannas at different times of the year, often below levels required to maintain body weight (Sinclair, 1974a & b; White 1978; Mattson, 1980; Demment & Van Soest, 1983; Dublin, Sinclair, Boutin, Anderson, Jago and Arcese, 1990; Ben-Shahar, 1993). As suggested by White (1978), carbohydrates do not appear to be in short supply and therefore, it is not the amount of energy flow through the ecosystem that limits the abundance of herbivores but rather differing amounts of spatially available nitrogen in the ecosystem. In a model, Owen-Smith & Novellie (1982) indicate that foraging performance by kudu, a browsing ungulate, was more sensitive to changes in food quality than changes in overall food abundance. Discrepancies between the model and observed foraging behaviour of kudu

suggested that energy rather than protein was the target nutrient. Mineral elements also vary in spatial and temporal availability and a variety of elements have been proposed to be important nutrients required by herbivores (Duncan, 1990; Georgiadis & McNaughton, 1990; McNaughton, 1990; Ben-Shahar, 1993; Grant, Meissner & Schultheiss, 1994).

Animal nutrition is complex and both nutrient requirement and availability varies broadly with animal and forage properties (McDowell, Conrad & Ellis, 1984; McNaughton & Georgiadis, 1986). Evidence for the complexity of the subject lies in the number of either conflicting or unsubstantiated ideas in the literature regarding nutrient availability and its influence on herbivore foraging behaviour, diet selection and animal distribution and movements. Nevertheless, ungulate requirements are broadly similar and it can be generally accepted that the quantity and nutrient quality of forage are important whether it be in relation to animal biomass (Phillipson, 1975; Coe, Cumming & Phillipson, 1976; Bell, 1984), population regulation (Sinclair, 1974b; Sinclair, Dublin & Borner, 1985; Dublin *et al.*, 1990), seasonal distribution (Ben-Shahar & Coe, 1992; Ben-Shahar & Skinner, 1988; McNaughton, 1990; Grant *et al.* 1994) or seasonal movement patterns (Novellie, Fourie, Kok & Van der Westhuizen, 1988; McNaughton, 1990).

Migratory zebra in northern Botswana range within a large area in the wet season but two areas of concentrated use were identified (Chapter 2). They grazed on the Savuti grassland for 4 to 5 weeks early in the wet season and

then moved to Mababe, some 70 km southward, into thorn savanna and stayed for a similar period. They returned to Savuti and spent between 5 to 6 weeks before moving to the dry season range. This wet season movement pattern of zebra was repeated in the two years studied and it was proposed in Chapter 3 that grass height (forage abundance) was the primary factor initiating these movements. There are, however, a number of factors relating to grass nutrient quality that may be influencing the wet season distribution pattern of the zebra.

No detailed information is available on soil characteristics for the Savuti / Mababe region. However, Shaw (1985) reviewed the origins of soils of the Mababe Depression in relation to past hydrological flow patterns and existing landforms. Historically the depression was a large lake and, although no time-frame is known, it dried up during successive phases. The present landform evidence indicates a central low lying 'sump' area within the depression and is clearly visible on aerial photographs where *Acacia* scrub vegetation is surrounded by *Colophospermum mopane* woodlands. The boundary between the two vegetation types is clear-cut and coincides with a 1 – 2 m ridge around the 'sump' (Shaw, 1985) which was more recently influenced by hydrological flow patterns than the outer edges of the depression. The soils of this basin are therefore of lacustrine origin (Shaw, 1985; Cooke, 1976) and are heavy montmorillonitic clays that characteristically have high ionic bonding properties (Millot, 1979). There is no evidence that the Mababe Depression ever had any outflows but that at least four river systems flowed into the lake. The lake dried

up because water flow in these river systems was either diverted into other rivers due to seismic activity or decreased due to long-term changes in rainfall patterns. At present no water flows into the Mababe and the most recent flow of water was via the Savuti Channel in the north (stopped flowing in the early 1980's) and the Mababe River in the south (stopped flowing in the 1950's). Both these rivers entered the basin and formed alluvial fans where they entered the dry central basin, each approximately 100 km^2. Water levels in these fans varied annually according to levels of the seasonal floods which also varied according to long-term weather patterns. Since the rivers have dried up, the flooded marshes have become open grasslands although the Mababe marsh, having dried approximately 30 years earlier than the Savuti marsh, has become encroached by *Acacia* scrub. Sediments of the Savuti grasslands would likely be nutrient rich due to the deposition of soluble nutrients by recent floodwaters. These soils may be expected to support grasslands of higher nutrient quality than the heavy clays of the basin (Bell, 1982, 1984). However, soil nutrient concentrations alone are not necessarily reflected in the nutrient and elemental concentrations found in grasses but might be attributed more to species attributes and their ability to accumulate nutrients (Downing, 1979; Chapin, 1980; McNaughton & Chapin, 1985; Ben-Shahar & Coe, 1992).

At the start of the wet season, zebra did not move directly to Mababe, possibly because they preferred to feed in the Savuti area. This may relate to the likelihood of more nutrient rich forage in Savuti compared to Mababe. Only once

their daily intake declined to a certain level did they move despite the higher quality of forage.

The peak foaling period for zebra in northern Botswana was February to March (Joos-Vandewalle, unpubl. data). The zebra may have moved to Mababe as a result of higher concentrations of phosphorus and calcium there as the timing of the movement was coincident with parturition (McNaughton, 1985; Duncan, 1992).

This study had three objectives. The first was to investigate the differences in concentrations of crude protein and some important minerals of grasses between Savuti and Mababe at the time of movement between the two areas. The second was to investigate the differences in nutrient content of grasses between the beginning and the end of the wet season. The third was to investigate the difference in estimated nutrient and mineral intakes of zebra between Savuti and Mababe by faecal analysis.

Methods

i. Available nutrients and mineral elements

In order to satisfy the first objective, grass leaf samples were collected in ten zebra feeding sites (Chapter 3) in Savuti and ten in Mababe in February 1993. Zebra ate a lot of immature seeds so inflorescence samples were collected from the same grass species as the leaf samples in the chosen feeding sites. To

assess changes in nutrient and mineral element availability over time, additional samples were collected in twenty feeding sites in Mababe (March) and fifteen in Savuti (May) when zebra were present in the area.

At least 10 tufts of the three most favoured species in each site were sampled within a radius of approximately 50 m from the identified central locus. To minimise sample variation due to differences in nutrient levels of different plant parts at different phenological stages (Duncan, 1992; Georgiadis & McNaughton, 1990), only the second terminal leaf blade on green tillers was collected. Samples were air dried in brown paper packets and stored for laboratory analysis.

The only grass species sampled that was common to Savuti and Mababe was the annual, *Urochloa trichopus* (Hochst.) Stapf. Species sampled in Savuti were the two perennials, *Brachiaria nigropedata* (Fical. & Hiern) Stapf and *Cynodon dactylon* (L.) Pers. Species sampled in Mababe were two annuals, *Chloris virgata* Swartz and *Dactyloctenium giganteum* Fisher & Schweick. and two perennials, *Digitaria eriantha* Steud. and *Echinochloa crus-galli* (L.) Beauv.

Estimates of dietary crude protein, CP_d, and dietary phosphorus, P_d were determined (modified from Duncan, 1992) in February in Savuti and Mababe, respectively. The proportion of grass tufts of a species grazed by zebra across all feeding sites (obtained from Chapter 3) was multiplied by the determined concentration of crude protein and phosphorus (see later) for that species.

These products were summed across all species sampled in Savuti and Mababe, respectively, to give an estimate of CP_d and P_d. Hence:

$$\% CP_d = \sum(S_{ij} \cdot CP_i) \text{ and}$$

$$\% P_d = \sum (S_{ij} \cdot P_i),$$

where S_{ij} = proportion of grazed tufts of all tufts of $Species_i$ ($i = 1, 2, 3, ..., n$) in $Area_j$. Area (j) included all zebra feeding sites on the Savuti grassland and in Mababe, respectively. CP_i & P_i = leaf crude protein and phosphorus concentrations (%) of the i^{th} species in the Savuti and Mababe areas, respectively.

Given that the youngest leaves contain the highest proportions of nutrient concentrations compared to older leaves and other plant parts, calculated nutrient intakes are likely to be overestimates.

ii. Faecal crude protein and phosphorus

In the same week of grass sampling, fresh faecal samples were collected from adult zebra mares in Savuti and Mababe. Herds were observed during feeding periods (as described in i. above) and when a zebra defecated a sample from the dung pile was immediately collected. Samples were collected from three zebra in the same herd (feeding site) and bulked for analysis. When collecting samples, it was ensured that the dung had not been contaminated with urine as this could influence the results of nutrient analysis. In February, ten bulked

samples from non-lactating mares were collected from Savuti and Mababe, respectively. As few mares had foaled at this time, faecal samples were not obtained from lactating mares. By March, many more foals were present and ten bulked samples from lactating mares and ten from non-lactating mares were collected in the Mababe feeding sites. The fresh samples were crushed by hand, placed in clean brown paper packets and placed in a warm (~40°C) oven until dry. The samples were then stored in a dry place at room temperature until laboratory analysis was carried out. Samples were checked regularly and any samples with signs of fungal growth were discarded.

iii. Laboratory and Statistical analysis

Laboratory analysis of the samples was conducted at the Department of Botany, University of the Witwatersrand by the plant physiology unit. Dried leaf and faecal samples were ground fine using an electric mill and divided into three replicates. The unsieved samples were analysed for nitrogen and phosphorus based on the standard Kjeldahl oxidation method according to the procedure outlined in Anderson & Ingram (1989). For analysis of other mineral elements, the detergent method was used (Anderson & Ingram, 1989). Total nitrogen (N), phosphorus (P), calcium (Ca), potassium (K), magnesium (Mg) and sodium (Na) concentrations (mg/g) were determined colorimetrically using an atomic absorbance spectrophotometer. Crude protein concentrations were calculated as the % CP of dry leaf and faecal mass.

No information could be found relating dietary to faecal crude protein and phosphorus levels in plains zebra but Duncan (1992) found a good correlation between these in domestic horses. Faecal nitrogen and phosphorus have also been shown to correlate with the levels of N and P in the fodder of cattle (Grant *et al.*, 1994). Hence, as indicators of dietary CP and P intake, concentrations of faecal CP and P were considered useful.

Results for leaf nutrient and mineral element property were analysed statistically using Kruskal-Wallace tests by site (Savuti / Mababe), longevity of plant (annual / perennial) and time of season (Sokal & Rohlf, 1972). Results of faecal nutrient and mineral element property were by site (Savuti / Mababe) and the presence or absence of foals.

Results

i. Available nutrients and mineral elements

Zebra moved from Savuti to Mababe in February. At this time, only CP and Mg concentrations in grasses did not differ but concentrations of all other measured mineral elements differed significantly between the two areas (Table 4.1). On the whole, grasses contained higher levels of these minerals in Savuti and only Ca occurred in higher concentrations in Mababe. *Urochloa trichopus* was the only species common to both areas and the distribution of nutrient and mineral element concentrations in this grass was similar to that measured across all the species sampled. The only difference was that Mg was significantly higher and

CP was notably lower in concentration in *U. trichopus* in Mababe. Annual grasses were richer in nutrients than perennials although there was no significant difference in Na and P levels, respectively. Only concentrations of Ca and Mg were higher in leaves compared to inflorescences.

Crude protein, P and K levels in leaves decreased significantly in samples collected at the end of the wet season compared to those collected at the start of the wet season in Savuti (Table 4.2). In Mababe, only CP decreased significantly from February to March while Na increased. The estimated dietary CP of zebra decreased when they moved from Savuti to Mababe in February while the dietary P increased (Table 4.3). As the season progressed, the estimated intake of both CP and P declined. Only late in the season did the estimated intake of CP decline below the recommended limited for domestic horses while P appeared to be limiting in the diet at all times, especially for lactating mares.

Table 4.1: Crude protein (%) and mineral element concentrations (mg/g) in the leaves of grasses and plant parts of grasses in sample sites in the wet season range of zebra.

	Site (February only)		Site (*U. trichopus*)		Longevity		Plant part		Kruskal-Wallace test			
Nutrient	Savuti	Mababe	Savuti	Mababe	Annuals	Perennials	Leaf	Seeds	Site (Feb)	Site (*U. trichopus*)	Longevity	Plant part
CP	23.0	20.9	22.6	12.6	18.4	10.5	14.8	13.9	N.S.	***	***	N.S.
Ca	3.0	7.2	3.0	7.5	6.6	3.9	5.4	2.4	**	***	***	***
K	30.7	15.1	30.7	16.3	18.8	12.9	16.2	-	***	**	**	-
Mg	2.5	3.8	2.5	6.3	4.1	2.5	3.4	1.3	N.S.	***	***	***
Na	5.8	2.6	5.8	4.5	4.2	4.2	4.2	3.4	**	N.S.	N.S.	N.S.
P	12.4	9.7	12.4	6.4	9	7.4	8.3	9.7	**	***	N.S.	N.S.
Ca/P	0.2	0.7	0.2	1.2	0.7	0.5	0.7	0.3	***	***	N.S.	*
Number of samples	6	10	6	9	26	21	47	24	–	–	–	–

*$P<0.01$, **$P<0.05$, ***$P<0.005$.
N.S., not significant.

Table 4.2: Available leaf CP (%) and mineral element concentrations (mg/g) in sample sites at different times of the wet season in the zebra range.

	Savuti		Mababe		Kruskal-Wallace test	
Nutrient	Feb	May	Feb	Mar	Savuti	Mababe
CP	23.0	8.1	20.9	12.9	***	**
Ca	3.0	3.1	7.2	6.7	N.S.	N.S.
K	30.7	6.3	15.1	18.8	***	N.S.
Mg	2.5	2.5	3.8	4.0	N.S.	N.S.
Na	5.8	3.8	2.6	5.0	N.S.	*
P	12.4	4.6	9.7	8.5	***	N.S.
Ca/P	0.2	0.7	0.7	0.8	**	N.S.
Number of samples	6	12	11	18	-	-

*P<0.01, **P<0.05, ***P<0.005.
N.S., not significant.

ii. Faecal nutrients and mineral elements

Concentrations of Ca and Na in zebra faecal samples were significantly higher in Savuti than in Mababe (Table 4.4). Faecal Mg on the other hand was significantly higher in concentration in Mababe while CP_f and P_f did not differ. Whether zebra mares had a newly born foal and were lactating or not, did not influence the levels of faecal mineral concentrations.

Table 4.3: Estimated dietary crude protein (CP_d %) and phosphorus (P_d %) in the Savuti and Mababe areas of the wet season range of zebra. Values below the recommended limit for domestic horses (Duncan, 1992) are bold and for lactating mares are italic.

	February		March	May
Nutrient	Savuti	Mababe	Mababe	Savuti
CP_d %	13.6	*10.7*	*12.1*	***9.4***
P_d %	***0.23***	*0.28*	***0.23***	***0.11***

Table 4.4: Faecal crude protein (CP_f %) and mineral element concentrations (mg/g) in sample sites and mares with and without foal in the wet season range of zebra.

	Site (February only)		*Presence of foal* (February & March)		Kruskal-Wallace test	
Nutrient	Savuti	Mababe	*Present*	*Absent*	Site	Presence of foal
CP	3.8	4.0	3.9	4.0	N.S.	N.S.
Ca	2.9	0.9	0.9	2.0	**	N.S.
K	-	-	-	-	-	N.S.
Mg	0.4	1.6	1.5	1.0	***	N.S.
Na	1.9	1.6	1.5	1.8	***	N.S.
P	4.5	4.7	4.5	4.7	N.S.	N.S.
Number of samples	12	9	12	21	-	-

*$P<0.01$, **$P<0.05$, ***$P<0.005$.
N.S., not significant.

Discussion

In February, when zebra moved from Savuti to Mababe, available nutrients and mineral elements, except Ca, across all grass species sampled were higher in Savuti than Mababe. The species composition of the zebras' diet (given the estimated CP concentrations in leaves of these species) reflected an apparent greater ingestion of CP in Savuti than Mababe. Despite a higher availability in Savuti, the estimated diet of zebra reflected an apparent greater intake of P in

Mababe although this difference was not very large. More importantly, however, it appears that P was below the required minimum for lactating mares at all times and, only in Mababe in February, was above the minimum for metabolic maintenance (Duncan, 1992). It should be noted that the intake of nutrient components measured was only estimated according to the species composition of grasses grazed by zebra and nutrient concentrations in the most commonly grazed species. Absolute differences could not be established because specific plant parts eaten and daily dry matter intakes were not measured. The concentrations of nutrient and mineral elements in the faeces were measured (Duncan, 1992; Grant *et al.* 1994) in order to try and overcome this limitation of the data. However, the faecal analysis showed no difference in either CP or P between the two areas, indicating a possible similar intake of both these elements by zebra.

Faecal CP is a good indicator of dietary CP as there is a direct relationship between the two so that $CP_{diet} \cong 0.85\ CP_{faeces}$ (for domestic horses; see Duncan, 1992). The ingestion of CP (as indicated by CP_f) was substantially lower than both the estimated availability and CP_d in Savuti and Mababe. The plant samples collected for analysis of nutrient property estimates were from the highest possible source of nutrients in the plant, namely the newly emerged green leaf. As mentioned earlier, zebra also grazed a variety of plant parts, especially high fibre parts (Chapter 3), resulting in a diluted intake of CP concentration compared to that found in the samples. So a discrepancy

between CP in the grasses in feeding sites and actual ingestion would be expected. Nonetheless, the CP levels in grasses sampled in this study were high (2 – 3 times higher) compared to studies of nutrient levels in grasses of zebra habitats elsewhere in southern Africa (*Novellie et al.*, 1988; Ben-Shahar & Coe, 1992). In Kenya, grasses sampled at increasing distances from water troughs were equal or higher in CP (up to 35 % of DM) compared to this study (Georgiadis & McNaughton, 1990). Grasses on nutrient rich volcanic soils of the Serengeti plains (McNaughton, 1990) were almost half as rich in CP compared to grasses on the Savuti grasslands. Concentrations of CP of green leaves in wild horse feeding areas in wetland grasses of the Camargue were similar to this study (Duncan, 1992). In all of these other studies, whole plants were sampled and would explain the higher levels of CP found in grasses during this study than in South Africa and Serengeti plains. The high concentrations recorded in the Kenya study would be expected because of the large amounts of dung found around the water troughs (Georgiadis & McNaughton, 1990). Wetland grasses are known to be high in nutrients which explains the high concentrations found in Camargue (Duncan, 1992). A high proportion of zebras' diet in northern Botswana comprised annual grasses that tend to be richer in nutrients than perennial grasses (Pratchett, 1976; Mattson, 1980). Most of the other studies reflected the nutrient levels in perennial grasses which further explains the high levels of CP found in the grasses of this study compared to the studies in southern Africa and on the Serengeti plains. Hence, because of the difference in plant parts of the grasses sampled in this study compared to

others, as well as the wide variation expected in CP levels with grass phenology, any absolute comparison in levels of CP with these other studies is limited.

Faecal CP concentrations were measured to try and overcome this limitation in the data. However, no studies could be found that investigated nutrient concentrations of zebra faeces. Most studies investigated ruminants and the only wild equid studies found were on wild horses in the Camargue (Duncan, 1992) and feral donkeys in Australia (Freeland & Choquenot, 1990). Ingestion of CP by zebra, as indicated by faecal concentrations, in Savuti and Mababe appeared to be less than half the CP intake of ruminants in the Kruger National Park (Grant *et al.*, 1994) and horses in the Camargue (Duncan, 1992) in similar seasons. Grasses grazed by feral donkeys in Australia during the early dry season were very low in CP (≈1.3 % of DM) and faecal CP concentrations were approximately a quarter of the zebra CP_f concentrations. The intake of CP by zebra in Savuti and Mababe, despite an apparent availability of protein rich forage, was low and below the minimum required level for maintenance of domestic horses.

Grasses in Savuti & Mababe in northern Botswana were particularly high in P concentration compared to other studies but, as stated above, sampling of the second terminal leaf makes comparison with other studies where the whole plant was sampled, difficult. Southern African grasses tended to have concentrations below 1.0 mg/g (Ben-Shahar & Coe, 1992) as did grasses in

Serengeti (McNaughton, 1990), Australia (Freeland & Choquenot, 1990) and the Camargue (Duncan, 1992). Grasses in areas of high use intensity by herbivores in Kenya were also high in P concentrations (Georgiadis & McNaughton, 1990) but still less than half the concentrations measured in Savuti. The concentration of zebra faecal P indicated that zebra were ingesting high quantities of this mineral and concentrations were similar only to faecal P in ruminants in the wet season in the Kruger National Park (Grant *et al.*, 1994). Although Ca was also higher in grasses in northern Botswana compared to other areas (as discussed above), the Ca / P ratio was low and less than the required minimum level for maintenance of body weight for domestic horses. Only in Mababe when zebra first arrived there was this ratio within the required limit but also only near the lower limit. Zebra faeces contained as much as three times the amount of Ca in Savuti than they did in Mababe, even though grass Ca levels in the latter area were twice as high. The reason for this is not clear. Possibly, because of the lower Ca / P ratio in Savuti the zebra were taking in more Ca in order to assimilate the P required and therefore were having to excrete greater quantities of Ca to maintain a mineral balance.

The concentrations of all the other minerals measured in the grass leaves in Savuti & Mababe were also higher than recorded values in studies elsewhere. Likewise, large amounts of these minerals were found in the faeces of zebra. Although animals have the ability of storing and releasing minerals through bones, and faecal analysis alone is not a good indication of dietary and

physiological functioning (Freeland & Choquenot, 1990), the general evidence from these nutrient analyses indicates that minerals might be playing an important role in the foraging behaviour of zebra. Exactly what this role is, is not clear but it appears as though many of the minerals assessed were not in short supply. However, CP levels were below required minimum levels for maintenance, let alone breeding, while the Ca / P ratio was also low and below minimum requirements. Possible limitations of protein and Ca/P ratio levels for breeding are further indicated in the lack of breeding success of the zebra population and may explain the observed trend of decreasing numbers since the drying of the channel and the marshes. Mineral deficiencies and imbalances can also have clinical symptoms affecting breeding.

Mineral imbalances in domestic horses, especially low Ca, high P and high or low Ca / P ratios can lead to clinical disorders such as nutritional secondary hyperparathyroidism which leads to weakened bone structure and lameness (Bertone, 1992). High dietary Ca can cause hyperparathyroidism while high dietary P can cause excessive Ca mobilisation from bones and excretion through the urine (Ott, 1992). The zebra did not show obvious clinical signs of bone deformity or lameness indicating such nutritional imbalances. However, the low fecundity of zebra, a high number of stillborn foals and low survival rate of foals (Joos-Vandewalle, unpubl. data) may well be indicators that nutritional deficits (or excesses) are an important consideration in northern Botswana (Ralston, 1992). Details of dietary nutrition and their effects on animal health

and breeding may well be an important aspect to investigate in northern Botswana given the present depressed numbers of zebra in the region.

The nutritional differences assessed between Savuti and Mababe do not explain the wet season movements of zebra. At present, the reduction in available biomass remains the more convincing argument for this movement (see Chapter 3). More detailed investigations of forage nutrient status in relation to dry matter intake, physiological levels in the animal and possible effects on the population structure are required. Predation is also a potential factor (Sinclair, 1985; Fryxell & Sinclair, 1988), on its own or as a compounding influence, which was not investigated in this study. Lions and hyenas preyed heavily on zebra whilst the migration was in Savuti, especially on the foals, and an estimated 7 foals a night can be killed (Cooper, 1990; Viljoen, pers. comm.). Although the densities and rates of predation between Mababe and Savuti are not known, more of these large predators appear to occur in the latter region (personal observation). Zebra may well be moving to Mababe to foal in order to avoid such high losses even if it means a payoff against nutrition. Wildebeest did not move far away from Savuti, even when foaling. While lions seldom killed wildebeest, hyena never did in three years (Cooper, 1990; Viljoen, pers. comm.). Predation would also be an important factor to investigate in the future to completely understand the movement patterns of zebra in their wet season range.

CHAPTER 5

Discussion

Zebra in the Linyanti – Savuti – Mababe region in northern Botswana undertook annual movements between spatially separate wet and dry season ranges that were up to 140 kilometres apart. Wildebeest in the same area moved between similar wet and dry season ranges as the zebra but only moved100 kilometres between the ranges. The pattern of movement can be categorised as a classic migration as the same distinct and non-overlapping seasonal ranges were used each year (Pennycuick, 1975; Baker, 1978; Sinclair, 1979; Fryxell & Sinclair, 1988). Permanent water in the region was limited to one source in the Linyanti River in the north. Zebra and wildebeest are water dependent (Skinner & Smithers, 1990) and their dry season distribution (range) was therefore restricted close to the river. Rainfall, and its influence on the seasonal availability of water, appeared to be the primary factor influencing the movement away from the dry season range, a common pattern elsewhere in African ecosystems (Smuts, 1972; Sinclair & Norton-Griffiths, 1979; Mills & Retief, 1984a & b; Western, 1985; Whyte, 1985; Williamson, Williamson & Ngwamotsoko, 1988; Kgathi & Kalikawe, 1993). However, an aspect not researched in migratory zebra and wildebeest elsewhere, the migratory herds in northern Botswana displayed a high fidelity in the annual use of seasonal ranges and all individuals in the populations moved seasonally.

In the wet season range, there were clear similarities and differences in the use of foraging patches between zebra and wildebeest. Both species preferred patches with

a high proportion of green grass and, within these patches, selected for higher proportions of green tufts, a pattern similar to wildebeest in eats Africa (Stewart & Stewart, 1970), zebra in South Africa (Smuts, 1972) and wild horses in France (Duncan, 1992). Although there was moderate selection of grass leaves by zebra and wildebeest, all above ground parts of the plant were eaten by both. Wildebeest appeared to be more selective for leaf than zebra and grazed in heavily utilised, short patches dominated by perennial grasses like zebra and wildebeest in Serengeti (Gwynne & Bell, 1968; McNaughton, 1976, 1979) and most studies in southern Africa (Skinner & Smithers, 1990). Zebra grazed in tall patches (Smuts, 1972; Jarman, 1974; Grobler, 1983; Novellie *et* al., 1988) with a high proportion of annuals, especially *Urochloa trichopus*. Zebra moved up to 50 kilometres between the Savuti and Mababe areas within the wet season range in response to decreased abundance of forage in each area. Wildebeest never ranged as far south as the zebra in the wet season and no clear relationship between the structure of the grasslands and movement was established.

Sampling of select grass leaves rather than the whole plant, as in studies elsewhere, for grass nutrient analysis precluded any comparison with grass nutrient levels in other ecosystems. Within the wet season range, however, at the time zebra moved to Mababe, grasses in Savuti were more nutrient rich and had higher levels of mineral element concentrations, except Ca, than grasses in Mababe. Despite these differences, the intake of CP and P, as indicated by faecal analysis, showed no significant difference between the two areas while Ca levels were much higher in Savuti. Although measured crude protein (CP) concentrations in forage were high throughout the wet season range, zebra faecal CP was below recommended levels

for maintenance of body weight (for domestic horses; Duncan, 1992). The relative differences in forage and faecal nutrient and mineral element concentrations between Savuti and Mababe showed no clear relationship with the use of, and movement between, these areas. Hence, the decrease in forage abundance (as measured by sward height) due to grazing was the more convincing evidence influencing movement between Savuti and Mababe. Predation might be a confounding influence by forcing zebra away from Savuti to avoid high losses of foals during the birthing period (Sinclair, 1985; Fryxell & Sinclair, 1988; Cooper, 1990).

Landscape ecology blended with hierarchical theory can be used as a means of enhancing the understanding of foraging theory (Senft, Coughenour, Bailey, Rittenhouse, Sala & Swift, 1987). The use of and movements between landscapes, plant communities and feeding patches by herbivores are described in this paper in relation to the decisions herbivores have to make at different temporal and spatial scales. Zebra and wildebeest in northern Botswana migrated annually through several landscapes within the region. In the late dry season, water availability rather than forage determined the dry season range. With the onset of the rains, the zebra and wildebeest migrated relatively quickly through woodlands with tall, coarse grass communities directly to Savuti. They returned through the same woodlands from the wet to the dry season range. The pattern, direction and rate of this migration was similar during the three study years implying that the animals knew where to find grasslands of relatively high nutrient quality in the region. The time scale at which this knowledge was acquired is not clear. Yet, evidence suggests that significant short-term ecological changes in the ecosystem must have influenced the migration. Less than two decades ago in the late 1970's and early 1980"s, the Savuti channel flowed

and the Savuti plains were seasonally flooded with high flood levels occurring in the dry season. Hence, the dry season distribution of water was quite different to that at the time of this study. Researchers believed that the annual pattern of movement by zebra and wildebeest at the time the channel flowed was the inverse of present movements and comprised a dry season concentration in, and a wet season dispersal away from, the Savuti region (indicated by periodic aerial surveys; Viljoen, pers. comm.). There were also resident zebra and wildebeest that remained year round in Savuti. Zebra and wildebeest numbers were also estimated to be three to four times higher than during this study. The drying up of the Savuti channel resulted in a significant reduction in dry season water availability in the region. Those zebra and wildebeest that used Savuti in the dry season would therefore have had to perceivably extend their annual range by moving to the Linyanti River in the north-west in the dry season. The channel flowed for more than thirty years prior to its drying in the early 1980's. It had been dry for more than a century before it flowed in the 1950's. If zebra and wildebeest previously migrated when the channel was dry, as they do today, it is inconceivable that this behaviour might have been carried over through more than two generations during the 30 years when the channel flowed. Hence, when the channel dried in 1983, it can only be presumed that the present day migration was established after this date. Unfortunately knowledge of the seasonal movement patterns and how these changed at the time the channel dried up is mostly circumstantial and hearsay but raises the question whether migrations are established at an evolutionary time scale. The drying of the Savuti channel was a major ecological perturbation that may have resulted in the establishment of the zebra and wildebeest migration at an ecological time scale.

The fidelity of the zebra and wildebeest seasonal ranges was largely due to the distinct boundaries between open and sparsely wooded grasslands, which they preferred, and the surrounding *Colophospermum mopane* woodlands. Landscapes with distinct boundary-contrast often also form distinct animal range boundaries because animals seldom cross these (Senft, 1981 in Senft *et al.*, 1987). Forage distribution within the open grassland and sparsely wooded grassland communities in Savuti / Mababe was such that the goals of diet selection by zebra and wildebeest were most likely synonymous with goals of landscape use. Hence, when zebra and wildebeest crossed landscape boundaries, they were simultaneously crossing community boundaries. Zebra and wildebeest grazed exclusively on open and sparsely wooded grasslands in the wet season range, and only moved into the neighbouring *Colophospermum mopane* woodlands to drink. In foraging, zebra movement between the two areas of concentrated use in Savuti and Mababe, respectively, in the wet season range (and coincident landscapes) involved long-distances between different grass communities in response to decreased forage abundance. At the end of the wet season, zebra reversed movement across landscape boundaries in response to intermittent rainfall events, something that seldom happens according to Senft (1981; in Senft *et al.*, 1987). Wildebeest did not respond to rainfall at this time of the year like zebra did. Hence non-forage factors appeared to occasionally have an important influence on zebra movements and decision-making in the wet season while wildebeest seemed to respond more exclusively to forage related factors. At the end of the wet season, wildebeest were more sensitive to water availability than to forage factors. The reverse was true for zebra.

Senft *et al.* (1987) concluded that large herbivore foraging theory must be based on decision-making mechanisms. They elaborate and state that i) learning or natural selection must act on these mechanisms when considering foraging optimality, ii) how foraging behaviour varies with ecological scale needs to be explained, iii) realistic goals must be applied to various ecological scales to explain objectives of foraging behaviour, iv) a mechanism for goal evolution must be provided and v) the theory needs to be put into an ecosystem context particularly with regard to plant responses. Aspects of this study were consistent with the recommendations of Senft *et al.* (1987). The study was conducted at different ecological scales once these had been identified. Plant response in previously grazed areas was inferentially investigated by monitoring grass abundance changes within the wet season range. Foraging goals at the ecological scale were investigated at the plant and faecal nutrient level to assess movement between Savuti and Mababe although inconclusive results indicated that the foraging goal for zebra was grass abundance rather than nutrient quality. Foraging behaviour at the evolutionary scale was not investigated.

I propose that the zebra and wildebeest populations in northern Botswana are an ideal test case for foraging and spatial models. Ecological noise is reduced because of the discrete spatial units and seasons, despite the unpredictable nature of the rains. Co-existing populations of a ruminant and a hindgut fermenter that principally use the same annual and seasonal ranges are ideal for comparative studies. In particular, zebra occur in greater numbers than wildebeest unlike most African ecosystems where medium body-sized ruminants are more successful than non-ruminants of similar body size and further study of these populations would therefore

enhance understanding through inter-regional comparison. Finally, the Savuti region experienced a major ecological disturbance two decades ago with the drying of the Savuti channel. Historically this has occurred at varying intervals. The chance that it will happen again is good and such an opportunity would provide an important opportunity to expand ecological understanding of migratory ungulates through 'experimental' research.

APPENDIX I

Tables of a) the number of zebra and wildebeest bearing active radio transmitters and b) the number of individual collar locations made each month during the study.

a)

	Year					
	1991		1992		1993	
Month	Zebra	W'beest	Zebra	W'beest	Zebra	W'beest
Jan			6	7	15	4
Feb			6	5	15	4
Mar			11	5	15	4
Apr	9	5	11	5	15	4
May	9	5	11	5	15	4
Jun	8	4	11	5	15	4
Jul	8	4	11	5	15	4
Aug	8	7	11	5		
Sep	8	7	11	5		
Oct	8	7	11	5		
Nov	7	7	9	4		
Dec	6	7	15	4		

b)

	Year					
	1991		1992		1993	
Month	Zebra	W'beest	Zebra	W'beest	Zebra	W'beest
Jan			0	0	30	8
Feb			24	11	29	0
Mar			27	10	30	10
Apr	10	10	40	22	32	10
May	33	19	10	20	59	16
Jun	0	0	0	0	14	4
Jul	0	0	0	0	15	4
Aug	0	3	0	0		
Sep	0	0	0	0		
Oct	32	13	11	5		
Nov	25	34	48	20		
Dec	22	28	53	16		
Total	122	107	213	104	209	52

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