CHAPTER 1

INTRODUCTION

In community ecology, food was initially thought to be an insignificant driving force after predation and parasitism, as herbivores in general appear to consume little of the plant primary production (Hairston, Smith & Slobokin 1960). However, it soon became apparent that food could potentially be limiting, as not all food was edible owing to structural and chemical differences that varied in time and space, and thus food became considered as one of the most important environmental factors in animal ecology (Sinclair 1975, White 1978). Food availability (Klein 1968, Coe, Cumming & Phillipson 1976, Sinclair 1977, Sinclair, Dublin & Borner 1985, Fryxell 1987a), in addition to predation, intraspecific competition and disease (Smuts 1978, Sinclair 1985, Berry 1982) have been suggested to limit many populations of ungulates, through changes in recruitment or survival rates as a function of population size (McCullough 1979, Fryxell 1987a). Furthermore, in shaping the structure of African ungulate communities, interspecific competition for the periodically limited food resources was thought to play the dominant evolutionary role (Sinclair 1979) but more recently, predation has also been suggested to be of importance in the process (Sinclair 1985, Fryxell, Greever & Sinclair 1988).

Interspecific competition and predation have caused the differential use of resources and the consequent morphological and behavioural differences between species, well illustrated in the wide assortment of African ungulates of varying body sizes that seem especially associated with the extensive African savanna vegetation, has characterised the continent since the Miocene (Cooke 1972, Owen-Smith 1982). The characteristics of the food have also been important in the above process, as plants are far from a homogenous food supply. Nutritional quality is dependant upon many plant factors such as: the ratio between the soluble cell contents and relatively indigestible cell wall constituents, secondary compounds, silica, physical structures like thorns, growth stage, season, distribution and soil nutrients (Owen-Smith 1982, Van Soest 1982, Demment & Van Soest 1985).

The well known relationship between mass specific metabolism and body mass (Kleiber 1961) compounds the above problems associated with the heterogeneous food supply, as small herbivores with their higher mass specific metabolic costs are forced to select for rarer high quality food items (Demment & Van Soest 1985). By contrast, larger herbivores are constrained more by the need to satisfy absolute energy costs and they too should select rapidly digesting high quality diets but because high quality items are often too rare to satisfy energy demands they are forced to utilize poorer quality, more abundant plant material. And as they have longer retention times they can afford to eat poorer quality diets. Consequently this has resulted in a wide range of ungulates of different body masses, particularly amongst the ruminants, with differing morphological (mouth sizes, salivary glands) and digestive (gut capacity, rumen subdivision) forms that can be broadly divided into concentrate, intermediate, and grass and roughage selectors depending on the extent of selection and efficient digestion of high quality food items (Hofmann & Stewart 1972, Hofmann 1989). Resource partitioning by ungulates occurs at the habitat, plant species and plant part levels and between herbivore sexes (Lamprey 1963, Gwynne & Bell 1968, Ferrar & Walker 1974, Field 1975, Clutton-Brock, Guinness & Albon 1982) and it appears that this separation, particularly amongst the grazers, is facilitated by the width of the mouth relative to body mass (Owen-Smith 1985, Illius & Gordon 1987), while for the browsers the separation is maintained by feeding at different heights (Du Toit 1990). Thus for example amongst the grazers, species of similar body and mouth sizes do not generally coexist in the same habitats in most African ungulate communities.

Cumming (1982) noted that grass and roughage feeders dominate most savanna ecosystems as a whole. However, this tendency in semi-arid and arid systems is sustained only with the availability of drinking water, as Western (1975) noted that non water-bound species tended to be intermediate and concentrate feeders, with one exception the oryx Oryx gazella callotis. In this regard the gemsbok O. gazella gazella of southern Africa is also the only ruminant grass and roughage feeder penetrating on a permanent basis into the waterless arid stretches of the Kalahari and Namib. Thus spheres of occupation of non water-bound species surrounding those of the water-bound species are characteristic of many ecosystems in the dry seasons, such as the Serengeti plains in the dry season (Pennycuick 1979). Failing to view the system without reference to seasons obscures the lines of division separating the preferred realms occupied by species and different feeding types.

The gemsbok's ability to survive in harsh waterless conditions of the southern Kalahari stems from a combination of morphological, physiological and behavioural adaptations (Taylor 1968, 1970a, 1970b, Root 1972, Lewis 1977, Hofmann 1989). Decreased water losses arising from a reduced metabolism, low evaporation rates, a flexible body temperature and the use of water rich underground tubers allows the gemsbok to survive independently of drinking water. While the lack of these characteristics in the blue wildebeest Connochaetes taurinus taurinus, makes them more dependant on drinking water and/or access to better quality food supplies. Hence, wildebeest are only able to penetrate more arid regions during the wet seasons through migratory behaviour. Does this inability to remain permanently in semi-arid areas result from physiological inadequacies to conserve water and energy or the incapacity to maintain a sufficient intake of water and protein through fine plant selection?

Water is accepted as the most important limiting factor for plants and animals alike in arid and semi-arid ecosystems, considered to receive less than 500 mm of rainfall per annum (Louw & Seely 1982, Noy-Meir 1973). This was revealed in the relationship between rainfall, primary productivity (i.e. the food supply) and large herbivore biomasses in Africa (Coe et al. 1976). The provision of water in semi-arid and arid systems has the effect of increasing the biomasses of herbivores dependant on drinking-water and these herbivores ultimately become limited by either the quality or quantity of the food supply (McNaughton & Georgiadis 1986). The drilling of boreholes to provide permanent waterholes in the Kalahari Gemsbok National Park (KGNP) in the southern Kalahari from the 1930's, a region naturally free of surface drinking-water for most of the year, has encouraged the establishment of a resident population of wildebeest from the once much larger migratory herds (Eloff 1966). This brought the gemsbok and wildebeest, both grass and roughage feeders of similar body masses (200 and 230 kg, respectively (Skinner & Smithers 1990) into permanent contact in this region. The provision of water, the most limited resource, makes the selection for the other important variables such as food quality, more accessible for study. Further, this allows one to test the degree of resource partitioning by similar sized ruminants and the extent to which such features like mouth-part size facilitates this separation. Most studies on ungulate resource partitioning have emphasised the influence of body size by comparing a range of different sized species (Jarman & Sinclair 1979, Belovsky 1986, Owen-Smith 1985). Few have compared similar sized ruminants, such as the gemsbok and wildebeest, resident in the same area.

The best evidence of resource partitioning emanates from experimental manipulations (Schoener 1986). Given the limitations of such methods with regard to manipulating ungulate populations, a more convenient approach is to compare niche overlap in periods of high and low resource availability (Gordon & Illius 1989). During lean periods (such as the annual dry season or periodic droughts), selection resulting from interspecific competition is likely to result in adaptations most suited for exclusive use of resources but in periods of abundance it may be more profitable to use food types other than the ones for which the phenotype has specifically been selected. Such adaptability is not only reflected in habitat and food selection but also at the population level. Long term studies of ungulate populations may reveal important insights about the relationships between precipitation, the food supply and ungulate population dynamics (Novellie 1983). Understanding the adaptability of two species at the food, habitat and population levels requires a multifaceted approach as attempted in the present study. Specific questions asked were:

1. To what extent did the two species differ in their seasonal food and habitat requirements and how did they differ in their abilities to select for plant quality?

2. Was this selection a result of morphological features, such as mouth parts and/or physiological differences?

3. To what extent did the population dynamics reflect the different adaptabilities of the two species to the harsh semi-arid conditions given the provision of drinking water, a major limiting factor in the system?

The results are presented in five chapters:

Chapter 3 describes the food supply and the differences between the gemsbok and wildebeests' ability to select plant species and quality, compared between seasons, and drought and post-drought years.

Chapter 4 describes the movement patterns, home range sizes and habitat use of the two species compared between seasons and drought and post-drought periods.

Chapter 5 describes the differences between seasonal activity patterns of the two species.

Chapter 6 describes the differential attractions of the two species to the waterholes of varying water quality in relation to their habitat and feeding habit differences.

Chapter 7 describes the population dynamics of the two species in relation to rainfall.