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Berry, Mark Philip Seager

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RAINFALL ORIENTATED MANAGEMENT FOR A MULTIHERBIVORE GRAZING SYSTEM

Mark Philip Seager Berry

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ABSTRACT

RAINFALL ORIENTATED MANAGEMENT FOR A MULTIHERBIVORE GRAZING SYSTEM

This dissertation investigated vegetation-herbivore interactions and formulated a strategy for managing multiherbivore systems under varying rainfall regimes. Specifically, the aim was to maximise springbok *Antidorcas marsupialis* when competing with blesbok *Damaliscus dorcas phillipsi* and black wildebeest *Connochaetes gnu*.

In the face of the complexity of multiplant-multiherbivore interactions, a discrete difference model was constituted to express interseasonal changes in an episodic arid system, where vegetation and herbivores varied in response to rainfall.

The model was used to identify important parameters in the plant-herbivore system and its sensitivity analysed and its output corroborated. Rainfall was spatially and temporally variable and unpredictable. Vegetation growth was the single most sensitive variable within the system and vegetation biomass changed rapidly in response to climatic factors.

The concept of herbivore functional response was a useful means for expressing interspecific differences between herbivores and was practically applied. The model performed plausibly with data from the field where vegetation biomass and herbivore populations

were seasonally determined. The model output was used to discern population trends under different rainfall regimes.

Under conditions of low rainfall herbivores were limited by low vegetation biomass. Under medium conditions of rainfall interspecific competition was evident whereas under high rainfall facilitation occurred.

The model was used to formulate a management strategy that maximised springbok under different rainfall regimes and provided a useful technique for improving management of multiherbivore systems.

DECLARATION

I declare that this dissertation is my own, unaided work, except where otherwise stated. It is being submitted for the degree of Doctor of Philosophy in the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other University.



12 day of March, 1991.

PREFACE

This thesis aimed to improve knowledge and understanding of vegetation-herbivore systems. This was attempted by seeking to find a solution to a real management problem through a process of ecological modeling.

The process was one of developing the philosophy; evolving a model; searching for data with which to explore the model; using the model to investigate vegetation-herbivore interactions; and finally formulating a strategy.

Developing a modeling philosophy and evolving the model demanded a sequential and logical approach. To facilitate this it was considered prudent to use the subject literature to support the argument. The literature therefore was incorporated into the relevant chapters and not treated separately in a specific review.

In order to retain parsimony and aid continuity, appendices were used to separate data complementary to the argument.

ACKNOWLEDGEMENTS

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I am indebted to Professor Michael Mentis, Director of the Resource Ecology Group of the University of the Witwatersrand, for his continual guidance and support throughout the study. I have relied heavily on his independent thinking and intellectual experience. These he has given with patience and understanding.

I thank Prof B. H. Walker for his help in the early stages. Prof A. M. Starfield and Dr N. Owen-Smith helped to formulate the concept and direct the study at the outset and their assistance is gratefully acknowledged.

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I also wish to thank Mr John Moleko and Mr Hans Bitterbos who helped with the watering and harvesting of irrigation plots in the study area.

I have been enthusiastically supported by my family throughout the study both in the field and in the office. The encouragement from Lesley and assistance from Matthew and Simon has provided the necessary incentive to persist and I thank them sincerely.

During the study I have been fortunate to be part of the Resource Ecology Group of the Department of Botany. I thank the many friends and colleagues with whom I have interacted and who have provided for a stimulating and rewarding experience.

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CHAPTER 1 : INTRODUCTION

1.1 Objective of the study

The broad objective of this study was to obtain the information and understanding to determine a management strategy that would maximise the number of springbok, *Antidorcas marsupialis*, on a given vegetation type known as The Pan on a game reserve, Rooipoort.

An important consideration of the study was that it should be directed at a real management problem and that it should seek to find a solution that had practical application.

The occurrence of panveld is limited and, in addition to being prime springbok habitat, is also the preferred habitat for two other herbivore species namely black wildebeest *Connochaetes gnu*, and blesbok *Damaliscus dorcas phillipsi*.

Prior to the introduction of black wildebeest and blesbok, springbok were, according to historic records, numerous and dominated the area. The establishment of the other two species was accompanied by a decline in the number of springbok.

The hypothesis is that black wildebeest and blesbok are more successful than springbok in competing for the herbage resources of The Pan and as a result their introduction has led to the decline of springbok. However, the springbok is an important component of the utilisation spectrum and the objective of

management is to manipulate the herbivore populations in such a way so as to maximise the number of springbok.

1.2 Specific objectives

The overall objective of the study was broken down into a number of specific objectives that identified the major components of the study. These were to

(i) study the interseasonal biomass changes in response to varying rainfall and temperature

(ii) study the herbage biomass changes as a result of herbivore utilisation

(iii) model the vegetation and herbivore responses to varying rainfall, and

(iv) develop a strategy that would best meet the overall objective of maximising springbok numbers.

The specific objectives were achieved through a number of sequential steps, namely

(i) evolving a modeling approach

(ii) identifying important parameters of the model

(iii) gaining understanding of the plant-herbivore system

(iv) seeking real data in the field

(v) refining the model in terms of structure and input

(vi) corroborating the data, and

(vii) using the model to determine a management strategy.

1.3 The modeling approach

A model is an intellectual tool used to define problems, organise thoughts, understand data and to communicate and test this understanding (Starfield & Bleloch 1986). Ecological models are either theoretical or predictive and are designed to compare ideas with reality (Caswell 1976).

Theoretical models are aimed at improving understanding and gaining insight into how ecological processes function and, as such, are analytical. Predictive models are designed to project behaviour and outcome and are used to simulate ecological processes. In predictive models, it is the performance and not the reality of the model itself that is of consequence. Inevitably both types of models include predictive and theoretical components. However, whereas predictive models may be validated and verified, theoretical models are primarily heuristic (aimed at discovery) and are not easily validated.

In this study a theoretical model was employed to analyse the important components of a plant-herbivore system. Once an understanding had been gained, the model was used to predict the outcome of various scenarios.

The approach adopted follows that of Starfield & Bleloch (1986) where the first step was to build a tentative model; the properties of the model were then investigated; the performance of the model was explored using hypothetical data; cautious conclusions were drawn and supportive evidence was sought.

Ecological models seldom, if ever, provide definitive outcomes because they lack both data and understanding. However, management decisions still have to be made despite these shortcomings. The procedure advances understanding and identifies important parameters which in turn refine the model. This process of adaptive modeling ultimately improves the management decisions.

The modeling of a single prey-single predator relationship is at best complex (May-Meir 1981). The task of either detailed analysis or accurate simulation of multiplant-multiherbivore ecosystems is unattainable. In any event the usefulness of such complex models is often questionable due to their numerous assumptions and lack of reliable data. The researcher is therefore obliged to simplify the system to manageable components and to a single objective, in this study, maximising springbok. Thus the focus is on a part of the system, not the ecosystem as a whole and the level of resolution is appropriate to the management objective. This is a compromise between total systems modeling on the one hand and the need to solve management problems on the other.

The approach was therefore one of successive iterations from little data and lack of understanding of the plant-herbivore system to some supportive data and improved understanding.

Inevitably the outcome was a simplification of a multi-optimisational problem. However, this approximation would at least provide a workable strategy from which to manage where, at present, no such strategy existed.

1.4 Important parameters

The purpose of this section was to identify those parameters that were likely to be relevant to the understanding and development of the model and thus avoid the risk of collecting the wrong data. The exercise was also intended to highlight the shortcomings and inadequacies in the existing data and therefore help to determine the appropriate resolution necessary.

In arid and semi-arid climates herbage production is primarily a function of moisture (rainfall) and season (temperature and daylength) (Noy-Meir 1973) of which rainfall is the dominant controlling factor (Barnes & McNeil 1978; Boutton et al. 1988; Sneeva 1982).

Another characteristic of arid and semi-arid climates is that precipitation is highly variable both spatially and temporally (Noy-Meir 1973; Seely 1978; Zuschini & Adamson 1984) and the variability increases with increasing aridity (Le Houerou 1984). Different grass species exploit different rainfall events (Dye 1983; Westoby 1979) and as a result arid communities exhibit episodic growth behaviour in response to rainfall (Milner & Hughes 1968).

A number of authors have noted that productivity is highly correlated with rainfall (Deshmukh 1986; Dye 1983; Emslie 1987; Le Houerou et al. 1988; Noy-Meir 1973; Owen-Smith 1982; Phillipson 1978; Rosenzweig 1968; Rutherford 1980; van den Berg 1983).

In the Serengeti, where the temperature was relatively constant throughout the year, grass production on alkaline soils of varying depth depended on rainfall alone (Hilborn & Sinclair 1979). McNaughton (1983) found that below 700mm of annual rainfall, grassland communities were distributed parallel to rainfall isohyets i.e. short grasslands occurred below 700mm of rainfall and tall grasslands above 700mm of annual rainfall.

Rosenzweig (1968) found that photosynthesis was a function of water availability and solar radiation and this bore a strong relationship to the evapotranspiration rate. Coe *et al.* (1976) noted that in arid and semi-arid environments the potential evapotranspiration exceeded actual precipitation and therefore the system was water limited. In these environments growth only took place when there was sufficient moisture for plants to evapotranspire. Thus primary production depended on evapotranspiration which in turn depended on precipitation. Hence precipitation showed a significant relationship to primary production and was a useful index as such. In a reverse process Seely (1978b) used production to calculate precipitation in very arid areas.

Where large temperature fluctuations occur plant growth is inhibited at extremes of both high and low temperatures (Noy-Meir 1973; Smeova 1982) and production is both water and temperature limited.

There is considerable confusion in the literature with respect to the use of the term 'production' and as Grossman (1982) has

pointed out productivity is equated with both peak biomass and peak standing crop when, in reality, they are decidedly different. For example he found that net aerial annual production (NAAP) was 2.57 times greater than peak biomass.

The confusion in the terminology is compounded by the unreliability of production measurements. Singh *et al.* (1975) found that, depending on the method used, both peak standing crop and net aerial annual production varied by as much as 90 per cent when applied to the same data set. Furthermore, productivity varied with plant species, plant diversity, frequency of sampling (Singh *et al.* 1975) and time of year (Morris & Muller 1970).

Given comparative estimates of production, the assumption that growth of intermittently cut swards is related to that in grazed swards is inappropriate and inaccurate (Crawley 1983; Johnson & Parsons 1985; McNaughton 1985).

A number of authors have noted that primary production cannot be estimated from harvest data alone and this gives rise to an underestimate (Deshmukh 1984; Deshmukh & Baig 1983; Grunow *et al.* 1980; Rutherford 1980; Williamson 1976).

Wiegert & Evans *in* Singh *et al.* (1975) found estimates of NAAP increased by as much as 4.9 times when mortality was included. Elsewhere, the inclusion of mortality increased NAAP estimates by ninety to 120 per cent (Deshmukh 1986; Donaldson 1967; Scholes 1984). Mortality was found to vary with soil type, climate and grazing intensity (Johnson & Parsons 1985; Scholes 1984).

The quality of the grass sward also varies with rainfall and there is a close correlation between monthly rainfall and protein content (Afolayan *et al.* 1978; Strugnell & Pigott 1978). This is attributed to a decrease in the protein content with age (Braun 1973). Rainfall stimulates growth which results in young shoots with a high protein content which declines as the plant matures (Owen-Smith 1982). Similarly protein content is maintained by frequent cutting (Braun 1973) and grazing (McNaughton 1985) as these actions stimulate the production of young shoots high in protein and low in fibre.

In summary, the most important parameter in determining herbaceous production is rainfall, the effect of which is tempered by extremes of temperature. In spite of the significant relationship between precipitation and growth, production is highly variable and its measurement both difficult and unreliable.

In terms of the modeling approach, therefore, the focus was on seasonal production. However, the degree of resolution required was one where detailed and accurate data were not justified due to the unreliability and variability of this measurement.

1.5 Improving understanding of plant-herbivore relationships

It has already been noted even single plant-herbivore systems are intricate and their description in the form of a mathematical model complex. In this study the purpose of modeling was not to "mimic nature" but rather to explore the mechanisms and improve understanding of plant-herbivore relationships which, in turn,

would aid the decision process.

The amount of vegetation removed by grazing varies considerably (Boutton et al 1988; Deshmukh 1986; Owen-Smith 1982; Owaga 1975; Strugnell & Pigott 1978). Deshmukh & Baig (1983) found the offtake was negligible and McNaughton (1985) noted that terrestrial herbivores typically consumed less than ten per cent of primary production. In the Serengeti consumption varied from fifteen per cent (Braun 1973) to ninety four per cent (McNaughton 1985).

Most herbivores are limited by food supply (Crawley 1983; Sinclair 1979) and the interaction between plants and herbivores is a complex one (Noy-Meir 1981).

Intake was found to be related to plant height and not herbage yield (Allden & Whittaker 1970). Herbivores generally have a preference for plant species with a high feeding value (Mentis 1980) which results in a diet overlap (Grunow 1980; Page & Walker 1978; Sinclair 1985; van Zyl 1965). Hansen *et al.* (1985) found that there was a 71 per cent overlap in the botanical composition in the diet of the 10 major herbivores in the Serengeti and most ungulates preferred a single species, *Themeda triandra*.

The question arises that if there is such a high overlap in herbivore diets and a preference for the same herbaceous species how might interspecific competition be reduced or overcome? In a similar way to which different plant species are able to exploit

different rainfall events (Westoby 1980) so herbivores exploit spatial and temporal variances in herbaceous growth which result in different grazing strategies.

Stelfox *et al.* (1986) found that grazing patterns depended on rainfall. Gwynne & Bell (1968) and Maddock (1979) described a grazing succession (facilitation) whereby different herbivore species used different levels in the herb layer and different proportions of the plant parts. These strategies led to a temporal resource partitioning and niche separation (Jarman & Sinclair 1979) because larger species were able to utilise lower quality swards (Bell 1971; Jarman 1974). Contrary to the above, de Boer & Prins (1990) could find no evidence of facilitation between buffalo *Synercus cafer*, zebra *Equus burchelli* and blue wildebeest *Connochaetes taurinus*. Overlap in zebra and blue wildebeest diets was concluded to be an anti-predator symbiotic relationship (de Boer & Prins 1990; Sinclair 1985).

Where herbivores co-existed within a more or less uniform habitat, it was common to find that they differed in body size or in timing of feeding, thereby reducing competition (Crawley 1983). Dublin *et al.* (1990) found no competition between blue wildebeest and Thomson's gazelle *Gazella thomsoni*. This was attributed by McNaughton (1985) to the fact that gazelles concentrated on short vegetation with low standing crop, whereas blue wildebeest selected for areas of high biomass concentration. Grazing reduced canopy height to produce a grazing lawn with increased food quality through preventing senescence and stimulating growth which gazelles were able to utilise and hence, gazelles concentrated on areas previously grazed by wildebeest

(McNaughton 1976; Maddock 1979). In spite of these strategies Borner et al. (1987) found that the decline of Thomson's gazelle in the Serengeti was, in part, due to interspecific competition.

Although temporal resource partitioning is apparent the mechanisms involved are unclear.

Illius & Gordon (1987) contended that energy intake and body weight were a function of bite dimension and biomass density of food source. Therefore, larger animals were obliged to seek taller, low quality swards which led to niche separation. Their model also accounted for the grazing succession first described by Gwynne and Bell (1968). Grazing exposed smaller food items and stimulated dense short regrowth that small animals were adapted to utilise and that could not support the large species. This was confirmed by Mills and Retief (1984a; 1984b) who found that springbok exhibited the most rapid response to rain as their small mouths enabled them to crop sprouting vegetation at ground level.

Thus there was a strong interaction between grazing animals, growth and utilisation of the grazed sward (Johnson & Parsons 1985; McNaughton 1976). Animal concentrations created grazing lawns which benefited individuals through greater food yield (McNaughton 1984). Schijf (1978) found that gregariousness was the most important factor influencing springbok dispersion and, although he realised cooperative foraging was beneficial, he did not attribute this to the benefit of grazing lawns which had higher productivities and were of a higher quality (McNaughton

1984). Biomass concentration also benefited the grass through increased canopy refuge (McNaughton 1984).

Springbok preferred young grass high in protein and low in fibre (Liversidge 1972) and therefore had a high grass component in their diet in spring and summer; in the absence of rainfall browse was more important and constituted the major part of their diet in autumn and winter (Bigalke 1972; Schijf 1978). Jarman & Sinclair (1979) similarly found that in impala, *Aepyceros melampus*, there was an inverse relationship between browse utilisation and rainfall.

The diet of black wildebeest was of predominantly short grass but included karoid shrubs (von Richter 1971b). Guthrie (1987) in an analysis of diet components found that blesbok and black wildebeest had very similar diets in winter when the diet of springbok was similar to that of other browsers namely kudu *Tragelaphus strepsiceros* and eland *Taurotragus oryx*. Blue wildebeest were found (Owaga 1975) to be highly selective for grass leaves .

The effect of nutrition on productivity is well established (Moen 1973) and both development rate and fecundity are affected by food availability (Crawley 1983).

Under poor climatic conditions (low food availability) the onset of sexual maturity was delayed (Crawley 1983). Clutton-Brock *et al.* (1982) found that in red deer *Cervus elaphus*, fecundity, calf survival and conception were negatively correlated with population size (food availability). Similarly conception rates

in buffalo were determined by the plane of nutrition (Sinclair 1977).

In summary, it is apparent that grazing herbivores select for the same herbaceous species which result in a high degree of diet overlap. Herbivores employ a grazing strategy that leads to a temporal partitioning of the resource and little interspecific competition. A complex interaction exists between predator (herbivores) and prey (plant) that has numerous outcomes and any attempt to model complex ecosystems is inevitably disappointing due to lack of both data and understanding. High resolution is therefore not warranted.

This complexity of multiherbivore-multiplant relationships demands that the system be simplified. The high overlap in diet permits the multiplant-multiherbovore system be reduced to that of a single plant-single herbivore. The lack of data on preference and selectivity at the species level are, in part, compensated for by some data for selection of plant size. There is also reasonable understanding of the effects of nutrition on animal productivity.

In conclusion, a context within which to model has been evolved and some relevant data identified. The degree of resolution suited to both the data and the understanding has been established. It is now possible to proceed to developing the model and applying real data to explore the consequences.

CHAPTER 2 : STUDY AREA

The aims of this chapter were to describe the study area and the abiotic and biotic elements found there.

This was necessary to determine what information was already available which in turn identified inadequacies in the existing data base.

2.1 General description

The study area falls within a private nature reserve, Rooipoort, situated some 60 km west of Kimberley (28° 40'S, 24° 10'E) in the northern Cape Province of South Africa (Fig. 2.1). The reserve is 42500 ha in extent and the study area constitutes approximately 600 ha of a homogeneous vegetation type found within this reserve.

The reserve is divided into an exclusively wildlife area totaling 34500 ha and an area of approximately 8000 ha where domestic stock (cattle) are grazed. The game area is bounded by a game-proof fence on three sides and the Vaal river on the fourth side.

2.2 Historical background

Rooipoort was acquired by the present owners, De Beers Consolidated Mines Limited, in 1894 for its alluvial diamond deposits. These deposits have never been exploited and the area has been maintained as a private nature reserve. From its

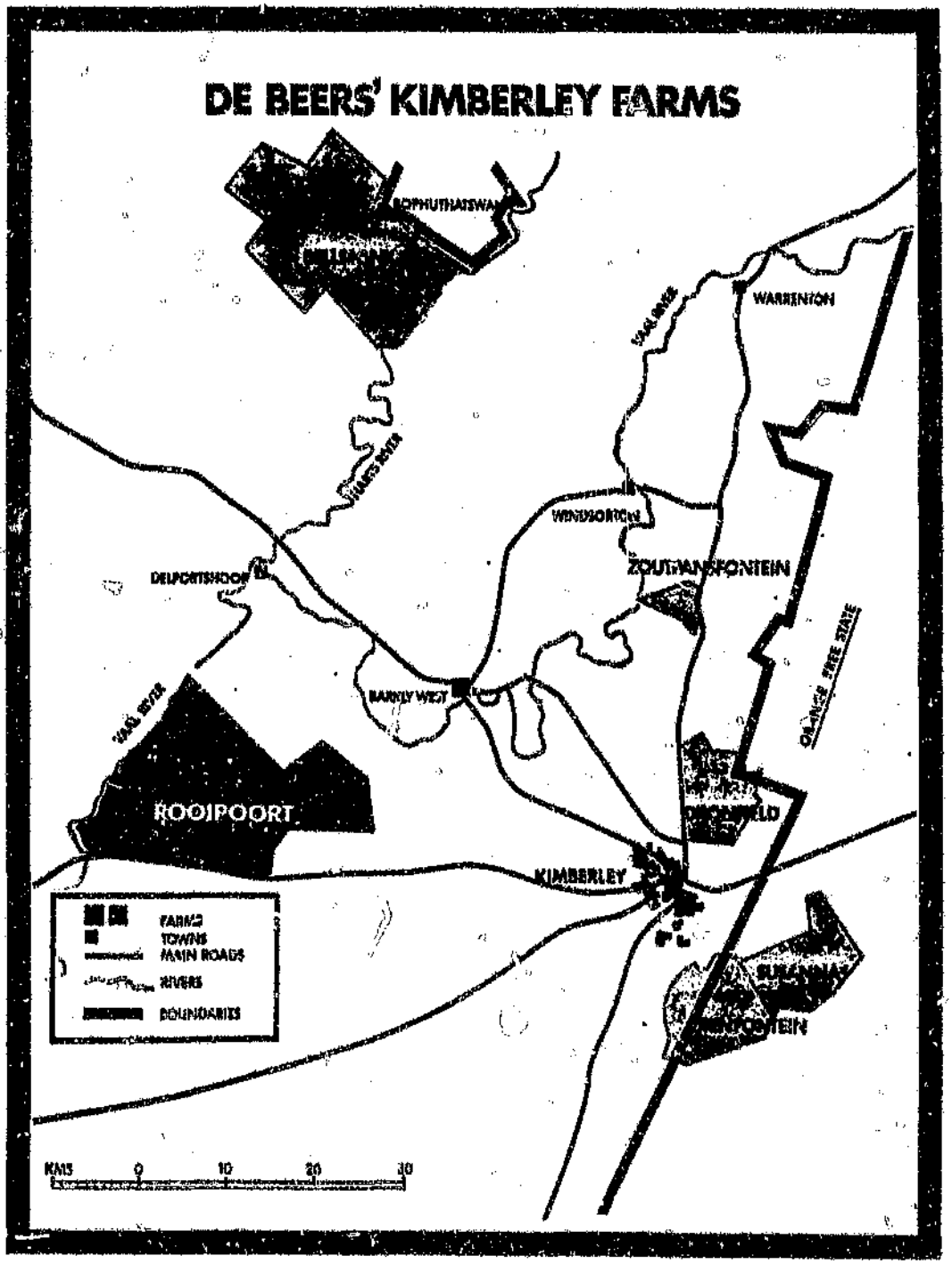


Figure 2.1 Location of Rooipoort.

inception, the reserve provided recreational hunting primarily of gamebirds (guineafowl *Numida meleagris*, sandgouse *Pterocles namaqua* and *P. buchelli*) and springbok for guests. At the turn of the century seven large herbivores species were to be found on the reserve. From 1960 onwards other herbivore species that previously occurred in the area were reintroduced and seventeen species are today found on the reserve.

2.3 Geology

Rooipoort lies at the base and east of the G[illegible] [illegible]teau. The area is underlain by several geological form[illegible] [illegible] koppies are mainly composed of andesitic lava (Ventersdorp super[illegible]roup) with outliers of dolomite (Transvaal sequence). Several low ridges of quartzite (Ventersdorp supergroup) are also to be found. The lower lying areas are covered by pedogenic calcrete of possible early Tertiary age and aeolian (Kalahari) sands (De Wit *pers. comm.*).

The study area (The Pan) is situated in a broad exhumed glacial valley bounded by andesitic ridges on either side (De Wit *pers. comm*). These rise steeply on the northern fringes of The Pan and gradually to the south. The Pan itself is a composed of a series of pan limestones (marls), calcified siltsands and muds. The former are extremely hard and impermeable close to the surface, which accounts for the absence of trees on The Pan. The sediments

---

De Wit, M. Regional Exploration Manager, De Beers Consolidated Mines Limited, P.O. Box 616 Kimberley. 8300.

are deposited on diamictites and shales of the Dwyka Formation (Karoo Sequence). The diamictites are believed to be glacial in origin (De Wit *pers. comm.*).

2.4 Climate

2.4.1 Rainfall

Kimberley is the nearest weather station for which long term rainfall records are available. There is evidence (Berry & Crowe 1985) that although the mean annual rainfall for Kimberley has increased marginally in recent years (1950 to 1982) the number of days within a year on which rainfall was recorded has decreased markedly during the same period. Thus rainfall for the last 38 years only was considered.

The mean annual rainfall for Kimberley for this period (1951 to 1988) was 421.9 mm. Rain occurs mainly in the summer months (Fig. 2.2) with the wettest months being January through to March.

The frequency distribution of annual rainfall over the same period was bi-modal (Fig. 2.3) with the highest frequencies between 250 mm and 350 mm and 460 mm and 560 mm of annual rainfall. This suggested that there was a tendency towards either dry years or wet years rather than "normal" (approximating annual mean) years.

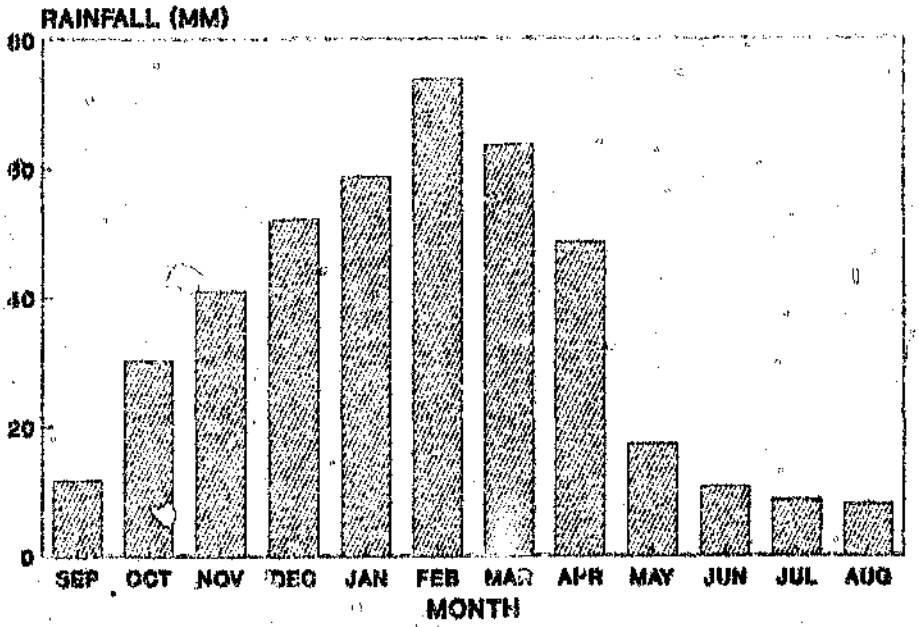


Figure 2.2 Mean monthly rainfall (mm) Kimberley 1951 - 1958.

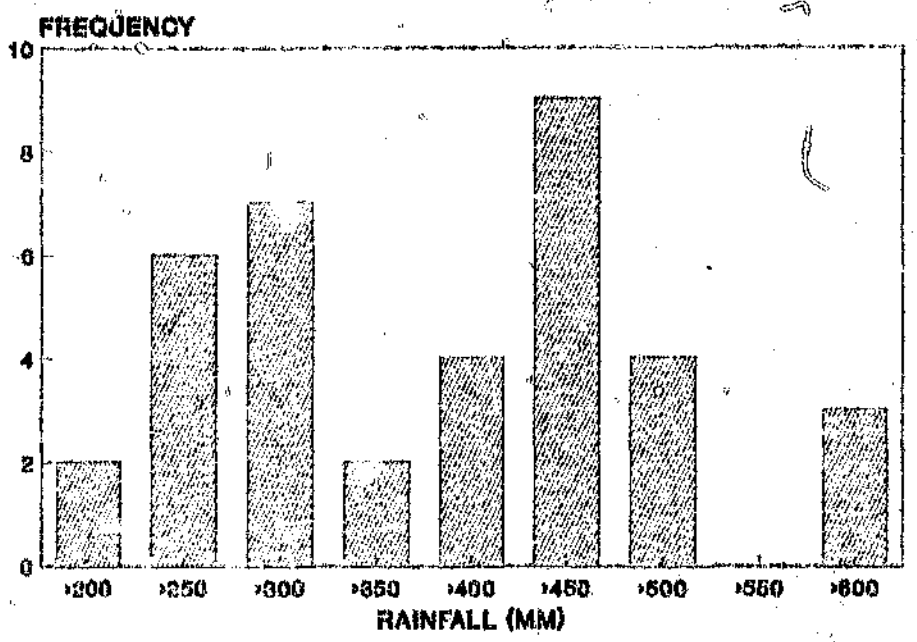


Figure 2.3 Mean annual rainfall frequency.

2.4.2 Temperature

Kimberley is subject to large seasonal temperature fluctuations. Summers are generally hot with the maximum temperature often exceeding 35 °C. The winters are cold often with sub-zero minimum temperatures. Mean monthly maxima and minima are given in Fig. 2.4, i.e. the mean of the average daily maximum and minimum for that month for the period 1951 to 1988.

2.4.3 Seasons

For the purpose of this study four seasons were identified on the basis of temperature with the hottest month being mid-summer and the coldest month mid-winter (Anon 1957). In conjunction with rainfall the seasons were described as follows:

spring	Sep-Nov	hot dry season
summer	Dec-Feb	hot wet season
autumn	Mar-May	cool wet season
winter	Jun-Aug	cool dry season

2.5 Vegetation

Rooipoort falls within Acocks's (1975) False Orange River Broken Veld and Kalahari Thornveld invaded by Karoo vegetation types. These are very broad descriptions of a variety of plant communities found on the reserve.

Bigalke and Leistner (1963) described eleven different vegetation types on Rooipoort (Fig. 2.5). Crowe, Schijf and Gubb (1981), on

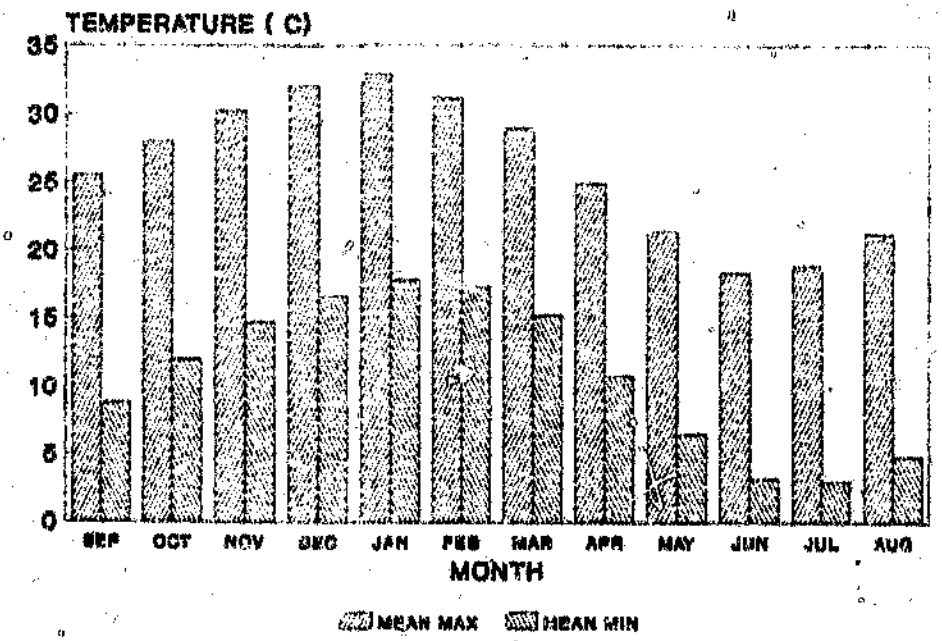


Figure 2.4 Mean monthly maximum and minimum temperatures.

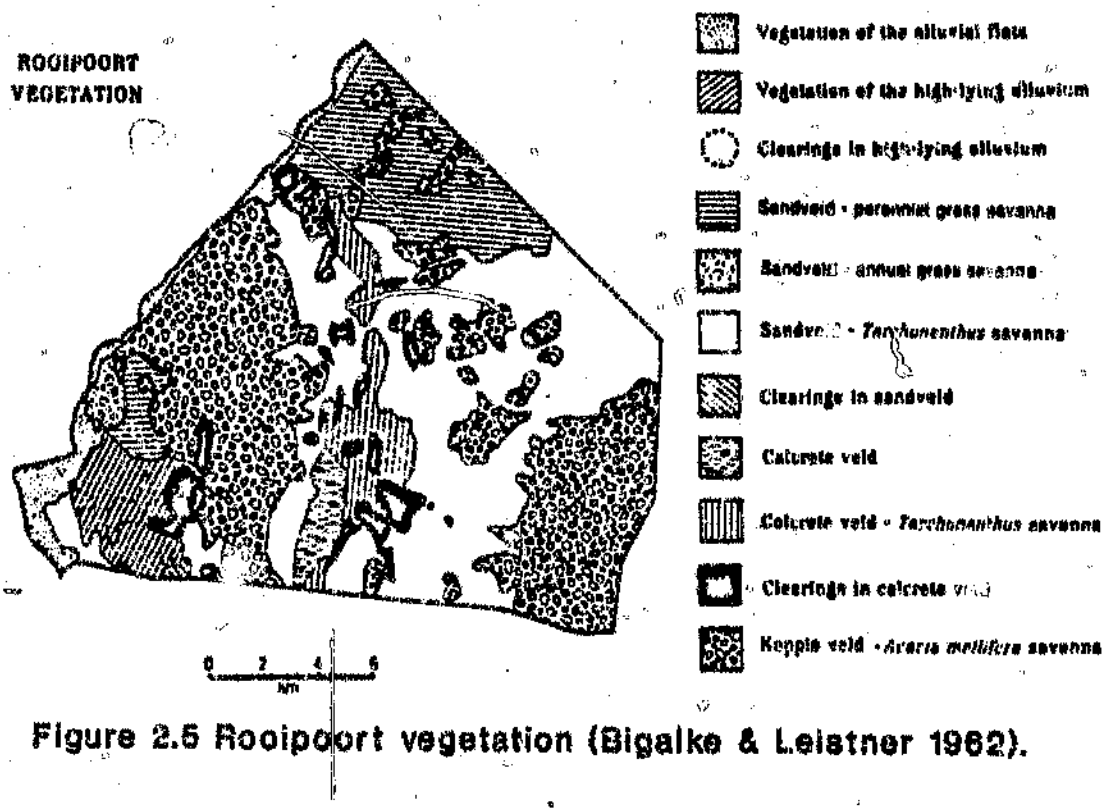


Figure 2.5 Rooipoort vegetation (Bigalke & Leistner 1962).

the basis of floristic and abiotic physiognomic characteristics grouped these into four major habitats, one of which was divided into four sub-habitats.

This study was confined to a single vegetation type known as The Pan. This perennial grassland was an area some 600 ha in extent and characterised by the virtual absence of trees. Pans act as nutrient sumps and as a result herbaceous growth on these areas is of a high quality. Some species e.g. black wildebeest and blesbok were also attracted to The Pan by its physiognomy i.e. a treeless short-grass plain.

The southern parts of The Pan that were periodically inundated tended to be bare or had a sparse cover of *Sporobolus albicans* and *Urochloa panicoides*. The northern areas of The Pan which were subject to flooding supported a taller grass community of *Eragrostis bicolor*. The remainder of The Pan was a mixed community of *Eragrostis truncata*, *Sporobolus ludwigii* and *Enneapogon desvauxii*. *S. ludwigii* tended to dominate on the moister, low lying soils and *E. truncata* dominated on the sandier soils towards the margin of The Pan. Karoo shrubs common on The Pan were *Lycium oxycladum*, *Pentzia incana* and *P. viridis*.

2.6 Herbivores

2.6.1 Historical

The earliest recorded census on Rooipoort was in 1903 when the numbers of large herbivores were estimated at 400 ostrich *Struthio camelus*, 500 red hartebeest *Alcelaphus buselaphus*, 1500

springbok and 3 kudu *Tragelaphus strepsiceros*.

These animals were naturally indigenous to the reserve and almost certainly steenbok *Raphicerus campestris*, duiker *Sylvicapra grimmia* and mountain reedbuck *Redunca fulvorufula* occurred but were not mentioned. These three species were present on the reserve and there is no evidence to suggest that they were ever introduced.

The first successful translocation took place in 1956 when blesbok were introduced. This was followed by eland (1959), black wildebeest (1959), gemsbok *Oryx gazella* (1961), warthog *Phacochoerus aethiopicus* (1961), zebra *Equus burchelli* (1963), giraffe *Giraffa camelopardalis* (1964) and blue wildebeest (1965).

Aerial censuses commenced in 1973 and thereafter were repeated at two year intervals until 1984. Since 1984 the aerial census has been carried out annually. The counts for major species from the first and the most recent aerial censuses are given in Table 2.1.

Table 2.1 Species and numbers of animals counted on Rooipoort in 1973 an 1988.

Species	1973	1988
springbok	1871	1498
hartebeest	774	864
ostrich	164	218
eland	57	456
kudu	58	226
gemsbok	25	742
blue wildebeest	65	425
black wildebeest	74	205
blesbok	92	171
zebra	9	188

2.6.2 Ecology of study species

2.6.2.1 Black wildebeest

Black wildebeest are associated with open treeless plains and prefer the shorter grasslands (von Richter 1971b). They are gregarious and are found in herds of varying size up to thirty animals.

Historically they occurred on the open grassveld and karoo regions of central and northern Cape Province, the Orange Free State, southern Transvaal and the foothills of the Drakensberg mountains (Von Richter 1971a; Skead 1980).

Social organisation consists of breeding herds made up of an adult territorial bull, adult and sub-adult females and calves; lone territorial males and bachelor groups of non-territorial adult and sub-adult males. Bulls although physically mature at 2-3 years of age only enter the breeding segment at the age of four to five years once they are able to maintain a territory.

Territorial bulls were found (von Richter 1971a) [illegible] their territories throughout the year which they ri[illegible]ously defended during the rut. Territories appeared to be stable and the same bull returned to the same territory in successive years . Female herds wandered throughout their home range and territorial bulls aggressively tried to retain these female herds within their territory during the rut. Home ranges varied with herd size and grazing condition but were usually of the order of 100 ha.

Females normally conceive for the first time at the age of 28 months and calve for the first time at the age of three years. Von Richter (1971b) recorded a small percentage of females under favourable conditions conceived at sixteen months for the first time and calved at two years.

Black wildebeest are synchronised seasonal breeders (Skinner *et al.* 1974) with a gestation period of 248 to 261 days (von Richter 1971b). Calves are born within the herd, are precocious and follow their mothers shortly after birth. The majority of calves were born at Rooipoort between the middle and end of December each year.

Three age groups were easily distinguishable by their body size and horn shape in the field. These were adults (> 2 yr), sub-adults (1 to 2 yr) and calves (< 1 yr). Adults were also distinguished from sub-adults by the colour of the hair on the forehead which tended to be brown in sub-adults and black in adults.

Black wildebeest are concentrate grazers (Mentis 1981) and prefer to selectively feed on short, palatable grasses (van Zyl 1965) with peak grazing periods in early morning and late afternoon/evening. The species are water dependent, generally drinking at sunset. During the middle of the day animals rest either lying down or standing. Black wildebeest show orientation to the sun, an adaption behaviour that allows them to stand in the mid-summer sun without seeking shade (von Richter 1971a).

Van Zyl (1965) found that the diet consisted mainly of grass (63 per cent) in summer and 37 per cent karoid bushes in the winter months. Preferred species included *S. ioclades* and *Pentzia spp.* which also dominated in this study area. Von Richter (1971b) noted that the sedentary nature of the species was of considerable ecological significance as black wildebeest were able to modify their habitat to produce favoured grazing. However, this area selection has given rise to management problems.

2.6.2.2 Blesbok

The habitat requirements of blesbok are in many respects similar to those of black wildebeest with a preference for open grasslands. Blesbok are also highly gregarious and exhibit similar territorial behaviour and social organisation.

Three sex-age classes were distinguished on body size, horn size and shape. Adult males were readily distinguished by the penal sheath.

Large breeding herds comprise females and juveniles and are attended by one adult ram. Bachelor herds are made up of predominantly young males. Territorial males live a solitary life on a restricted area. Outside the breeding season solitary rams cease to be territorial and join the large breeding herds (Du Plessis, 1972).

Some females are sexually mature at 16 - 18 months of age but the majority only become sexually active at 28 months of age

(Kettlitz 1967; Marchant 1983; Smithers 1983).

Du Plessis (1972) found calving coincided with growth of green grass in early summer. New born lambs were able to run within five minutes after birth and were weaned at four months of age. Calving on Rooipoort normally took place from the middle of November to the end of December. A number of calves were also born in late summer probably to heifers calving for the first time at the age of 28 months under favourable conditions.

Blesbok are also selective grazers with a preference for young sprouting grass (Du Plessis 1972; Smithers 1983). Du Plessis (1972) found in grassveld blesbok grazed exclusively, whereas, van Wyl (1965) found that 21.5 per cent of the diet consisted of karoid shrubs. Blesbok drink regularly.

2.6.2.3 Springbok

Springbok are characteristically associated with the arid and semi-arid areas of southern Africa. Although they occur in wooded habitats they have a preference for open areas, more particularly pan systems (Bigalke 1972; Schijf 1977).

Large aggregations made up of animals of both sexes and of all ages are common. Immature rams and non-territorial rams form bachelor herds. Adult males are territorial during the rut but join large herds outside of the breeding season.

Due to the rapid growth of springbok only two age classes, adults

and juveniles were easily identified. Males were readily distinguished from females by their heavier lyrate horns.

Contrary to the findings of Smithers (1983), in this study springbok were found to exhibit a bimodal calving peak as reported by Bigalke (1970) and Bigalke et *al.* (1975). Skinner (1989) considered springbok to be opportunistic breeders that bred at any time of year but with a spring/summer peak. On Rooipoort the majority of lambs were dropped in early summer (Sep-Oct) with a smaller lamb crop in autumn (March) which was similar to the findings of Bigalke et *al.* (1975).

Females normally lambed once a year from the age of 24 months. However, under favourable conditions ewes started breeding at five months of age (Skinner 1989) and were recorded to lamb at the age of one year and thereafter at six month intervals (Livoreidge 1989). Bigalke et *al.* (1975) found that the percentage of females that conceived for the first time at the age of six months varied from 20 per cent to 80 per cent and depended on veld condition.

Lambs lie up for the first ten days after birth and thereafter join the breeding herds. Weaning takes place at the age of three months although lambs readily feed from the age of three weeks.

Springbok are termed intermediate (mixed) feeders (Mentis 1981). Grass was found to constitute 39 per cent of diet and browse 61 per cent (Bigalke et *al.* 1975). Grass is taken for only short periods in the summer months after rain (Mills & Retief 1984a) and in winter springbok switch to browsing, particularly karoo

shrubs, e.g. *Pentzia spp.* and other Savanna elements viz. *Rhus, Olea* and *Zizyphus* (Bigalke 1972; Liversidge 1972).

In conclusion the study area lies within a complex and varied ecosystem. The Pan itself is by comparison relatively simple with clearly defined physical, floral and faunal elements.

CHAPTER 3 : MODEL DEVELOPMENT, VERIFICATION AND SENSITIVITY

The purpose of this chapter was to investigate the model's properties and determine if the model was appropriate to the objectives of the study.

This was achieved by starting with a simple expression that could plausibly model the plant-herbivore relationship. This expression was expanded and refined to a more complex model. The various parameters of this model were then tested to determine their sensitivity on the output.

This procedure sought to identify the important elements in the model and the inadequacies in the data and, through successive refinement, to evolve a model that displayed the descriptive and predictive properties required.

3.1 Introduction

The uses and benefits of ecological modeling have been discussed by Jeffers (1982), Starfield and Bleloch (1986) and Swartzman (1979). Models have been used extensively in ecology and wildlife management (Caughley 1982; Dye 1983; Hilborn & Sinclair 1979; Mentis 1982; Noy-Meir 1975; Pellew 1983; Starfield *et al.* 1982a & 1982b; Starfield & Bleloch 1986; Walker 1978) to facilitate decision making where data and understanding were deficient. In spite of their use in predator-prey relationships (Bleloch 1982; Caughley 1976; Johnson & Parsons 1985; Noy-Meir 1975; Noy-Meir 1981; Owen-Smith & Novellie 1982; Pellew 1983; Starfield *et al.*

1976; Swart *et al.* 1986; Venter & Hopkins 1988) the role of herbivory particularly for large herbivores has remained poorly understood (Crawley 1983).

From the outset the modeling approach was heuristic (serving to discover) as there were limited means of validating the model in the normal way by testing with independent data. Rather, the model set out to determine the data required, the functioning of the system and the role of management.

Starfield & Bleloch (1986) have pointed out that the quality of a model depended not on its realism but rather its performance in relation to the purpose for which it was built. In this case the model was specifically developed to meet the descriptive and predictive needs of the plant-herbivore system.

3.2 Model development

In arid and semi-arid environments conditions for growth are highly variable.

Consequently, the approach of Noy-Meir (1975) and the use of a logistic model was inappropriate for modeling interseasonal changes in vegetation growth when the effects of rainfall and herbivory were large.

Furthermore, the logistic model assumed that the growth rate of vegetation depended on the quantity of vegetation present when, in fact, plants were able to use below ground reserves and grow rapidly even at low aerial plant biomass.

Starfield and Bleloch (1986) proposed an alternative model to express vegetation growth between seasons. The simple form of the model was given by

$$dV/dt = a - pV \qquad (1)$$

where a was the new growth and p was a decay constant.

The growth, a, was a function of rainfall and temperature and was independent of the value of V. The model assumed that there were always sufficient reserves to respond to rainfall and that there was only one vegetation type.

These assumptions were not unreasonable. Arid adapted plants have evolved a rapid response to rainfall though the use of below ground reserves (Westoby 1980). The high overlap in herbivore diet (Grunow 1980; Page & Walker 1978; Sinclair 1985) to the extent of a single preferred species (Hansen et al. 1985) permits the assumption of a single vegetation type.

The model was elaborated to include a constant grazing rate C

$$dV/dt = a - pV - C \qquad (2)$$

The properties of C under fluctuating rainfall regimes were explored by Starfield & Bleloch (1986) and it was shown that provided consumption was less than growth there was only one equilibrium point which was always stable.

The ability of the herbivore to meet its consumption requirements (c) depended on the quantity and the quality of the vegetation (V), for example, grass length, leaf to stem ratio, patchiness etc. The model was improved by allowing the consumption to be modified by the state of the vegetation and this was termed the functional response f(V) (Appendix 2).

The consumption rate was then given by

$$C = cf(V)H \qquad (3)$$

Functional response was a complex concept that varied with herbivore species and vegetation composition. However, the resolution of the model permitted that the concept be simplified and used to good effect in herbivore population dynamics. This was so because herbivore productivity was dependent largely on food availability.

In order to use the model to investigate the changes from year to year or season to season the differential equation (Eq. 1) was changed to a difference equation, a form that was easily solved numerically and, therefore, could be built into a computer program. That was

$$Vi = Vo + a - pVo \qquad (4)$$

Here Vi was the new vegetation after a given period t + 1, Vo was the vegetation at the start of the period t, a was the growth between time t and t + 1 and p was the fraction of the original vegetation that was lost during this period.

The equation was rewritten as

$$Vi = a + Vo(1 - p) \quad (5)$$

and simplified by substituting k for 1 - p

$$Vi = a + kVo \quad (6)$$

where k was the proportion of vegetation that remained.

The vegetation equation (Eq. 4) was expanded to include herbivores

$$Vi = Vo + a - pVo - cf(Vo)H \quad (7)$$

This is the discrete model of Starfield & Bleloch (1986). The model represents net growth over the period under consideration, not a growth rate and hence is capable of expressing interseasonal changes in the vegetation.

The discrete form of the model was well suited to the resolution and objectives of this study. Vegetation growth in semi-arid systems was event (rainfall) driven. Furthermore, herbivore births were also seasonal and synchronised. In effect the

was best expressed in time intervals of several months.

The simple herbivore equivalent model to Eq. (1) was

$$dH/dt = bH - mH \qquad (8)$$

where H was the herbivore population, b the number of births and m the number of deaths.

It is well established that herbivore productivity is a function of food availability (Crawley 1983; Moen 1973). Therefore, the concept of functional response (Appendix 2) was useful for manipulating the population dynamics of a herbivore.

If the number of births and the number of deaths in the herbivore population were a function of the vegetation and the herbivores' ability to meet their food requirements, then

$$dH/dt = bf(V)H - mf(V)H \qquad (9)$$

where f(V) was the functional response of the herbivores.

Births were highly seasonal and the discrete difference equation was more appropriate for expressing this seasonality than was the differential equation (Eq. 9).

$$Hi = Ho + bf(Vo)Ho - mf(Vo)Ho \qquad (10)$$

Hi was the new herbivore population at time t + 1 and Ho was

the herbivore population at time t.

The scope and limitations of the vegetation-herbivore model (Eq. 7) were governed by its assumptions and these are listed below.

1. Vegetation growth was variable and dependent on rainfall and season.
2. There were always sufficient reserves for vegetation growth. This assumed that growth occurred in the absence of residual vegetation.
3. There was only one type of vegetation and it was all grazable i.e. woody components were ignored.
4. The vegetation loss affected all plants equally and was dependent on the amount of vegetation. Vegetation loss varied with season and rainfall.
5. The grazable biomass was equally available to herbivores on The Pan i.e. it was of equal palatability and quality.
6. Herbivores were expressed as a single variable.
7. Food preferences were not affected by sex or age of herbivore.
8. Herbivore productivity was only determined by diet.
9. Only springbok, blesbok and black wildebeest consumed the vegetation. Other herbivores were ignored.

In order to reduce unnecessary detail the model was constructed as parsimoniously as possible. The aim was to include no more than was absolutely necessary for the desired description and prediction. Although the variables, like lumped vegetation and a single herbivore lacked detail, they were adequate to model the plant-herbivore system at the desired resolution.

3.3 Model verification and sensitivity analysis

3.3.1 Introduction

The purposes of this section were to (i) explore the properties of the model (Eq. 7) (ii) determine the sensitivity on the output of the various input parameters, and (iii) verify the plausibility of the output.

This was achieved by means of a sensitivity analysis whereby each parameter was systematically changed and the effect on model output observed. This identified those parameters in the model that were important, gave a feel for the model's performance and allowed a comparison of model output with what was perceived to be reality.

In order not to confound the outcome, the model was simplified wherever possible. This reduced the number of variables and hence improved interpretation. The model was then elaborated with successive sensitivity analyses and the output studied. In the simplified model the effect of each parameter was more readily apparent than in a more complex model where it was often difficult to discern which parameter was most affecting output change.

It was determined, for example, whether growth was more important than senescence, and in what way herbivory affected production. This also avoided the mistake of gathering irrelevant data in the field and thus concentrated the research effort.

3.3.2 Methods

The aim was to determine which of the vegetation factors, growth (a), senescence (p) or residual vegetation (Vo) most affected net primary productivity.

The simplified vegetation model (Eq. 6) which excludes herbivores was considered first

$$Vi = a + kVo \qquad (11)$$

The vegetation at the end of the season Vi was the growth during the season (a) plus the vegetation remaining from the previous season. The equation was linear and permitted a direct comparison of the different parameters in the model.

For the purpose of verification it was assumed that the starting biomass (Vo) was 400 $kg.ha^{-1}$ (eyeball estimate) and the proportion of vegetation remaining was 0.4 (after Starfield & Bleloch 1986). The maximum growth during the season was 1000 $kg.ha^{-1}$ (guess).

The growth (a) in each season was determined by applying a "growth factor" to the maximum possible growth (1000 $kg.ha^{-1}$). In terms of the model assumptions, this growth factor was a product of rainfall and temperature. Therefore growth was higher in summer when temperatures were high and rain fell and low in winter when there was little or no rain and temperatures were

low. In spring and autumn growth was intermediate. Similarly more growth occurred in wet years than in dry years.

This reasoning was applied to develop a set of growth factors (Table 3.1) for different seasons and different rainfall regimes.

Table 3.1 Seasonal growth factors for sensitivity analysis.

Rainfall	Season			
	spring	summer	autumn	winter
low	0.3	0.4	0.3	0.0
medium	0.5	0.7	0.4	0.1
high	0.7	1.0	0.6	0.2

The growth (a) for spring during a high rainfall was

$$0.7 \times 1000 = 700 \text{ kg.ha}^{-1}.$$

The production was determined using Eq. 11

(i) seasonally for each rainfall regime i.e for each season (3 months) with a starting biomass (Vo) of 400 $kg.ha^{-1}$ each time, and

(ii) annually for each rainfall regime with a seasonal time step (3 months) i.e. the cumulative seasonal production (12 months) with a starting biomass (Vo) of 400 $kg.ha^{-1}$ and the derived Vi was used as the Vo for following season.

The simplified vegetation model (Eq. 11) was expanded to include herbivores and the importance of herbivory and its effect on production was determined using

$$Vi = a + kVo - cf(Vo)H \quad (12)$$

Initially to facilitate interpretation the herbivore model was also simplified. It was assumed that the herbivores were able to fully satisfy their intake requirements i.e. to satiation, in which case, it was possible to simplify the functional response to f(Vo) = 1 and cf(Vo)H was simplified to cH. Therefore

$$Vi = a + kVo - cH \quad (13)$$

A realistic estimate of the number of herbivores was made from herbivore counts carried out on The Pan between 1982 and 1988. The three herbivore species were considered as a single species and expressed as a single variable. The herbivores were reduced to animal unit equivalents (AU) (Appendix 1) and a value of 100 herbivores (AU) was used. The Pan was approximately 600 ha in extent, thus the assumed stocking density was equivalent to 1 AU to 6 ha or 0.17 H per ha.

Consumption per AU was assumed to be 10 kg dry matter per day (Tainton 1981). Therefore each animal unit (herbivore) required approximately 3600 kg per year (10 kg x 360 days). If each AU grazed 6 ha per annum then each ha had to supply 600 kg of forage per year. Thus the annual consumption c was 600.

The sensitivity analysis was carried out with crude values that approximated those in the field. Their accuracy was unimportant for the analysis. Sensitivity was determined by varying each

parameter over realistic ranges and observing how this affected production with a single time step (one season of three months). Each input value was varied separately i.e. one at a time with all other variables held constant and the percentage change in the output (Vi) noted. The model was linear and therefore the variables were compared directly. Those variables that gave the greatest percentage change in the output were the most sensitive and the most important in determining production.

The expanded model (Eq. 7) was then subjected to verification and sensitivity analysis to determine the interaction of all variables in the model. In this case both the residual vegetation from the previous season (Vo) and the functional response [f(Vo)] of the herbivores were also considered in conjunction with those parameters already examined in the simplified model (Eq. 13).

Finally, the sensitivity of the herbivore model (Eq. 10) was investigated.

3.3.3 Results

The seasonal production for varying rainfall is given in Table 3.2. As expected production was high in summer and low in winter. The production in spring was marginally higher than in autumn. This does not seem unreasonable given that spring temperatures generally tended to be higher. There was a net increase of vegetation for all seasons except winter. The production under high rainfall was approximately twice that under low rainfall.

Table 3.2 Seasonal production in $kg.ha^{-1}$.

Rainfall	Season			
	spring	summer	autumn	winter
low	460	560	460	160
medium	660	860	560	260
high	860	1160	760	360

The seasonal and annual productions using the biomass of the previous season Vi as Vo for the next season are given in Table 3.3.

Table 3.3 Seasonal and annual production in $kg.ha^{-1}$.

Rainfall	Spring	Summer	Autumn	Winter	Total
low	460	584	534	213	1791
medium	660	964	786	414	2824
high	860	1344	1138	655	3997

There was an increase in seasonal production using the previous seasons' production as the starting biomass. This is not surprising as the net seasonal production was higher than the fixed value for all seasons except winter. The annual production under high rainfall (3997 $kg.ha^{-1}$) was slightly more than double that under low rainfall (1791 $kg.ha^{-1}$). Assuming high annual rainfall was 500 mm and low was 250 mm gave a production of 8.0 and 7.2 $kg.ha^{-1}.mm^{-1}$.

The sensitivity analysis with the simplified herbivore equation (Eq. 13) demonstrated that vegetation parameters were more important than herbivore parameters (Table 3.4). Furthermore, the model was most sensitive to changes in production. This was useful for it indicated that temperature and rainfall, rather than starting biomass and decay, were more important determinants

of vegetation change.

Table 3.4 Summary of percentage change in vegetation biomass (Vi) for a 5x change in input parameter for simple model.

Parameter		Variation	% biomass change
production a	($kg.ha^{-1}$)	250-1250	223
starting veg Vo	($kg.ha^{-1}$)	250-1250	67
% veg loss k		0.1-0.5	52
herbivore H	($AU.ha^{-1}$)	0.1-0.5	29
consumption c	($kg.ha^{-1}.AU^{-1}$)	200-1000	16

The sensitivity analysis of variables in the expanded model which included herbivore functional response (Eq. 12) gave a similar result to that found above. Growth, and to a lesser extent standing biomass, were the most important parameters (Table 3.5). The effect of herbivory was small particularly when compared to the sensitivity of production to change.

Table 3.5 Summary of percentage change in vegetation biomass (Vi) for a 5x change in input parameter for expanded vegetation model.

Parameter		Variation	% biomass change
production a	($kg.ha^{-1}$)	250-1250	167
starting veg Vo	($kg.ha^{-1}$)	250-1250	93
% veg loss k		0.1-0.5	26
herbivore H	($AU.ha^{-1}$)	0.1-0.5	24
consumption c	($kg.ha^{-1}.AU^{-1}$)	200-1000	13
funct resp f		0.2-1.0	8

In the herbivore model, model output was most sensitive to the number of herbivores at the start Ho (Table 3.6). The effect of mortality on the herbivore population was marginally higher than the birth effect whereas mortality functional response affected output the least.

Table 3.6 Summary of percentage change in herbivores (Hi) for a 5x change in input parameter for herbivore model.

Parameter	Variation	% biomass change
herbivores Ho (AU)	50-250	400
birth rate b	0.1-0.5	40
mortality rate m	0.1-0.5	53
birth func resp bf(Vo)	0.2-1.0	21
mortality func resp	0.2-1.0	7

3.3.4 Discussion

In general the model's performance was plausible. The output for seasonal and annual production reflected relative rainfall and temperature regimes and total production fell within accepted norms for semi-arid environments. The output of the elementary model was not very different from that of the complex model which illustrated that much can be gleaned even from simple equations.

The sensitivity analysis clearly identified growth as the most important parameter. The effect of the herbivores on the vegetation was small even at a density three times, and a consumption rate almost double, that considered normal. This was fortuitous in that the two most difficult variables to define and measure were probably consumption and functional response (Crawley 1983).

If the role of herbivory was small relative to vegetation growth it suggested that the management should rather be aimed at manipulating production than at manipulating herbivore numbers. However, production was primarily governed by rainfall which, unless applied artificially, was beyond the control of management.

The importance of growth in determining production indicated that the model could be improved by increasing resolution in deriving this parameter, perhaps by separating temperature and rainfall in developing the growth factors.

The annual vegetation production generated by the model under low and high rainfall varied from 7.2 to 8.0 $kg.ha^{-1}.mm^{-1}$ rainfall. Elsewhere it has been found that in semi-arid rangelands above-ground production varied from 5 $kg.ha^{-1}.mm^{-1}$ (Rutherford 1980) and 8 $kg.ha^{-1}.mm^{-1}$ (Deshmukh 1984) to 20 $kg.ha^{-1}.mm^{-1}$ (Noy-Meir 1973).

The high production in spite of little residual vegetation is a feature of arid adapted plants that rapidly exploit conditions when favourable (Westoby 1990). The model seemed to incorporate this essential element of semi-arid environments.

McNaughton (1985) has noted that herbivores typically consumed less than 10 per cent of primary production. Deshmukh and Baig (1983) found that the removal by herbivores was negligible. The results of the sensitivity analysis concurred with these findings.

In conclusion, the objectives of this chapter were to develop a model, verify it and analyse its sensitivity. This was, by and large, achieved and, in the process, some understanding of a plant-herbivore system was acquired. The important parameters were identified and the emphasis was then to collect the relevant data in the field.

CHAPTER 4 : CLIMATIC DATA

4.1 Introduction

The purpose of this chapter was to collect accurate climatic data relating to temperature and rainfall.

The sensitivity analysis (Ch. 3) singled out growth as the most important parameter in the model. This corroborated conventional wisdom that growth is determined primarily by rainfall (Deshmukh 1986; Hilborn & Sinclair 1979; Le Houerou et al. 1988; Rosenzweig 1968) and to a lesser extent by temperature and daylength (Noy-Meir 1973).

It was surmised that precise climatic data would improve the model's performance since the model's output had a seasonal time step which was largely controlled by rainfall and temperature.

The hypothetical inputs used to verify the model and test its sensitivity (previous chapter) are refined in this chapter with real data obtained from the field. The aim was to enhance model realism and improve the output.

4.2 Methods

4.2.1 Temperature

Temperatures were not recorded at Roolpoort and it was therefore necessary to use an alternative data source. The

nearest official weather recording station was Kimberley, some 60 km east of the study area. Monthly maximum, minimum and mean temperatures for Kimberley Airport were provided by the Weather Bureau, Pretoria.

Temperature was used to determine season with the hottest month being mid-summer and the coldest month mid-winter (Anon 1957). The year was divided into four seasons (Section 2.4.3).

4.2.2 Rainfall

Rainfall data were required to classify rainfall regimes into high rainfall (wet), medium rainfall and low rainfall (dry). In addition, monthly rainfall figures were used in production (net aerial plant biomass gain) trials where the standing biomass of vegetation was periodically determined with natural rainfall and artificial irrigation.

There was evidence (Berry & Crowe, 1985) that for the thirty three year period 1950 to 1982 there was a significant decline in the number of days on which rain was recorded when compared with a similar period of 1907 to 1940. It was therefore decided that although records from 1897 for Kimberley were available it was more realistic to use only those records for the last thirty eight years from 1951 to 1988 for determining the rainfall regimes.

Rainfall data were available from three sources

(i) Long term data from 1951 - 1988 from the official weather station at Kimberley some 60 km east of the study site.

(ii) Rooipoort data from 1980 to 1988 collected some 10 km east of the study site.

(iii) Data collected at the study site from September 1987 to April 1988 while the irrigation trials were in progress.

The absence of long term data from Rooipoort necessitated the use of rainfall data from Kimberley. In order to test the reliability of using Kimberley rainfall figures a correlation was carried out using data sets for those periods for which records at both stations (Rooipoort and Kimberley) were available.

Three rainfall regimes wet, medium and dry and were determined using mean annual rainfall (Sep-Aug) for the last 37 years (1951 to 1988) (Anon 1957). The totals for mean annual rainfall (Sep-Aug) were arranged in descending order. The median was determined and the upper and lower halves divided into two equal periods of 9 years each giving four periods (quartiles). The upper quartile was then defined as "wet" and the lower quartile as "dry" and the years between the upper and lower quartiles were periods of "medium" rain (Anon 1957). The ranges for each rainfall regime were then determined.

Using the same data set (1951 to 1988) the mean monthly rainfall was determined and expressed as a percentage of the annual mean. Monthly percentages for each quarter were then added to give a seasonal percentage. This percentage was then applied to the value for each rainfall regime to determine seasonal values for wet, medium and dry years of rainfall. These were rounded off to the nearest 5mm.

4.3 Results

4.3.1 Temperature

Monthly temperatures varied from very hot (maximum > 30 °C) in summer to cold (minimum < 10 °C) in winter (Table 4.1).

Table 4.1. Monthly maximum, minimum and mean temperatures (°C) for Kimberley 1951 to 1988 (Weather Bureau).

Month	Maximum	Minimum	Mean
Jan	32.6	17.7	25.2
Feb	31.1	17.3	24.2
Mar	28.8	15.1	22.0
Apr	24.8	10.8	17.8
May	21.1	6.5	13.8
Jun	18.2	3.2	10.7
Jul	18.8	3.0	10.9
Aug	21.1	4.7	12.9
Sep	25.6	8.7	17.2
Oct	27.9	11.9	19.9
Nov	30.2	14.6	22.4
Dec	31.9	16.6	24.3

During the latter part of the study period (Sep. 1987 - Apr. 1988) when irrigation trials were in progress, the summer was particularly dry and hot and the autumn was exceptionably wet. This was reflected in the higher than normal temperatures

recorded in December and January and the lower than normal temperatures in March and April (Table 4.2).

Table 4.2 Monthly maximum, minimum and mean temperatures (°C) for Kimberley September 1987 to April 1988.

Month	Maximum	Minimum	Mean
Sep	21.4	8.5	15.0
Oct	28.1	12.4	20.3
Nov	31.4	15.3	23.3
Dec	33.0	17.1	25.1
Jan	35.6	18.6	27.1
Feb	28.6	18.0	23.3
Mar	26.9	15.8	21.3
Apr	20.9	9.1	15.0

4.3.2 Rainfall

The long-term mean for Kimberley (1951 to 1988) was found to be 422 mm. It is well establish that an east-west gradient of decreasing rainfall exists over central South Africa (Anon 1957). Therefore, it was assumed that the long term annual mean for Rooipoort was about 400 mm.

Rainfall data for Kimberley and Rooipoort for the period 1981 to 1988 are listed in Appendix 4. A correlation analysis of annual (Sep-Aug) and monthly rainfall data from both sites for this period gave correlation coefficient values of 0.9596 ($P < 0.001$) and 0.9660 ($P < 0.0001$) respectively.

Rainfall was measured at the eastern and western ends of The Pan as well as at the eastern irrigation trial site. It was apparent that a rainfall gradient existed on The Pan with rainfall decreasing from east (Stone Dam) to west (Hoffman's Pan) (Table 4.3).

Table 4.3 Comparison of rainfall (mm) at three sites on The Pan.

Month	Stone Dam	Block A	Hoffman's Pan
Sep	117	no record	76
Oct	20	16	18
Nov	74	57	20
Dec	42	32	30
Jan	9	no record	8
Feb	288	222	no record
Mar	50	41	no record
Apr	124	94	no record

On average, the western end of The Pan (Hoffman's Pan) received 58 per cent of the rainfall measured at Stone Dam. The two rain gauges were 5.5 km apart and it was calculated that Block A received 0.77 and Block B 0.69 of the Stone Dam rainfall (Table 4.4). A paired t-test found there was indeed a difference between rainfall at Block A and Block B ($t_{0.95}$=2.713; df=7).

Table 4.4 Calculated rainfall (mm) at irrigation plots September 1987 to April 1988.

Month	Block A	Block B
September	90	81
October	15	14
November	57	51
December	32	29
January	7	6
February	222	199
March	39	35
April	94	86

Determinations of rainfall regimes for the last 37 years showed that "wet" years had an annual (Sep-Aug) rainfall of greater than 475 mm and "dry" years of less than 300 mm. "Medium" rainfall lay between these two values. Given these values the seasonal rainfall for the different regimes was computed (Table 4.5).

Table 4.5 Seasonal rainfall (mm) for wet, medium and dry regimes.

Regime	Spring	Summer	Autumn	Winter	Total
Wet	>90	>210	>145	>30	>475
Medium	60-90	130-210	90-145	20-30	300-475
Dry	<60	<130	<90	<20	<300

It was found that summer was the wettest season (44% of annual rainfall) followed by autumn (30 % of annual rainfall). In addition to low temperatures little rain fell in the winter.

4.4 Discussion

There was a gradient of increasing temperature from east to west (Anon 1957) and it was probable that temperatures at Rooipoort were marginally higher (1 to 2 degrees °C) than at Kimberley. If growth was impaired at temperature extremes (Osmond et al. 1980) then temperature was most likely to limit growth in mid-summer and mid-winter. In any event growth in winter was water-limited.

All three herbivore species have distinct and synchronised birth pulses that are highly predictable for a given three month period. It was evident that quarterly seasons derived from temperature provided a time step that was well suited to the biological parameters of the herbivores in the study.

The absence of actual temperature and rainfall data for the study area was not a shortcoming. The data for Kimberley were highly correlated and more than adequate for the resolution of the model. By comparison to other variables in the model the long

term data for rainfall and temperature were precise and reliable.

The derivation of a climatic index to provide a reliable growth factor is extremely complex (Rutherford & Westfall 1986) due to the difficulty in determining effectivity of precipitation. Not only is soil moisture affected by temperature and wind, but also run-off, soil characteristics, aspect, etc. It was therefore impracticable to accurately record these variables at every rainfall event.

Rainfall in arid and semi-arid areas is characteristically unpredictable spatially, temporally and in terms of quantity (Le Houerou 1984; Zucchini & Adamson 1984).

The rainfall gradient exhibited on Tho Pan, therefore, was not unusual. Seely (1978) found a change of 360 per cent over a distance of eight km and Noy-Meir (1973) reported a difference of forty per cent within one km.

In summary, the climatic data provided a useful, objective method for determining seasons and identifying different rainfall regimes. It was evident that the climatic regime was one of extremes and subject to episodic variation. These data were adequate to compare both vegetation and herbivore productivity and their interaction inter- and intra-seasonally under different moisture regimes.

CHAPTER 5 : VEGETATION DATA

5.1 Introduction

The purpose of this chapter was to refine the vegetation model inputs namely, standing biomass, growth and senescence.

The research effort was focused on net aerial standing crop and how above ground vegetation responded to varying rainfall and season (temperature and daylength).

It has been shown (Ch. 3) that vegetation parameters in the model were the most important in determining its performance. It was therefore necessary that the understanding of these, particularly the rate of process, be improved.

5.2 Methods

5.2.1 Herbaceous biomass

The herbaceous standing crop was determined with and without grazing using the difference method (Milner & Hughes 1968). Grazing by herbivores was estimated by comparing caged and uncaged biomass, the difference being the herbaceous biomass removed by grazing.

During the summer of 1986/87, 50 circular cages (Van Dyne et al. 1963) each with an area of 0.5 m^2 were randomly placed along five transect lines (10 cages per line) randomly selected over

the study area. After a period of one month the herbaceous biomass under each cage along one of the transect lines was harvested. It was intended to harvest the biomass along all five transects after one month. However, due to the paucity of rain no growth occurred and the trial was continued for a further two months. At the end of three months the herbaceous biomass under the remaining cages was harvested and a similar sample randomly collected that had not been protected from grazing. The mean biomass after one month (ungrazed) and after three months (grazed and ungrazed) was determined.

5.2.2 Irrigation trials

An irrigation trial was set up to determine the potential herbage production in $gm.m^{-2}$ under different moisture regimes during the growing period (Sep-Apr). This was intended to show how growth would vary both seasonally and under high, medium (normal) and low rainfall.

An area approximately 30 x 15 m was fenced off with a wire netting fence 1.8 m high. The wire netting (mesh size 80 mm) was such that small herbivores e.g. rodents and insects would have access, but the larger herbivores (ungulates) were excluded.

Each irrigation treatment was applied to a plot 5 x 10 m within which ten 1 x 5 m subplots were situated. Only one subplot (5 m^2) which was randomly selected was treated each month. The treatment plots were 1 m apart and four different moisture regimes (treatments) were used.

(i) Cumulative irrigation - 25 mm applied to all plots in that trial at each successive watering for the entire growing season (September to April) i.e. the April plot received 25 mm (applied twice a month) from September through until the plot was harvested at the end of April.

(ii) 25 mm only to that plot harvested in that month.

(iii) 50 mm only to that plot harvested in that month.

(iv) Control (no irrigation).

Each treatment was applied during the first and third week of the month and the plot was harvested at the end of the fourth week. The trial was replicated twice (Block A; Block B).

Water was drawn from a near-by reservoir that was supplied by windmill from a borehole. The water was transported in 210 l drums which were marked off in such a manner that 125 litres, equivalent to 25 mm, could be accurately applied to the plot undergoing treatment. An earth wall some 50 mm high was made along the border of each plot. The area within this wall was flooded, using a hosepipe to siphon the water out of the drum. In this manner the water was uniformly applied over the entire plot. The 125 litres of water was applied once to treatments (i) and (ii) and twice to treatment (iii) at irrigation times (first and third weeks).

Harvesting took place at the end of the fourth week. The area to be harvested was marked with string. This was placed 50 mm inside the border to allow for edge effect. Thus the area harvested was 0.9 x 4.9 m. All grass within this area was cut to ground level. The grass samples were placed in plastic bags to reduce moisture loss and loss of dry material (Milner & Hughes, 1968) and stored in a deep freeze for subsequent analysis.

At an appropriate time the sample was oven dried to constant mass at 80 °C for 24 hours and the dry matter standing crop at harvest was determined.

In order to determine the important parameters affecting growth an analysis of variance was carried out with results obtained from the irrigation trial. Parameters examined were rainfall, amount of irrigation (treatment), temperature (month) and replicates (block).

Because of the wide difference in monthly rainfall the analysis was repeated with the log of both production and rainfall. It was obvious that the effect of rainfall was not instantaneous (high rainfall in February only produced growth in March). A further analysis was carried out with the log of the rainfall lagged by 1 month.

5.3 Results

5.3.1. Herbaceous biomass

At the start of the trial (January 1987) there was virtually no above ground standing crop on The Pan. The harvestable herbacecus biomass was found to be 0.12 ±0.14 $g.m^{-2}$ (n = 10; 95% cl) which is equivalent to 1.2 $kg.ha^{-1}$. In half the samples there was no vegetation at all. Rainfall during the previous month was 31 mm. There being so little vegetation on The Pan it was decided that there was no point in collecting further samples until such time as reasonable rain had fallen.

After a period of three months (Feb-Apr) 112.5 mm of rain were recorded in the study area and the remaining plots were harvested. The mean herbaceous biomass was found to be 1.44 ±1.63 $g.m^{-2}$ (n = 30; 95% cl) and 1.54 ±1.40 $g.m^{-2}$ (n = 30; 95% cl) for uncaged and caged plots respectively. The difference in harvested biomass between grazed and ungrazed plots was 6.5 per cent.

5.3.2 Irrigation trial

The trial period (September 1987 to April 1988) was characterised by exceptionally heavy rains at the beginning and the end (Table 4.3). The dry matter production under each treatment is given in Table 5.1.

Table 5.1 Dry matter production ($g.m^{-2}$) for different treatments on Rooipoort Pan September 1987 to April 1988.

Month	Block	Dry matter production cumul	25 mm	50 mm	control
Sep	A	7.4	12.2	11.1	12.3
Sep	B	not sampled	15.0	14.5	13.1
Oct	A	10.2	22.5	10.7	13.8
Oct	B	14.9	17.6	6.5	8.3
Nov	A	79.2	91.1	111.6	57.5
Nov	B	63.7	85.3	100.0	60.7
Dec	A	125.3	86.1	131.8	49.3
Dec	B	84.2	52.5	45.2	26.8
Jan	A	44.3	49.0	21.7	29.6
Jan	B	49.3	28.3	43.1	14.9
Feb	A	67.5	29.5	11.1	10.8
Feb	B	59.6	11.4	26.2	6.2
Mar	A	105.3	53.7	44.1	37.6
Mar	B	204.2	80.9	69.5	96.1
Apr	A	82.0	33.8	46.1	31.4
Apr	B	120.1	37.8	26.7	36.1
monthly mean		74.5	44.2	45.0	31.5
95% CL		± 51.2	± 29.2	± 38.9	± 24.5
growing season average		595.8	353.4	360.0	252.3

Standing biomass peaked at 204.2 $g.m^{-2}$ in March under cumulative irrigation of 350 mm supplemented by 222 mm of rain in late February. This was more than twice the production under 50 mm (80.9 $g.m^{-2}$) and 25 mm (69.5 $g.m^{-2}$) irrigation and was a 33 fold increase over the lowest biomass (6.2 $g.m^{-2}$) recorded on the control plot the previous month.

A comparison of mean monthly growth showed little difference in production between the 25 mm and 50 mm treatments and cumulative production was some 2.4 times greater than that of the control.

In any one month the cumulative treatment was equal to the 25mm treatment and there was little difference in production for the early part of the trial. However, from February onwards production under continual irrigation was considerably more than

either the 25 mm or 50 mm irrigation.

Under continual irrigation the total average production (month mean x 8 months) was 595.8 $g.m^{-2}$ which is equivalent to 5958 $kg.ha^{-1}$. The total production for other treatments varied from 2523 $kg.ha^{-1}$ for the control (528mm rainfall) to 3600 $kg.ha^{-1}$ with 100 mm supplementary irrigation per month. The production on each plot and the mean production for both plots is expressed graphically in Figs. 5.1, 5.2 and 5.3.

In spite of both rain and irrigation, relatively little growth took place in September and October. This can be attributed to low temperatures. Even though daily air temperatures had risen, it is probable that ground temperatures remained too low for rapid growth. The limiting effect of temperature is further evidenced by the lack of difference between irrigation treatments in September and October.

According to the literature a minimum amount of moisture is required for growth to commence (Deshmukh 1984; Le Houerou 1984; McNaughton 1985; Noy-Meir 1973).

The highest rainfall event recorded at the irrigation plots in October was 14 mm and growth was probably limited by insufficient ground moisture as well as low ground temperatures. Growth in early summer (Nov, Dec) was greater than in autumn even though considerably less moisture was available. However, growth in mid-summer-early autumn (Jan, Feb) appeared to be limited by too high a temperature at the available moisture levels.

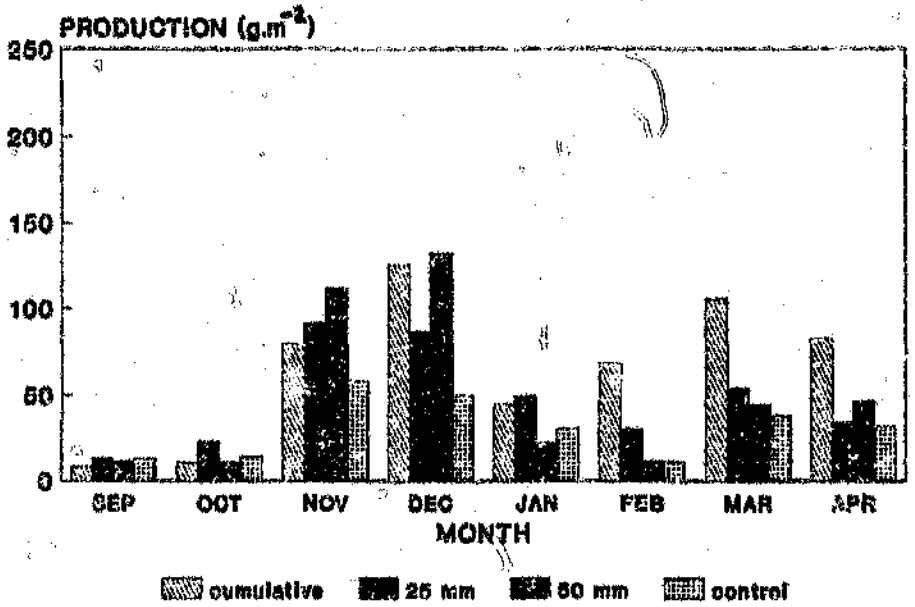


Figure 5.1 Monthly production ($g.m^{-2}$) under different treatments on Block A.

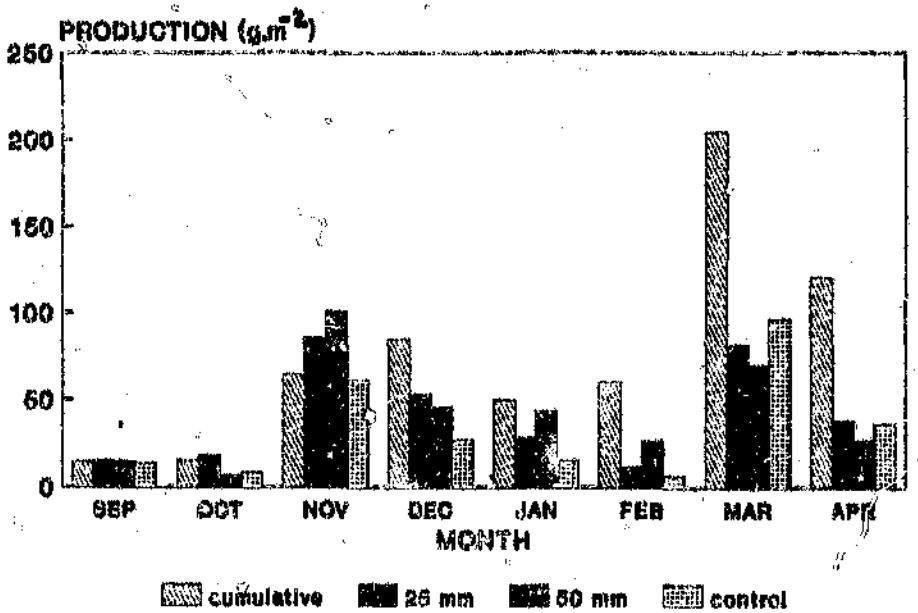


Figure 5.2 Monthly production ($g.m^{-2}$) under different treatments on Block B.

When moisture was limited and under conditions of high temperature (Dec, Jan, Feb) there was a rapid loss in herbage biomass as a result of senescence. This is illustrated in Fig. 5.4.

The highest herbage losses (percentage decline in aerial standing crop of previous month) recorded in a single month where irrigation was applied were 84 per cent followed by 65 per cent. However, these differences may in part have been due to variability between plots sampled. Even where rainfall was relatively high (> 20mm) there was a net loss of herbage the next month which was only halted following the very high rainfall of February.

An analysis of variance for production (Table 5.2) showed that there was no significant difference between blocks ($p = 0.9688$) and it was therefore concluded that the two blocks could be considered replicates. Month had the most significant effect and rainfall the least significant in determining growth. Some 33 per cent of the variance was not predicted by the model.

Table 5.2 Analysis of variance for production.

Covariate	Main effect	Signif. level
rain		0.0361
	treatment	0.0005
	month	0.0000
	block	0.9688

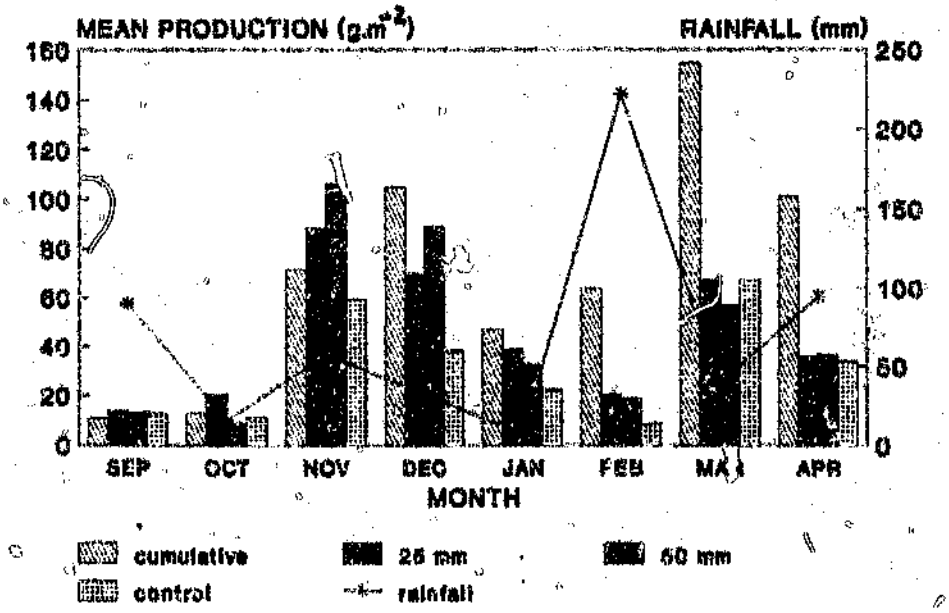


Figure 5.3 Mean monthly production ($g.m^{-2}$) under different treatments for Block A and Block B.

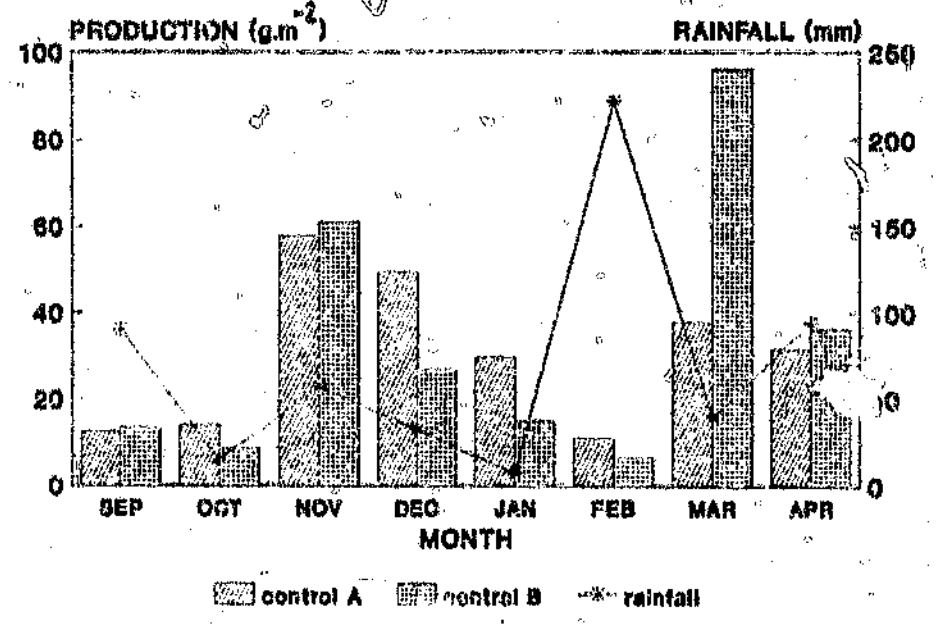


Figure 5.4 Monthly production without irrigation (control).

As expected the lagged log rain was more significant (Table 5.3). This model predicted all but 8.3 per cent of the variance.

Table 5.3 Analysis of variance for log of production.

Covariate	Main effect	Signif. level
log rain		0.5948
lag log rain		0.0000
	treatment	0.0000
	month	0.0000

The month effect in the model was large (52.3 per cent of variance). Month in itself is meaningless and it was probable that this was mainly a temperature effect although presumably day-length would also have affected growth. An analysis of variance for log production and temperature showed minimum and maximum temperature to be the most significant (Table 5.4).

Table 5.4 Analysis of variance for log of production.

Covariate	Main effect	Sig level
Temp min		0.0002
Temp max		0.0006
Temp mean		0.0374
	treatment	0.0389

A multiple range analysis of the log of production and treatment showed that there was no significant difference in production with plots that received 25mm and 50 mm. There was a difference between cumulative irrigation and the control. There was a reasonable correlation of production in one month with that of the previous month ($r = 0.54$; $p < 0.0001$).

5.4 Discussion

Herbaceous production was negligible at low ground moisture and the grazing effect was small. There were considerably more herbivores present on The Pan than could be maintained by the low grazeable biomass at the time (summer 1987). Given a herbivore intake of 10 $kg.AU^{-1}.day^{-1}$ (Tainton 1981) at a standing herbaceous biomass of 15.4 $kg.ha^{-1}$ it would require 234 ha to maintain one animal unit. During the period the herbivore biomass averaged 58.8 AU or 10.2 $ha.AU^{-1}$. This suggested that herbivores were supplementing intake from areas adjacent to The Pan and the model should be refined to cater for this.

At low stocking rates the usefulness of consumption determinations is questionable (Deshmukh & Baig 1983). The grazing effect (6.5 per cent) was small even at low herbaceous biomass. This compared with herbivore consumption rates of 7.5 per cent (Owaga 1980) and 4 per cent (Deshmukh 1986) determined elsewhere.

The cumulative treatment amounted to 528 mm rainfall (average of two plots) plus 600 mm irrigation and would be a decidedly wet season (wet regime = annual rainfall > 475 mm). The duration of the trial was eight months and covered most of the growing season (spring to autumn). From rainfall distribution it was estimated that the remaining four months (May to August) could account for 9 per cent of annual production. Considering that the cumulative treatment gave a production of some 6000 $kg.ha^{-1}$ then the total annual production would have been of the order of 6500

$kg.ha^{-1}$. This must approximate the potential maximum annual production for The Pan.

The maximum potential production of 6500 $kg.ha^{-1}$ compared favorably with the maximum net aerial annual production of 6000 $kg.ha^{-1}$ for semi-arid zones reported by Noy-Meir (1973) and was similar to biomass production figures obtained elsewhere (Rutherford 1978).

The total production (monthly mean x eight months) of 5958 $kg.ha^{-1}$ was 2.92 times greater the peak biomass of 2042 $kg.ha^{-1}$ recorded which was comparable to the figure of 2.5? times reported by Grossman (1982). This illustrated the degree of vegetation loss (senescence) and the importance of its consideration when determining production.

The ability to lose above ground standing biomass is an arid climate adaptation where the rapid loss of photosynthetic material reduces moisture loss through transpiration and thus conserves moisture (Westoby 1980).

The loss of herbaceous biomass has been referred to as mortality (Deshmukh & Baig 1983; Donaldson 1967), senescence (Johnson & Parsons 1985) and decay (Starfield & Bleloch 1986). It has been shown to markedly affect production (Deshmukh 1986; Wiegert & Evans *in* Singh *et al.* 1975) and a number of authors (Deshmukh 1984; Deshmukh & Baig 1983; Grunow *et al.* 1980; Rutherford 1980; Williamson 1976) have noted that primary production cannot be estimated from harvest data alone due to senescence and resultant loss of biomass. Scholes (1984) showed that mortality was

decreased by soil moisture and grazing.

McNaughton (1985) recorded rapid rates of change in green biomass from +20 $g.m^{-2}.d^{-1}$ to -20 $g.m^{-2}.d^{-1}$ in the Serengeti over short periods (1 week). Underestimates of net annual aerial production may be as high as 120 per cent (Deshmukh 1986) and 490 per cent (Wiegert & Evans *in* Sing *et al.* 1975).

In spite of large losses in biomass there was no accumulation of litter within the plots. Montana *et al.* (1988) found that under arid conditions surface litter was lost through weathering and physical fragmentation.

It was evident that the vegetation system was water and temperature limited. Growth was reduced at temperature extremes and when plants were moisture stressed. When both temperature and moisture conditions were ideal growth took place rapidly. This is characteristic of arid adapted species that exploit favourable conditions when they occur (Westoby 1980).

Growth in early summer (Nov. Dec) was greater than in autumn even though considerably less moisture was available. This slowing in growth is attributed primarily to phenophase where vegetative growth is rapid in spring but slowed in autumn when winter reserves are being assimilated (Sauer 1978) but may also be due to biomass accumulation.

McNaughton (1985) also noted that grassland productivity was more sensitive to rainfall early in the wet season than later in season. Dye (1983) demonstrated that some grass species had a

quiescent period of growth mid-season even when moisture was not limiting.

Lack of growth may have been as a result insufficient ground moisture for growth to commence. Deshmukh (1984) found that the minimum requirement or "zero interception" for growth was 23 mm of rain. Similarly, Noy-Meir (1973) reported values of 25 to 75 mm; Le Houerou (1984) 50mm; McNaughton (1985) 25mm and Seely (1978b) 17-21 mm.

It was also apparent that growth was affected by the amount of residual vegetation present. This was evident in late autumn when the growth was far higher under continual irrigation (25 mm) than under 50 mm irrigation. This was thought to be a result of a higher proportion of green (photosynthetic) material with continuous irrigation which allowed the grass to respond rapidly when conditions of high moisture prevailed.

In hindsight the experimental design of the irrigation trial was poor. Within each block, a single square plot would have been preferable to the four separate sub-plots in each replicate. In spite of the sites having been selected for their apparent homogeneity, biomass per unit area varied over a short distance and it was difficult to compare variation between separate plots. Within each plot five separate samples of 1 x 1 m rather than a 5 x 1 m sample would have allowed a more meaningful comparison of variance within each sub-plot. The results were confounded by the exceptionally high rains at the start and the end of the trial and below average rain in mid-summer. This tended to mask the effects of irrigation.

Hurlbert (1984) demonstrated that supposed replicates were not necessarily statistically independent and that pseudoreplication occurred in many experiments where ANOVA was used for testing treatment effects.

In the irrigation trial a randomised block treatment was used which was an acceptable approach for giving spatial interspersion. However, some segregation did occur within each treatment. A further disadvantage of the method was that, according to Hurlbert (1984), as much as a six-fold replication was necessary before significant differences could be demonstrated by some statistical tests.

In summary, the data required for input into the vegetation model have been refined. The production was higher than was anticipated for the system but so was the rate of vegetation loss. The estimates of high growth in summer and low growth in winter were confirmed.

Contrary to what was expected growth was higher in autumn than in spring probably due to low spring temperatures. Residual vegetation was important but this was thought to be as a result of quality (greenness) rather than quantity. The effect of herbivory was small and this also corroborated what was found in the sensitivity analysis.

The response of vegetation (rapid-growth, rapid-loss) illustrated the episodic nature of the system and reaffirmed the suitability of a discrete model with a seasonal time step.

CHAPTER 6 : HERBIVORE DATA

6.1 Introduction

The purpose of this chapter was to refine the herbivore model through studying the population dynamics of the three herbivore species and to improve understanding of the vegetation-herbivore interactions on The Pan.

It is widely acknowledged that herbivore performance is a consequence of food availability (Crawley 1983).

It was reasoned that herbivore population and sex-age structure were appropriate indicators of vegetation state. The population dynamics of each species were investigated under varying rainfall regimes and the seasonal vegetation-herbivore interactions on The Pan analysed.

6.2 Methods

Population estimates were divided into three parts.

(i) Total counts which were estimates of the species population total on the entire reserve.

(ii) Sex-age counts which were determined from sampling the total population.

(iii) Pan counts which were monthly estimates of the number of each species in the study area.

6.2.1 Total Counts

Total counts were derived from aerial censuses. These were carried out annually in February or March from a helicopter. The reason for this time of year was that the probability was high of having a green background against which the animals, particularly springbok, were more easily seen. Aerial counts were carried out in 1982 and yearly from 1984 to 1988.

The helicopter contained four observers, two in front (including the pilot) and two in the back. The front observer recorded all observations made by both himself and the pilot. The back observers recorded independently on their side only and their totals were added together. This resulted in a total for the front observers and a second total for the back observers. The highest count was used. All the censuses were carried out with the same observers sitting in the same positions in the helicopter.

The entire reserve was divided into five separate blocks approximating the major vegetation types. Within each block, flight paths 800 m apart, were marked and numbered. The helicopter flew at an altitude of 70 m above ground level and at a ground speed of 110 $km.h^{-1}$. All animals, 400 m either side of the flight path were recorded either into a tape recorder or directly onto data sheets. The 35000 ha game area was counted in

a single day. Counting did not take place during the middle of the day from 11h00 to 15h00 when animals were inclined to be resting.

During the study period a number of animals were cropped from time to time. This took place during the winter months (May to July). Cropping was either by live capture or by hunting.

6.2.2 Sex-age counts

To determine the sex age structure of the population sex-age counts were carried out in January and February of each year. At that time juveniles were approximately three to four months old and sub-adults 15-16 months old having been born in September (springbok), November (blesbok) and December (black wildebeest).

In the case of black wildebeest and blesbok as many herds as possible were sampled post-calving. Where possible, three age classes (adult, sub-adult and juvenile) and the sex were determined using body size, colour and horn shape (Section 2.6.2).

Springbok were difficult to sex and age due to the large flight distance of this species on Rooipoort. However, irregular sex-age counts were done. The population structure of springbok on other Kimberley properties was determined and these data were used for the Rooipoort population. Due to the rapid growth of springbok only two age classes (adult and juvenile) were distinguished.

6.2.3 Pan counts

A total of forty eight counts of herbivores on The Pan were carried out from a vehicle periodically for different months of the year between August 1982 and July 1988. Counts were conducted only when animals were active during the late afternoon on days on which there had been no prior disturbance on The Pan. The entire circumference of The Pan was travelled. Springbok tended to take flight on sight of the vehicle and were counted immediately. Blesbok and black wildebeest were sedentary and distinct herds could be identified and counted at leisure. A 20-power telescope mounted on the door of the vehicle was used for determining sex and age. Data were recorded into a tape recorder and later transcribed.

The herbivore totals were converted to a common biomass using animal unit equivalents (Appendix 1) and correlations sought between herbivore biomass, rainfall and between the different herbivore species. The counts were not done at the same time each month. In order to get a better appreciation of the correlation, the rainfall for each of the four weeks preceding the count was correlated separately and in combination. This was repeated with the log values of weekly rainfall.

A time series analysis (Groebner & Shannon 1989) of herbivore numbers on The Pan was carried out. The long-term trends, seasonal, cyclical and random components were examined.

The Pan counts were carried out periodically and the time series analysis approach of Cryer (1986), which is better suited to the

analysis of discontinuous data, was used to test significance.

6.3 Results

6.3.1 Total counts

Total annual counts and corresponding removals for black wildebeest (Bk), blesbok (Bb) and springbok (Sb) from aerial censuses are summarised in Table 6.1

Table 6.1 Summary of aerial counts and removals, Rooipoort 1982-1988.

Year	Total count			Removals		
	Bk	Bb	Sb	Bk	Bb	Sb
1982	263	194	2207	9	12	30
1983	no count			42	37	390
1984	237	188	1207	84	20	75
1985	188	153	989	68	6	486
1986	174	235	1001	14	43	42
1987	228	120	1185	76	5	73
1988	205	171	1112	5	8	79

Population totals remained relatively constant with the exception of high counts for black wildebeest and springbok in 1982 and blesbok in 1986. Removals varied with species and year in accordance with the objectives of management at the time.

The isolation of population trend in the time series analysis showed that, over the study period, the springbok and blesbok populations increased marginally and that of the black wildebeest declined (Fig. 6.1).

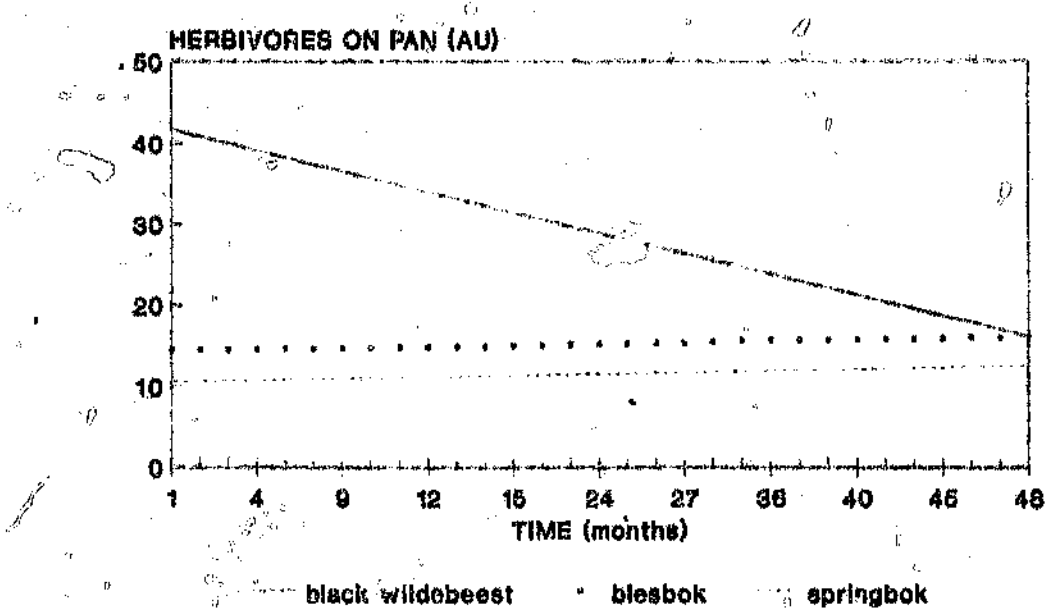


Figure 6.1 Time series analysis isolating population trend.

It was found that black wildebeest had a slope co-efficient of -0.3863 were seasonal ($p < 0.01$) with a significant trend ($t=-2.9067$; $df=30$; $p < 0.01$). Blesbok had a slope co-efficient of 0.1328 were seasonal ($p < 0.01$) with no trend. Springbok had a slope co-efficient of 0.0529 were not seasonal and have no trend.

6.3.2 Sex-age counts

The results of sex-age counts for each species are summarised in Tables 6.2, 6.3 and 6.4.

Table 6.2 Summary of black wildebeest sex-age counts Rooipoort.

Year	Adult M	Adult F	Sub-adult	Juv	Total	F/M	% sub-ad of tot	% juv of F	% juv of tot
1985	23	50	17	31	121	2.2	14.0	62.0	25.6
1986	19	50	16	23	108	2.6	14.8	46.0	21.3
1987	19	83	40	37	179	4.4	22.3	44.6	20.7
1988	25	54	16	24	119	2.2	13.4	44.4	20.2
Total	86	237	89	115	527				
Mean						2.8	16.9	48.5	21.8

Nineteen eighty five to 1988 were dry years thus one would expect similar birth rates and survival over this period. It seemed probable that breeding herds were over-sampled in 1987, hence the high proportion of adult females and sub-adults in the count. Assuming that sub-adults normally made up about 14 per cent of the total and if the 1987 adult females was reduced proportionally, an adult sex ratio of 1:2.7 was obtained. This was in line with other years.

Table 6.3 Summary of blesbok sex-age counts Rooipoort.

Year	Adult M	Adult F	Sub-adult	Juv	Total	F/M	% sub-ad of tot	% juv of F	% juv of tot
1985		83	12	29	124		9.7		23.4
1986		47	16	23	90		17.8		25.6
1987	26	49	22	28	125	1.9	17.6	57.1	22.4
1988	28	81	29	57	195	2.9	14.9	70.3	29.2
Total			79	137	534				
Mean						2.4	14.8	65.4	25.7

A relatively wet summer was experienced in 1988 which resulted in improved grazing conditions. The availability of green grass in early summer is believed to increase blesbok lamb survival and this would have accounted for the high percentage of lambs in that year.

Table 6.4 Summary of springbok sex-age counts Susanna.

Year	Adult M	Adult F	Juv	Total	F/M	% juv of F	% juv of tot
1985	99	286	204	589	2.9	71.7	34.6
1986	160	353	262	775	2.2	74.2	33.8
1987	52	157	95	304	3.0	60.5	31.3
1988	108	185	146	439	1.7	78.9	33.3
Total	419	981	707	2107			
Mean					2.3	72.1	33.6

In 1985 and 1987 sample counts of springbok on Rooipoort gave a lamb percentage of 31.2 and 27.8 per cent of total. On other properties lambs constituted 47.3 per cent of the total springbok population after the good summer rains of 1988. This lambing percentage was 1.33 times the number of ewes which suggested that either a proportion of the sub-adult segment lambed or a number of ewes lambed twice.

6.3.3 Pan counts

Average seasonal biomass for each species (Table 6.5) showed that black wildebeest biomass remained relatively stable throughout the year with a marginal decline in winter. Blesbok biomass in summer was roughly four times that in winter whereas that of springbok was approximately two times that of winter biomass.

Table 6.5 Mean seasonal biomass on Pan 1983 to 1988.

	Biomass (AU)					
	spring	summer	autumn	winter	mean	CL
black wildebeest	26.2	28.4	29.2	20.6	26.1	±3.4
blesbok	9.4	25.1	18.5	6.5	19.4	±9.9
springbok	14.4	15.7	10.9	8.1	17.0	±8.9

A correlation analysis of herbivores and rainfall (Table 6.6) showed that there was a negative correlation for all three species and the rainfall during the month. However, significant correlations were obtained for both blesbok and springbok, but not for black wildebeest, for rainfall in the month preceding the count.

Table 6.6 Correlation of monthly rainfall (mm) with herbivores (AU) on Pan.

Rainfall		Bk	Bb	Sb	Tot AU
Month	co-eff	-.35	-.16	-.23	-.35
	signif	.0244	.3139	.1440	.0256
Previous month	co-eff	-.20	.40	.47	.20
	signif	.2202	.0097	.0020	.1987
Log prev month	co-eff	-.03	.54	.37	.33
	signif	.8484	.0003	.0170	.0367

No correlations existed for herbivore numbers and rain in either the first or fourth weeks preceding the count (Table 6.7). Both blesbok and springbok showed highly significant correlations with rainfall two weeks prior to the count. Blesbok, and to a lesser degree springbok, showed correlations with rainfall three weeks preceding the count.

Table 6.7 Correlation of log weekly rainfall (mm) with herbivore biomass (AU) on Pan.

Rainfall		Bk	Bb	Sb	Tot AU
Week -1	co-eff	-.23	.17	-.04	-.08
	signif	.1451	.3037	.8212	.6378
Week -2	co-eff	-.01	.48	.66	.44
	signif	.9623	.0015	.0000	.0041
Week -3	co-eff	-.05	.48	.28	.29
	signif	.7701	.0017	.0765	.0719
Week -4	co-eff	-.12	.13	.05	-.00
	signif	.4563	.4682	.7430	.9992

Considering the weeks in combination (Table 6.8) a similar result was obtained in that black wildebeest were not correlated with any combination. Blesbok had significant values for all combinations with the highest correlation being rain two and three weeks prior to the count. Similarly springbok numbers were significantly correlated with all combinations except weeks three and four. Springbok showed the highest correlation two and three weeks after rain.

Table 6.8 Correlation of log accumulative weekly (preceding) rainfall (mm) with herbivore biomass (AU) on Pan.

Rainfall		Bk	Bb	Sb	Tot AU
Week 1-2	co-eff	-.11	.41	.47	.28
	signif	.4949	.0078	.0023	.0765
Week 1-3	co-eff	-.07	.56	.41	.38
	signif	.6764	.0002	.0082	.0248
Weeks 1-4	co-eff	-.05	.49	.37	.32
	signif	.7414	.0014	.0199	.0474
Weeks 2-3	co-eff	-.01	.59	.56	.46
	signif	.9361	.0001	.0002	.0032
Weeks 2-4	co-eff	.00	.49	.48	.39
	signif	.9977	.0013	.0018	.0133
Weeks 3-4	co-eff	-.06	.43	.22	.24
	signif	.7286	.0056	.1748	.1411

Correlations were also carried out between the biomass of each species (Table 6.9). Blesbok and springbok numbers were significantly and positively correlated.

Table 6.9 Correlation between biomass (AU) for each species on The Pan.

		Bb	Sb
Bk	co-eff	.25	.04
	signif	.1142	.8248
Bb	co-eff		.54
	signif		.0003

Isolation of the seasonal trend (Fig. 6.2 & 6.3) showed that generally numbers for all three species were high in summer and low in winter. Black wildebeest were most common on The Pan in autumn, blesbok in summer and springbok in spring. Wildebeest numbers fluctuated the least and blesbok numbers the most.

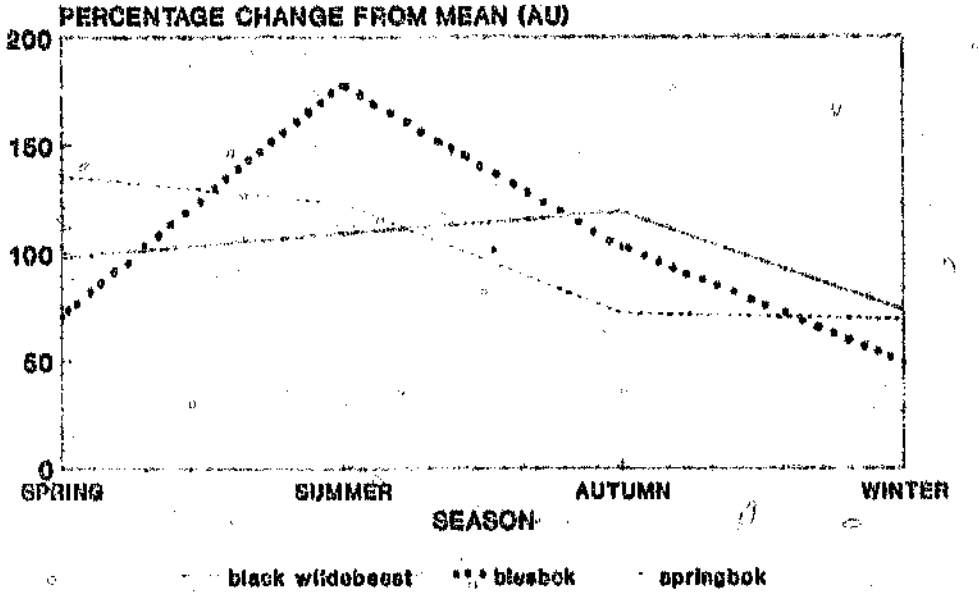


Figure 6.2 Time series analysis showing seasonal trend by season.

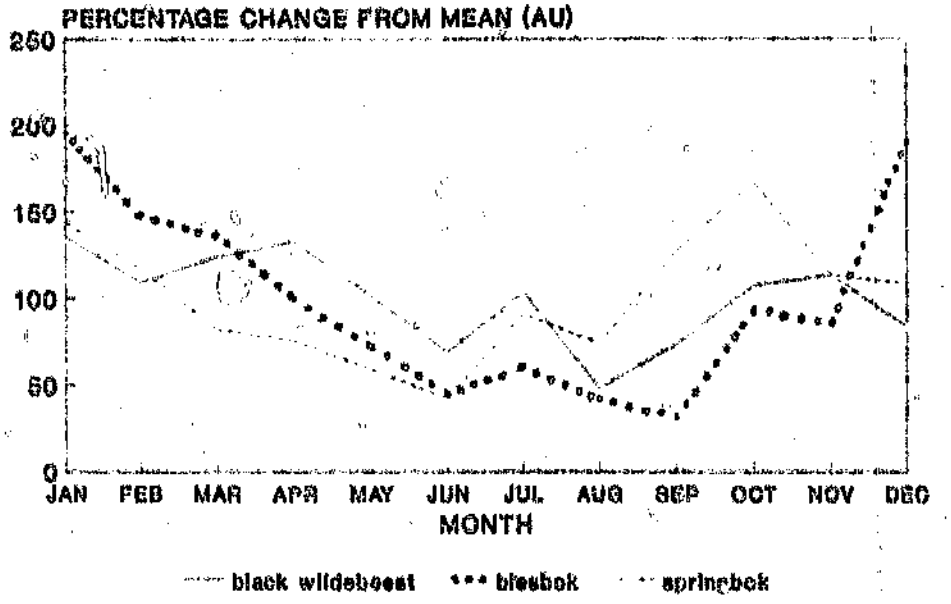


Figure 6.3 Time series analysis showing seasonal trend by month.

Isolation of the cyclical component (Fig.6.4) showed a peak in August for all three species.

6.4 Discussion

The black wildebeest and blesbok were invariably found in open, treeless habitats on Rooipoort and were considered highly visible from the air. The counts for those two species were believed to be consistently more accurate than those for other species. Conversely, springbok were widely dispersed in all vegetation types and notoriously difficult from the air. The figures for springbok were almost certainly under-estimates of the true population. This is a common error of aerial censuses (Melton 1978).

No measure of error in sexing and ageing was determined but it was thought to be small in the case of black wildebeest. Error was more likely to arise through non-random sampling of the various herds than through incorrect sex identification.

It is widely acknowledged that under high rainfall the plane of nutrition improves and this results in higher lambing percentages through increased fertility, higher conception, shortened lambing intervals and increased survival of lambs (Crawley 1983; Moen 1973; Sinclair 1977).

The low calving success of black wildebeest in this study was attributed to the poor grazing availability under low rainfall conditions (von Richter 1971a).

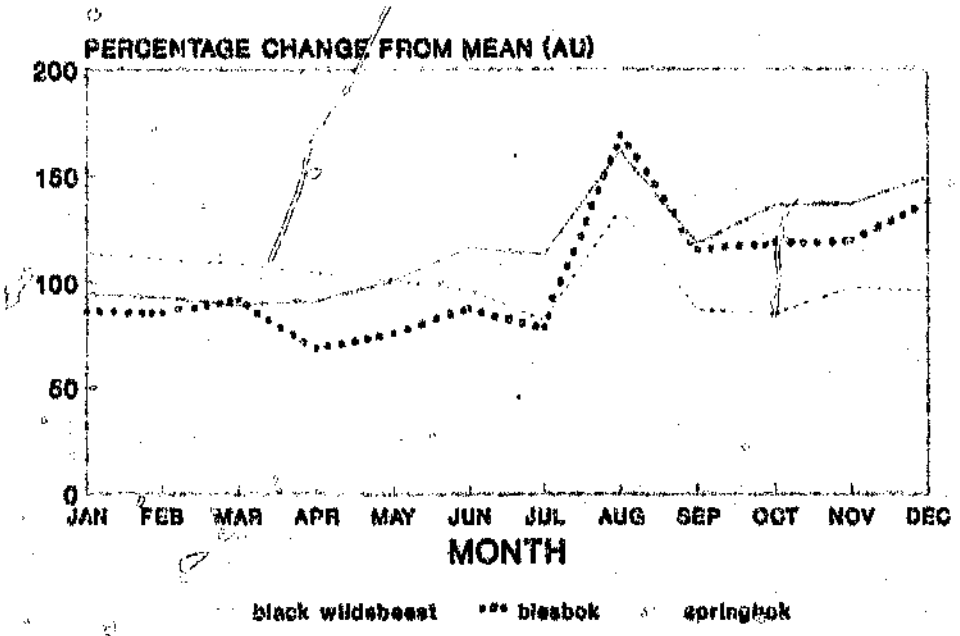


Figure 6.4 Time series analysis isolation of cyclical component.

Predation on springbok lambs on Rooipoort was thought to be higher than on other properties and, as a result of decreased survival, a lower recruitment rate was expected. Furthermore, the Rooipoort springbok population was not managed and only a small proportion (4% to 7%) was removed annually during the past three years which resulted in a higher proportion of males in the population. This, in turn, would further reduce the percentage of lambs in the population.

The correlations and time series analyses showed that black wildebeest were resident on The Pan and unlike the other two species did not move on and off The Pan in response to the amount of green grass. It was evident that green grass was really only available in the second and third weeks after rain. The high correlation of springbok in the second week confirmed that this species was able to take advantage of the short green grass ahead of the blesbok. By the third week bleshok were still able to meet their grazing requirements probably as the species was better able to cope with the more mature, drier grass. By the fourth week, the grass was either too dry or was too rank for both blesbok and springbok. Alternatively the green flush had been removed by grazing.

This would suggest that if interspecific competition for grazing resources existed, it was highest between blesbok and springbok and lowest between black wildebeest and the other two species.

There was no suggestion in this study that black wildebeest facilitated springbok grazing in the dry season. To the contrary

springbok biomass declined relative to that of black wildebeest during winter (Table 6.5). The absence of any correlation indicative of competition between wildebeest and springbok suggested that the hypothesis (Section 1.1) that the introduction of black wildebeest has resulted in the decline of springbok was questionable. It seemed more likely that blesbok and not black wildebeest were competing with springbok.

The accuracy of aerial counts varies considerably with observer experience, species and vegetation type (Caughley 1977) and there is a tendency to undercount many ungulate species (Melton 1978).

The population trend was more important than absolute numbers. It was assumed that the degree of error in these population estimates remained similar with the use of the same observers and presumably with consistent bias.

The calf to adult female percentage found for black wildebeest was low and compared with percentages for black wildebeest in marginal habitats (von Richter 1971b). Under ideal conditions percentages as high as 79.1 and 85.7 per cent have been recorded (von Richter 1971b).

The blesbok annual calf recruitment i.e. the calf crop expressed as a percentage of the pre-calf population, averaged 33,8 per cent (range 28.9% to 41.3%) which compared well with the average of 33 per cent found by Marchant (1987). The highest recruitment rate recorded by Marchant (1987) was 53.9 per which was comparable with values of 55.0 per cent and 52.1 per cent given

by Du Plessis (1972). Lambing percentages greater than 80 per cent have been recorded elsewhere (Marchant 1987).

It is known that under good conditions springbok ewes lamb at the age of one year and at six monthly intervals (Bigalke 1972; Skinner & van Zyl 1970).

Mills & Retief (1984a & 1984b) found springbok show a rapid response to rain and were found to be significantly correlated to rainfall of the previous month whereas blue wildebeest were not significantly correlated. They concluded the rapid response by springbok was their ability to crop sprouting vegetation ahead of other species.

McNaughton (1985) also found the gazelle population to be highly correlated ($r=0.986$, $p < 0.0001$) with primary productivity and that the gazelle population increased and decreased with increase and decrease in green biomass.

This concurs with the findings of van Zyl (1965) who found that blesbok and springbok both selected for green leaves in winter and there was greater overlap in preferred species by blesbok and springbok than blesbok and black wildebeest.

In the Serengeti, Maddock (1979) found that facilitation occurred between Thomson's gazelle and blue wildebeest. Gazelle preferred areas already grazed by wildebeest which exposed dicotyledonous plants favoured by the gazelles (McNaughton 1976). In the present study it was probable that the herbaceous biomass was too sparse to impair accessibility for the springbok.

Hansen et al. (1985) found a high diet similarity between wildebeest and topi (70 per cent), between wildebeest and Thomson's gazelle (70 per cent) and between topi and Thompson's gazelle (68 per cent) in the wet season. Contrary to what was predicted the overlap declined in the dry season. It seemed that facilitation occurred during the dry season but interspecific competition occurred in the wet season (Sinclair & Norton Griffiths 1982). de Boer & Prins (1990) found no evidence of facilitation or that one species benefited from the grazing of another species earlier in the succession.

It can be concluded that the African ungulate community is shaped by a complex interaction of inter- and intraspecific competition, facilitation, predation and disease (Dublin et al. 1990; Sinclair 1985; Sinclair & Norton Griffiths 1982).

In summary, the parameters required for the herbivore model were investigated in a field and reasonable data on population numbers and structure were obtained. Further insight into herbivore-herbivore and vegetation-herbivore interactions was gained. There was now sufficient knowledge to replace crude inputs with real data and examine model output.

CHAPTER 7 : GRAZING SYSTEM DYANAMICS

7.1 Introduction

The purpose of this chapter was to explore the output of the vegetation-herbivore model.

This was accomplished by, where available, replacing crude values with real data obtained from field studies (Ch. 4 to Ch. 6). Where no such data existed the crude data were refined in the light of the field experience. This was achieved through a series of successive iterations until it was thought the outcome was plausible. These real and refined data were then applied to the model and the consequences examined.

It was necessary to evolve a reasonably competent and realistic model with which to develop a management strategy to meet the objective of the study.

7.2 Data

The data inputs to be refined were growth and senescence in the vegetation model and population size, birth and mortality rates for all three species in the herbivore model.

7.2.1 Methods

From the irrigation trials (Section 5.3.2) the applied irrigation and natural rainfall were combined to arrive at an estimate of

total precipitation (mm). The high rainfall total of 528 mm included some 200 mm that fell in the space of a few days and was not considered to be effective due to considerable run off. The rainfall total was therefore reduced to 400 mm which equated with the long term annual mean. There was no difference in herbaceous production between the 400 mm and 800 mm irrigation treatments and the lower figure was therefore used. Thus the total moisture amounted to 400 mm rainfall and 400 mm irrigation.

The maximum production was estimated to be 6500 $kg.ha^{-1}$. This was divided by the total moisture to give a production rate in $kg.ha^{-1}.mm^{-1}$. This production rate was then applied to mean seasonal precipitation figures for different rainfall regimes to derive a seasonal production total.

It was also found in irrigation trials that senescence resulted in a herbaceous biomass loss that increased rapidly under dry conditions. This loss was of the order of 50 per cent of the total biomass in the control and increased to over 80 per cent where biomass was high. The loss of herbage was ameliorated by rainfall and/or irrigation. A table was constructed of factors for vegetation loss (senescence) varied with season and rainfall regime. The greatest rate of loss was when temperatures were high (summer) and when moisture was low (winter).

The starting value for each herbivore species was the mean of the annual total for the past five years for that species. This was determined from the aerial census data.

From sex age counts (Section 6.3.1) the percentage juveniles in the population was known. This percentage increased, due to increased survival and reduced mortality, under favourable (wet) climatic conditions. From the percentage juveniles the recruitment rate r to the population was calculated by

$$r = 1 + [j/(P - j)]$$

where r is the recruitment rate, j the number of juveniles and P the population size.

The ability of each species to meet its consumption requirements depends on the vegetation biomass (Crawley 1983). There exists a grazing threshold which is defined as the vegetation biomass below which (= minimum grazing threshold) and above which (= maximum grazing threshold) a herbivore is unable to feed. At a point intermediate between minimum and maximum lies an optimum vegetation biomass at which the herbivore is able to meet all its intake requirements.

The vegetation biomass was used to derive minimum and maximum grazing thresholds and thus, the functional response f(V) (Appendix 2) of each species under variable rainfall regimes. The f(V) value was used to derive population f(P), birth f(w) and mortality, f(m) functional response values for each species (Appendix 2).

7.2.2 Results

The average production rate was found to be 8.1 $kg.ha^{-1}.mm^{-1}$ and the derived seasonal figures for different rainfall regimes are given in Table 7.1.

Table 7.1 Derived seasonal and annual production ($kg.ha^{-1}$) for varying rainfall on The Pan.

Rainfall regime	Season spring	summer	autumn	winter	Annual total
wet	720	1680	1160	240	3800
medium	600	1360	936	200	3096
dry	480	1040	720	160	2400

Given that senescence was ameliorated by moisture the following decay rates were used (Table 7.2).

Table 7.2 Assumed seasonal decay rates for herbaceous vegetation on The Pan expressed as a fraction of the vegetation remaining.

Rainfall regime	factor	Season spring 0.70	summer 0.65	autumn 0.75	winter 0.55
wet	0.9	0.630	0.585	0.675	0.495
medium	0.8	0.560	0.520	0.600	0.440
dry	0.7	0.490	0.455	0.525	0.385

Vegetation loss was highest in winter (low moisture, low temperatures) followed by summer (high temperatures, high moisture) and spring (low temperatures, medium moisture) and autumn (mild temperatures, high moisture). The decay rates varied from a low of 32.5 per cent (100-67.5) in a wet autumn to 61.5 per cent (100-38.5) in a dry winter.

The starting population totals for each species used were 1100 springbok, 170 blesbok and 200 wildebeest. The percentage juveniles (actual) in the population and the recruitment rates (calculated) for each species are given in Table 7.3.

Table 7.3 Percentage juveniles and recruitment rates for each species under different rainfall regimes.

	Percentage juveniles			Recruitment rate		
	dry	medium	wet	dry	medium	wet
black wildebeest	21	24	29	1.27	1.32	1.39
blesbok	24	27	30	1.32	1.37	1.43
springbok	30	35	40	1.43	1.54	1.67

Birth of juveniles for all three species was synchronised and seasonal. Springbok lambing had two seasonal peaks, one in spring and another in autumn. For the purpose of the model 75 per cent of lambs were born in spring and 25 per cent in autumn. Blesbok gave birth in November (spring) and black wildebeest in December (summer).

The minimum and maximum grazing thresholds for all three species were estimated (Table 7.4) based on the feeding type of animal (Mentis & Duke 1976), mouth size (Illius & Gordon 1987) and body size (van Soest 1982).

Table 7.4 Minimum, optimum and maximum vegetation biomass (kg.ha^{-1}) used to model functional response.

	Biomass (kg.ha^{-1})		
	minimum	optimum	maximum
black wildebeest	400	2000	20000
blesbok	300	1000	10000
springbok	200	800	6000

The ability of a herbivore to harvest vegetation is related to mouth (bite) size (Illius & Gordon 1987).

It was reasoned that springbok were able to exploit shorter vegetation than blesbok which in turn exploited shorter vegetation than wildebeest. Therefore under dry conditions springbok had a higher f(V) than blesbok and wildebeest. Conversely wildebeest were better able than both blesbok and springbok to utilise the tall vegetation.

It is known that springbok avoid tall grasslands preferring short panveld vegetation (Smithers 1983). It followed that under high rainfall their f(V) value would not necessarily increase. Therefore, under high rainfall wildebeest had a high f(V) value and springbok a low value. Blesbok were intermediate.

Derived vegetation functional response values are given in Table 7.5.

Table 7.5 Species functional response f(V) for different rainfall regimes.

Rainfall regime	Species		
	springbok	blesbok	black wildebeest
wet	0.4	0.3	0.25
medium	0.6	0.6	0.5
dry	0.6	0.8	0.1

Springbok were the most selective feeders and utilised The Pan at a higher f(V) value (closer to 1) than either blesbok or black wildebeest. For the same reason springbok populations were high on The Pan only when the species had a high f(V) value.

The species specific f(V) values were used to establish movement onto and off The Pan. This was known as the 'population functional response' (Table 7.6) and determined that proportion of the total population that was feeding on The Pan.

Table 7.6 Minimum [f(P)=0] and maximum [f(P)=1] f(V) values used to determine population functional response.

Species	f(V) value minimum	maximum
black wildebeest	0.0	0.25
blesbok	0.1	0.50
springbok	0.2	0.75

The breeding success of each species was also determined by the f(V) value. Black wildebeest were the least selective feeders and therefore met their nutritional requirements for breeding at a lower f(V) value than either blesbok or springbok. Similarly, they reached a maximum breeding rate (f(w) = 1) at a lower f(V) value than blesbok and springbok. Springbok were the most selective of the three species and started to breed and attained maximum at higher f(V) values. Blesbok were intermediate (Table 7.7).

Table 7.7 Minimum [f(w)=0] and maximum [f(w)=1] f(V) values used to determine birth functional response.

	f(V) value minimum	maximum
black wildebeest	0.15	0.50
blesbok	0.20	0.60
springbok	0.30	0.75

For the purpose of the model it was assumed that the birthrate off The Pan was 75 per cent that on The Pan.

Mortality increased linearly when f(V) values were less than 0.4, 0.3 and 0.15 for springbok, blesbok and black wildebeest

respectively. The habitat off The Pan was marginal for all three species. Mortality for animals off The Pan was fixed at 25 per cent higher than that for animals occupying The Pan.

7.2.3 Discussion

The total production of 3800 kg.ha^{-1} under wet conditions was reasonable and similar to that obtained in the irrigation trial (section 5.3.2) and elsewhere (Rutherford 1978). The total annual production for dry conditions (2400 kg.ha^{-1}) generated by the model was higher than that obtained experimentally but was consistent for the amount of rainfall.

The percentage loss of herbaceous biomass due to senescence was comparable to figures obtained experimentally.

The functional response was a useful means for developing species specific population parameters. There was no way of establishing the real value of functional responses for the different species. The values derived rather reflected the difference between species and not absolute values. In spite of this inadequacy the benefit of species specific f(V) estimates were apparent in the model output and for this reason their use was justified.

The production rate of 8.1 kg.ha^{-1}.mm^{-1} derived in this study was similar to the values of 8.2 kg.ha^{-1}.mm^{-1} found by Stugnell & Pigott (1978) and 8 kg.ha^{-1}.mm^{-1} of Deshmukh (1984). Its use to calculate seasonal production figures was legitimate.

An assumption of the model was that conditions on The Pan were more favourable and preferred to those off The Pan. It was therefore logical that the birth rate for animals on The Pan was higher than for animals elsewhere.

Sex-age counts were carried out mainly on The Pan but also on other vegetation types. The data for recruitment rates were representative of the whole population and not just that on The Pan. Furthermore, The Pan population was not fixed and the incorporation a variable population into the model was difficult and the data were unreliable.

The population counts suggested that over the study period, during which dry conditions prevailed, significant mortality occurred in the blesbok population, which declined and in the springbok population which remained virtually static. High percentages of blesbok and springbok were removed in some years and this affected population numbers. However, in other years the numbers of animals cropped were insignificant. There were no reliable mortality figures for any of the species and this was a shortcoming.

The recruitment rates were considered representative of the species under the various rainfall regimes. Marchant (1987) recorded growth rates in blesbok of 45 per cent under good conditions and von Richter (1971b) recorded a black wildebeest population growth rate of 36 per cent. Sinclair (1979) noted that, in the absence of predation, calves comprised 30 per cent of total population in blue wildebeest and this compared well with the 28 per cent used in this study.

7.3 Model structure

The model was divided into two sub-models, a vegetation sub-model and a herbivore sub-model. The climatic factors of rainfall and season were applied to various parameters in both sub-models. The herbivore sub-model was further divided into three different models, one for each species, but this was not shown in the algorithm (Fig. 7.1). The loop was seasonal and the vegetation biomass and herbivore numbers at the end of the season were the starting values for the following season.

A spread sheet (Lotus 1985) was used for the model. The program was found to be particularly suited to sequential steps and for seasonal looping. Furthermore, it was possible to build parameter tables for both season and rainfall which considerably simplified the mathematics. The detail of the model is given in Appendix 3.

7.4 Model output

The model output was explored in a number of ways

(i) vegetation output under varying rainfall regimes in the absence of herbivores

(ii) vegetation output under varying rainfall under grazing

(iii) each herbivore species in the absence of the other two species under varying rainfall

(iv) all three herbivores together under varying rainfall, and

(v) a comparison of modeled and real populations.

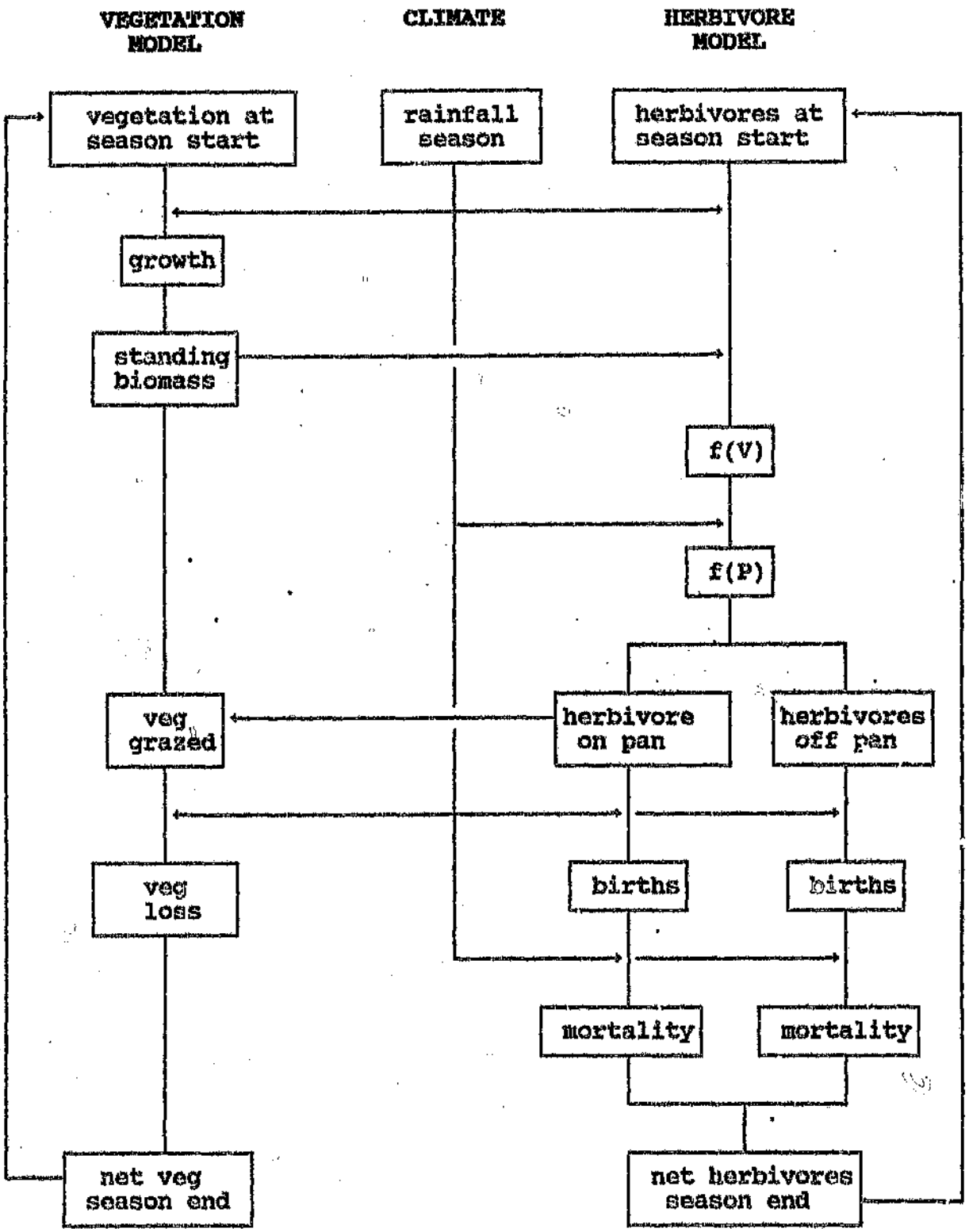


Figure 7.1 Algorithm of plant-herbivore model.

7.4.1 Vegetation output

In the absence of herbivores vegetation standing biomass (residual vegetation plus net growth) averaged 2200 $kg.ha^{-1}$ under high rainfall, 1200 $kg.ha^{-1}$ under medium rainfall and 800 $kg.ha^{-1}$ under low rainfall (Fig. 7.2).

The high moisture figure compared well with the 2450 $kg.ha^{-1}$ obtained in the irrigation trial and the other outputs were also plausible. There was a large oscillation due to the loss of biomass (senescence) in winter when moisture conditions were low. This was also evidenced in the field.

The vegetation biomass stabilised at approximately 700 $kg.ha^{-1}$ with grazing under all three rainfall regimes (Fig 7.3). This showed that the herbivores cropped all the 'grazable' biomass but were unable to remove all the vegetation due to the minimum grazing threshold. This was realistic.

7.4.2 Herbivore output

The number of each species on The Pan in the absence of other herbivores and cropping is given in Figs. 7.4 to 7.6.

The springbok population declined under dry conditions from the starting population of 1100 animals to around 300. Under medium rainfall the population was stable at approximately 1600 animals and under wet conditions the population increased to a level of some 3200.

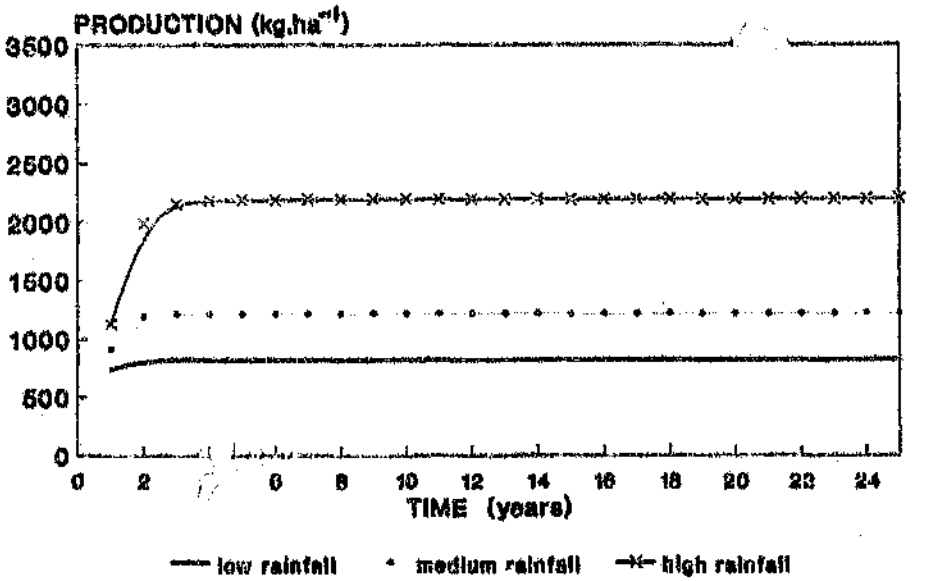


Figure 7.2 Vegetation biomass ($kg.ha^{-1}$) without grazing.

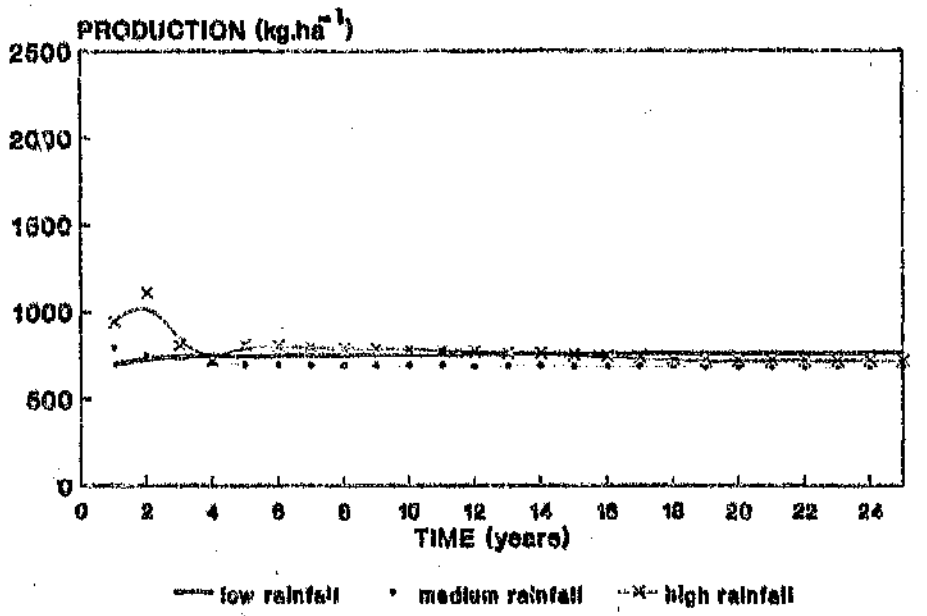


Figure 7.3 Vegetation biomass ($kg.ha^{-1}$) with grazing.

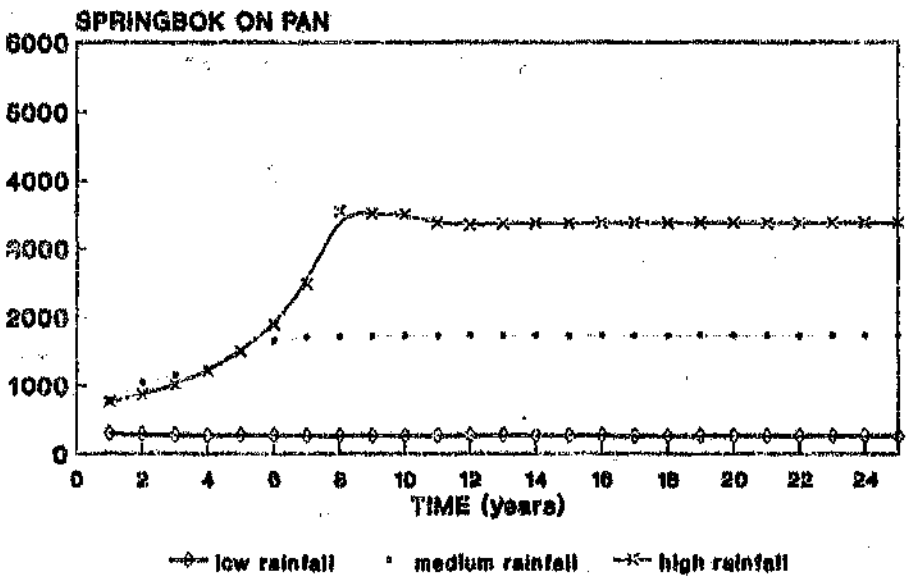


Figure 7.4 Springbok populations under different rainfall regimes.

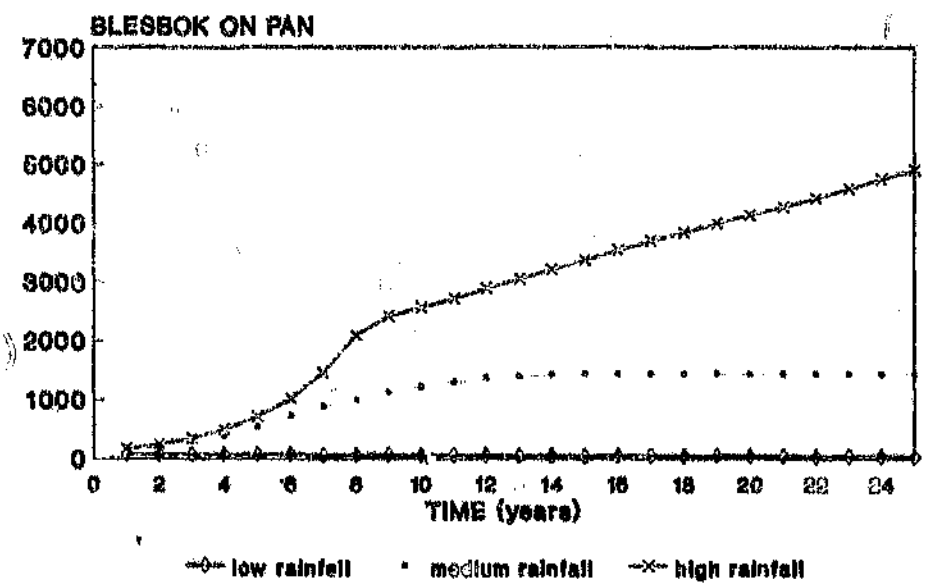


Figure 7.5 Blesbok populations under different rainfall regimes.

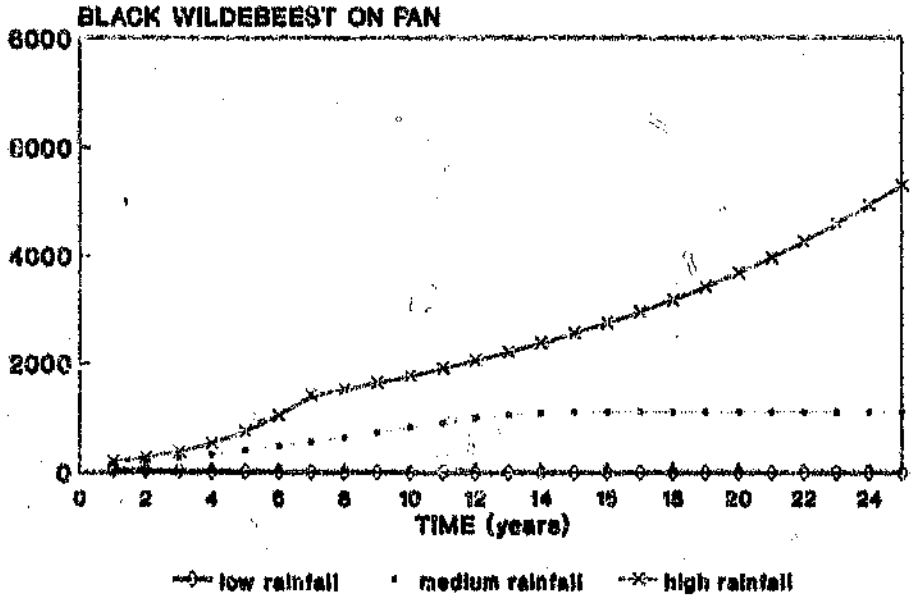


Figure 7.6 Black wildebeest populations under different rainfall regimes.

Blesbok populations were virtually absent from The Pan under continual dry conditions, stable at about 1400 under medium rainfall after 10 years and were still increasing after 25 years under high rainfall. There were large oscillations at high population levels due to animals removing all the grazable biomass and then vacating The Pan.

Black wildebeest declined to zero under dry conditions. Under medium rainfall the population increased for the first 13 years and thereafter stabilised at 1000. Under wet conditions the population continued to increase throughout the 25 year period.

These outcomes reflected the ability of springbok to crop short vegetation and hence the species was able to survive arid conditions. All three species reached equilibrium under medium rainfall which suggests the ecological carrying capacity was reached. Had the model been operated for a longer period a stable herbivore population level would ultimately also have been attained under wet conditions.

A comparison of herbivore numbers on The Pan under low, medium high and randomly varying rainfall is given in Figs. 7.7 to 7.10.

Under low rainfall species population levels were similar to those found by examining each species on its own. This suggested that there was little competition between the three species when vegetation biomass was low. Only springbok were able to crop the vegetation and hence were limited rather by rainfall than by either blesbok or black wildebeest.

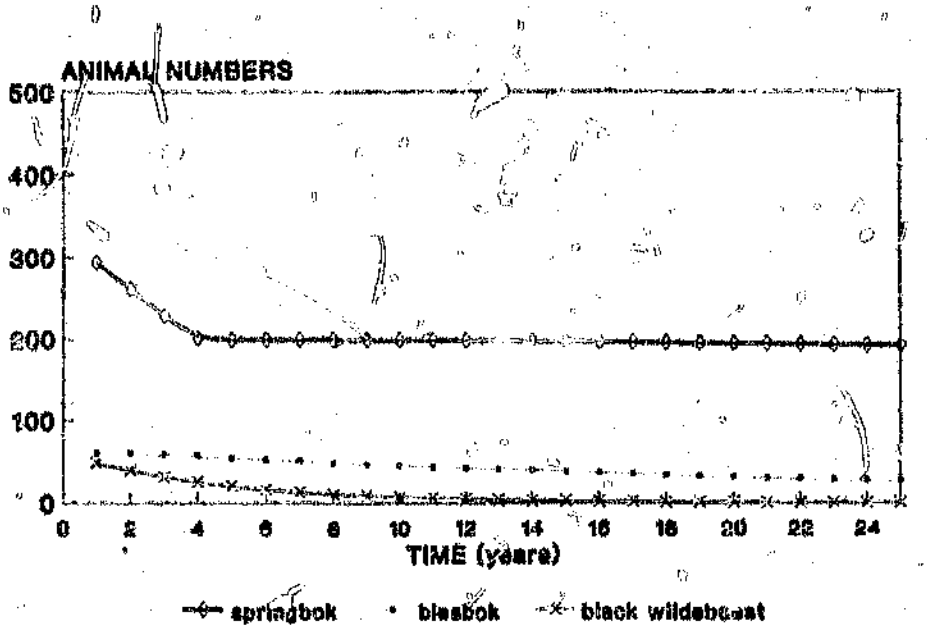


Figure 7.7 All three species on The Pan under low rainfall.

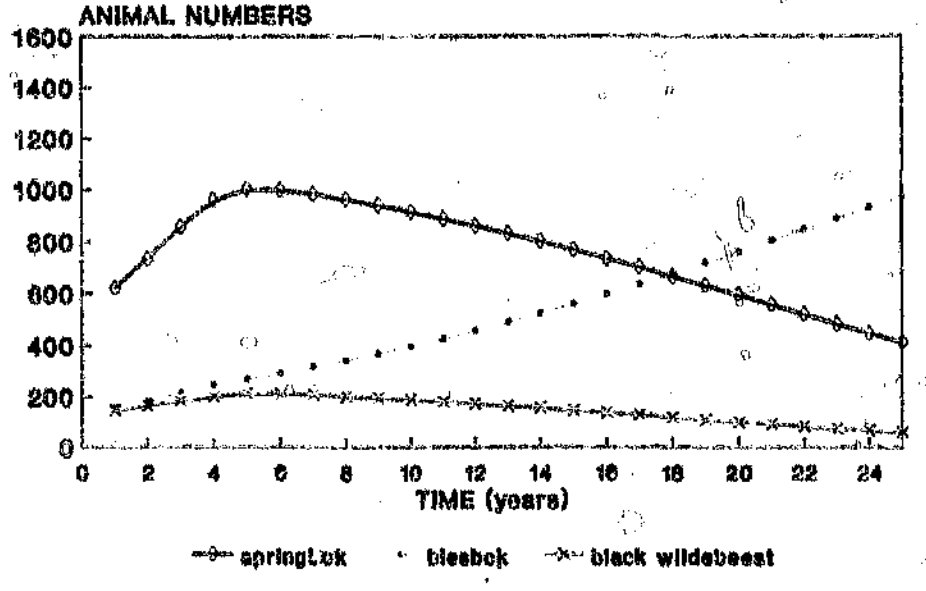


Figure 7.8 All three species on The Pan under medium rainfall.

For the comparison of modeled output with reality, actual seasonal rainfall from 1982 to 1990 was classified into wet, medium or dry according to Table 4.5. This actual rainfall sequence was then applied to the model and the population totals for 1982 (Table 6.1) were used as the herbivore data for autumn 1982. The actual number of each species removed (Table 6.1) each year were also included. The model was then run for the period 1982 to 1990 and the predicted output compared with the actual counts for each species.

The modeled springbok population (Fig. 7.14) compared well with actual counts over the period 1982 to 1990.

In the case of blesbok (Fig. 7.15) the comparison was also reasonable. The model confirmed the earlier suspicion that the 1986 blesbok count was an over estimate. Under conditions of high rainfall (1988 to 1990) actual counts were higher than modeled output. This suggested that, under these conditions, blesbok performed better than what the model predicted.

In contrast to springbok and blesbok output, the modeled black wildebeest population (Fig. 7.16) compared dismally with actual counts. The model predicted black wildebeest declined to zero in 1984, whereas the population, in reality, has remained above 200 animals.

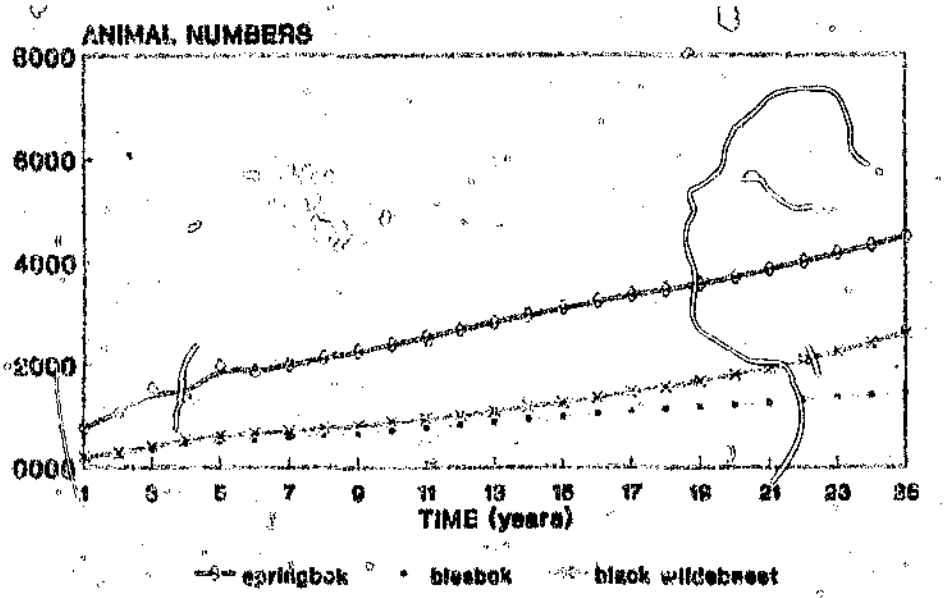


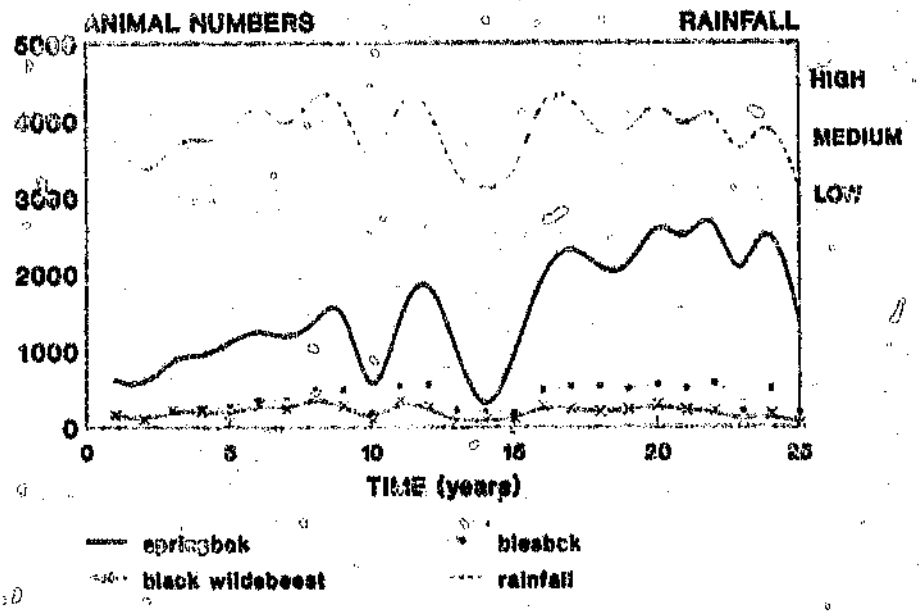
Figure 7.9 All three species on The Pan under high rainfall.

Under medium rainfall the extent of interspecific competition was evident in all three species. Population levels of all three species initially increased with improved grazing conditions. Springbok peaked at 1000 after about five years and then declined as competition from other species increased. Black wildebeest showed a similar trend. Blesbok were the most successful and increased through the 25 year period at the expense of the other two species.

Under high rainfall all three species increased rapidly for the first five years and thereafter gradually. The black wildebeest population exceeded that of the blesbok after about 10 years. The model output showed all three species benefited from the high rainfall conditions.

Under random rainfall populations varied in response to prevailing climatic conditions. It was interesting to note that different "random" rains produced widely different population levels depending on the run of "wet" or "dry" years. This is illustrated in Fig. 7.10a and Fig. 7.10b which were modeled with the same starting vegetation biomass and herbivore populations. However, herbivore population levels differed markedly after 25 years.

A comparison of springbok populations with and without competition (Figs. 7.11 to 7.13) showed that under dry conditions springbok numbers were marginally depressed through competition. Under medium rainfall springbok declined from 1700 to 400 animals and under wet conditions springbok increased in the presence blesbok and wildebeest.



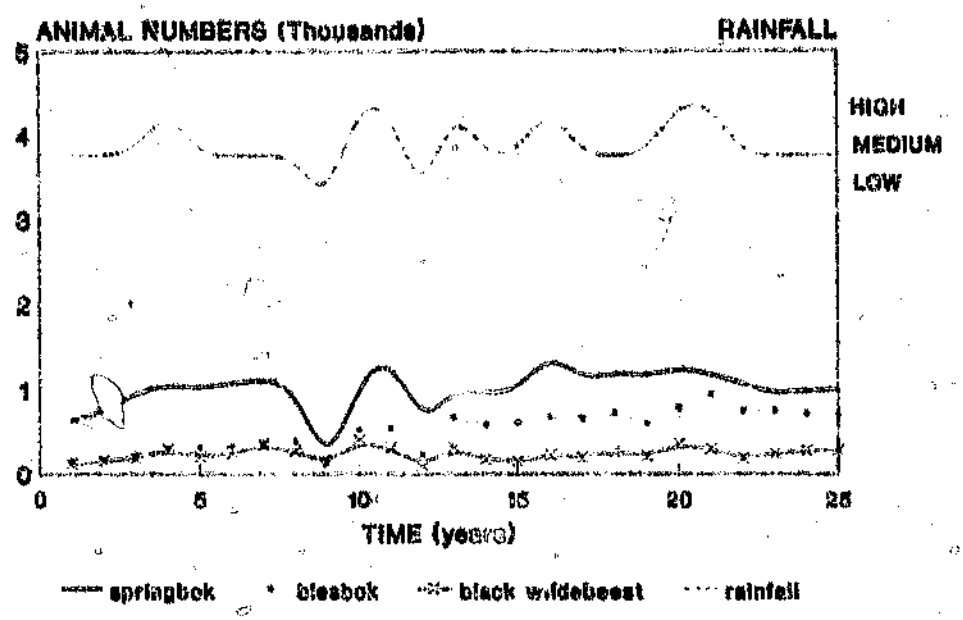


Figure 7.10a & Figure 7.10b All three species on The Pan under random rainfall showing different outcomes with the same model and starting herbivore populations.

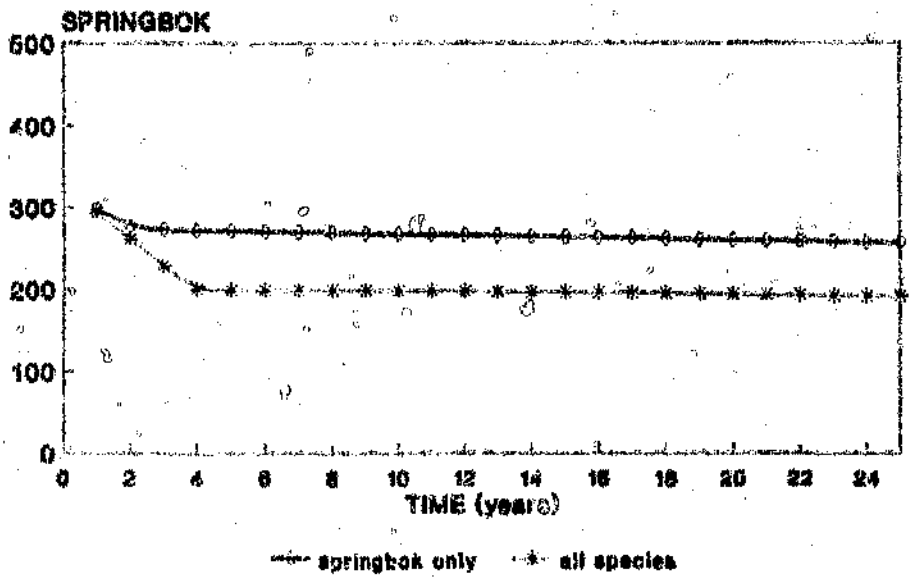


Figure 7.11 Springbok with and without competition under low rainfall.

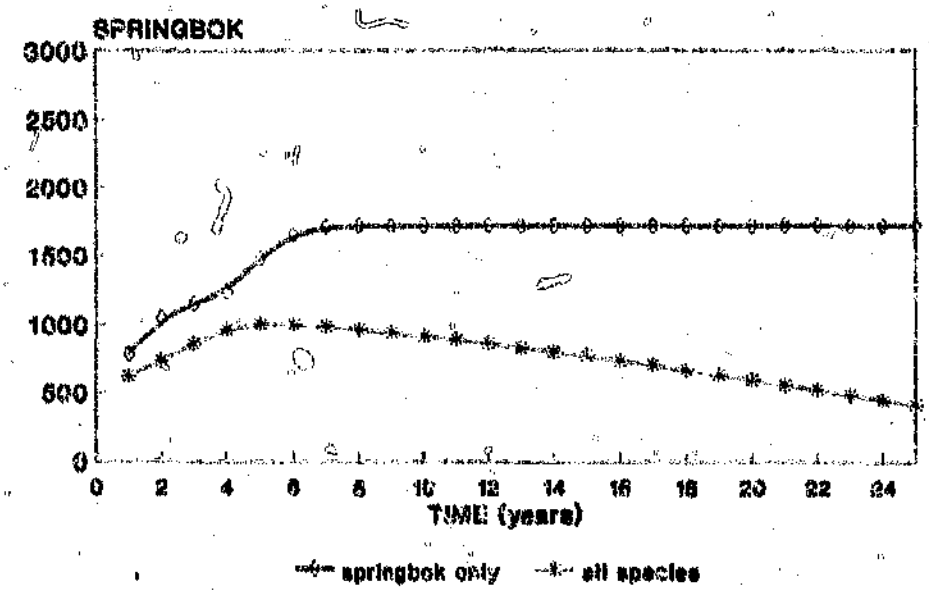


Figure 7.12 Springbok with and without competition under medium rainfall.

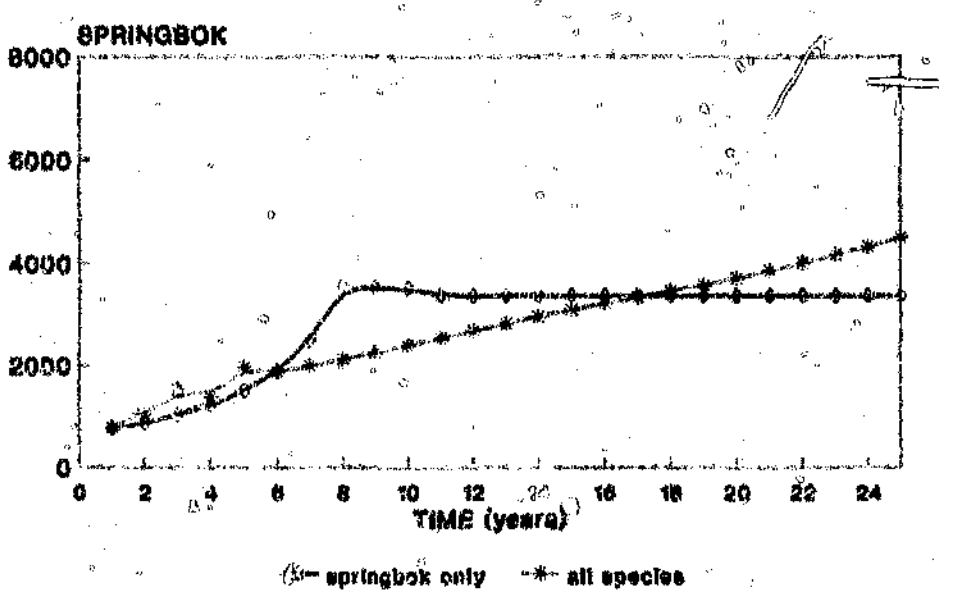


Figure 7.13 Springbok with and without competition under high rainfall.

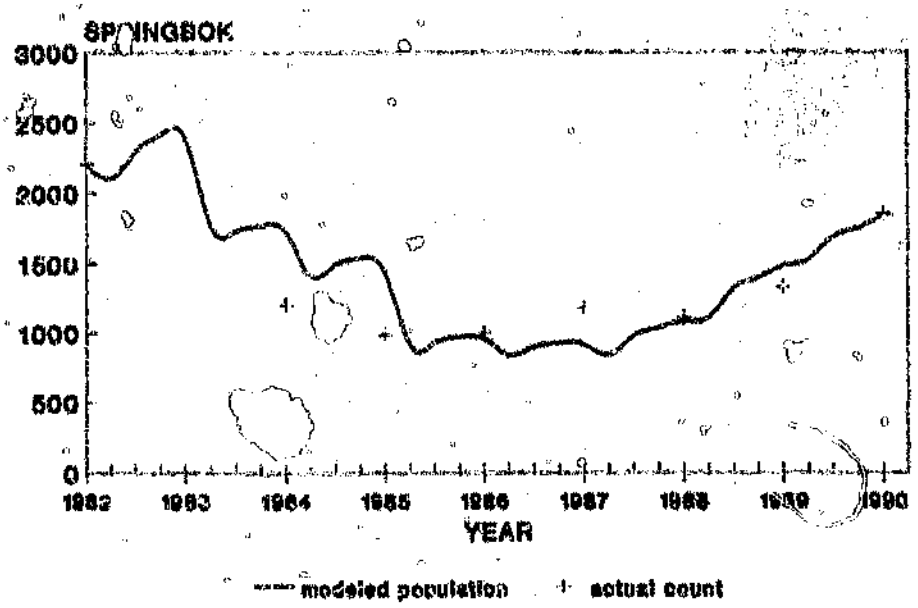


Figure 7.14 Comparison of modeled springbok population with actual counts.

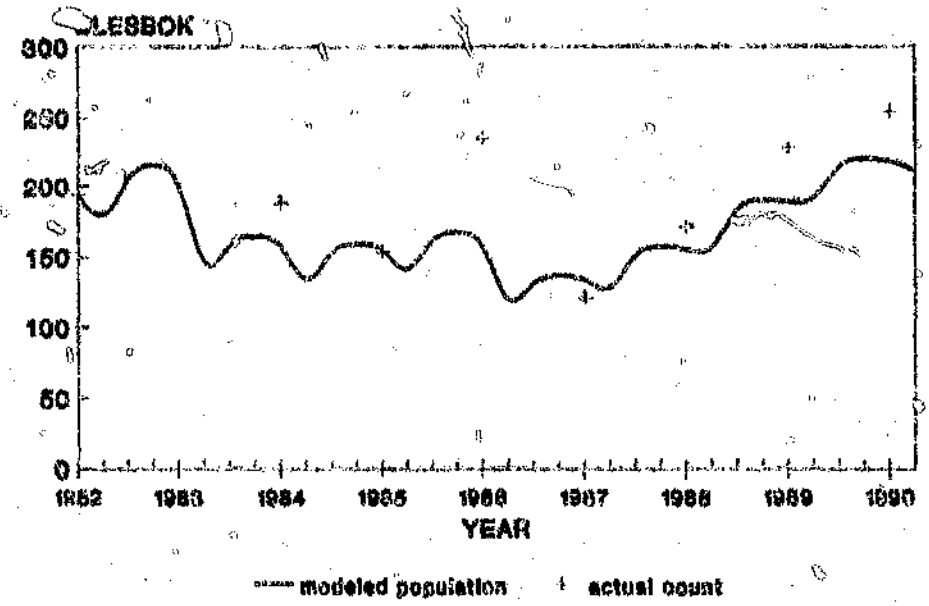


Figure 7.15 Comparison of modeled blesbok population with actual counts.

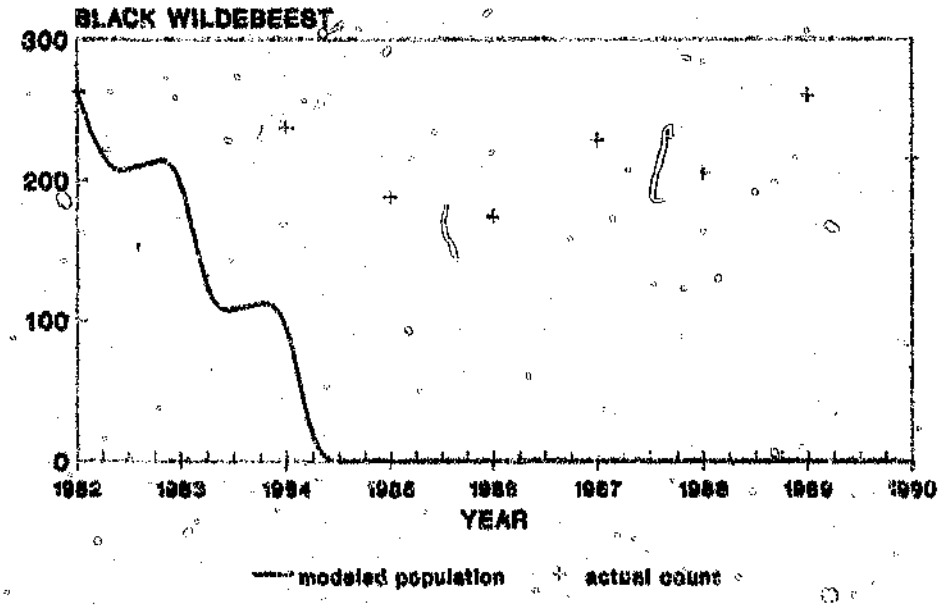


Figure 7.16 Comparison of modeled black wildebeest population with actual counts.

7.4.3 Discussion

The model output showed that the springbok population on The Pan was primarily limited by vegetation biomass. This was either a consequence of low rainfall which resulted in a low vegetation biomass or competition with other species. Competition was minimal at low plant biomass because bleshok and black wildebeest were unable to graze the short vegetation. Under medium rainfall springbok on The Pan were reduced considerably. At high plant biomass springbok benefited from the presence of other species presumably as a result of grazing to produce shorter green grass as preferred by springbok.

The implications of the model output included that there was scope for managing and increasing springbok numbers under medium and high rainfall but this was limited under low rainfall.

The model also demonstrated that initial output was misleading. In Figs. 7.8 and 7.12 springbok numbers increased for the first five years and thereafter declined. It was therefore important to explore the output for sufficient time for trends to be established.

The model assumed that resources off The Pan were unlimited. This permitted the populations to increase to unrealistically high numbers. On the one hand this was advantageous in that, given high populations, the animals concentrated on The Pan when grazing was available. This revealed the potential for the species. On the other hand it was far-fetched and a shortcoming of the model.

Population regulation would also have been refined by introducing a number of age classes with age specific mortality. This would improve the herbivore model but such detail is beyond the resolution of the vegetation model.

The widely different outcomes under "random" rainfall were particularly revealing and illustrated the complexity of plant-herbivore and herbivore-herbivore interactions. In reality, every rainfall event, and therefore, every rainfall regime was unique and no two outcomes were the same.

The comparison of modeled output with actual counts is a tautology. Generally, models are "tested" with independent data and not data from which the model is built. However, the comparison remains an acceptable test, albeit a weak one.

The springbok and blesbok models predicted well and passed this test.

The model output for black wildebeest was disappointing when compared with actual counts. The fact that there was such a difference between modeled and actual populations was attributed to the ability of the species to meet its intake requirements off The Pan. That is, vegetation biomass on The Pan did not affect black wildebeest to the same as extent as springbok and blesbok. The time series analysis and correlation with rainfall of black wildebeest on The Pan (Ch. 6) have demonstrated this.

In essence, the model underestimated the productivity of black wildebeest, particularly under low and medium rainfall conditions, which led to a predicted population decline when actual removals were applied to the modeled population. However, the model was easily refined by increasing the f(V) values (and therefore recruitment) for black wildebeest under low and medium rainfall which improved its performance. In many respects the model has served its purpose for it has identified shortcomings in the existing data and weaknesses in model design.

In general, the performance of the model concurred with work elsewhere. Allden & Whittaker (1982) found herbivore intake was related to plant height and van Zyl (1965) noted that there was a high overlap in diet between the three species. Guthrie (1987) also recorded that blesbok and black wildebeest shared similar diets. Springbok were able to graze a much shorter sward (Mills & Retief 1984a; 1984b) and were therefore more arid adapted than the other two species.

Facilitation was evident at high plant biomass. Although not previously described for black wildebeest and springbok, facilitation has been described for similar species (Thomson,s gazelle and blue wildebeest) in the Serengeti (Maddock 1979; McNaughton 1976).

At low and medium vegetation biomass there was conspicuous competition between springbok and the other two species which resulted in a decline in springbok numbers. Competition has been reported between Thomson's gazelle and blue wildebeest by Borner et al. (1987) and Dublin et al. (1990).

The ability of springbok to increase to very large numbers under wet conditions without competition suggests springbok were able, through grazing, to beneficially modify the food resource. McNaughton (1984) has surmised that gregariousness in grazing animals increased foraging efficiency by modifying vegetation structure to improve food yield per bite. The model suggested springbok employed such a strategy.

In conclusion, the output from the model was both realistic and plausible. The model implicated blesbok as a more important competitor than black wildebeest. This was contrary to what was first thought but in hind sight logical.

The useful application of modeling was apparent, particularly in discerning vegetation-herbivore interactions and long term trends.

A notable feature of the model, that sets it apart from other vegetation-herbivore models, has been the incorporation of variable vegetation and herbivore inputs. Had this model remained a constant-growth, constant-requirement model, much of its sensitivity would have been lost and the various responses by both vegetation and herbivores would not have been elicited.

The model was sufficiently corroborated to now explore management options.

CHAPTER 8 : MANAGEMENT STRATEGY

8.1 Introduction

The aim of this chapter was to formulate a management strategy to maximise the number of springbok on The Pan.

This was achieved by

(i) clearly identifying the objective

(ii) noting other management considerations, and

(ii) using the model to meet the objective.

In this way the goals were defined and the strategy was impartially determined. The process promoted logical decision making by identifying the reasons why certain actions were undertaken. This facilitated adaptive management.

8.2 Overview

The overall objective of the study was to gain understanding of the mechanisms that drive a plant-herbivore system so that the system could be manipulated to meet the aims of management.

A primary consideration at the outset was that the strategy be practicable. This required that other management constraints be incorporated in defining the objective.

These were that

(i) viable populations of blesbok and black wildebeest be maintained on the reserve

(ii) cropping be restricted to the winter months, and

(iii) income be derived where possible.

Provided reasonable numbers of animals were on the reserve a high proportion of the population would be on The Pan. Therefore any management action should be aimed at the total population and not just those animals on The Pan. This applied to all three species.

Whereas the vegetation response was rapid that of the herbivores was lagged. For example, favourable vegetation conditions gave rise to an increase in birth rate only a year later. This compounded decision making as the future climatic regime was unknown.

In the current model application the future was ignored, although with refinements to the approach, it could be included.

8.3 Model application

The model was used to (a) determine the degree of interspecific competition between herbivores (b) explore the outcome of management intervention, and (c) devise a practicable strategy.

8.3.1 Interspecific competition

Springbok population levels were examined separately with those of blesbok, black wildebeest and both species together under varying rainfall regimes. In each instance the starting population was 1100 springbok, 170 blesbok and 200 black wildebeest. The results are given in Table 8.1 and expressed graphically in Figs. 8.1 to 8.3.

Fig. 8.1 Modeled total springbok population after 25 years when competing with other species under different rainfall regimes.

Rainfall	Competing species			
	sb only	sb+bb	sb+bk	sb+bb+bk
dry	250	220	220	180
medium	1700	500	1350	400
wet	5000	11000	6500	4500

The results concurred with earlier model output from The Pan. Under low rainfall competition was minimal and springbok numbers were, by and large, limited by rainfall (vegetation). Under medium rainfall blesbok limited springbok numbers to almost the same degree as with both wildebeest and blesbok together. Conversely, under high rainfall springbok were limited only by the competitors.

Contrary to what was expected blesbok and black wildebeest individually benefited springbok numbers when wet conditions prevailed.

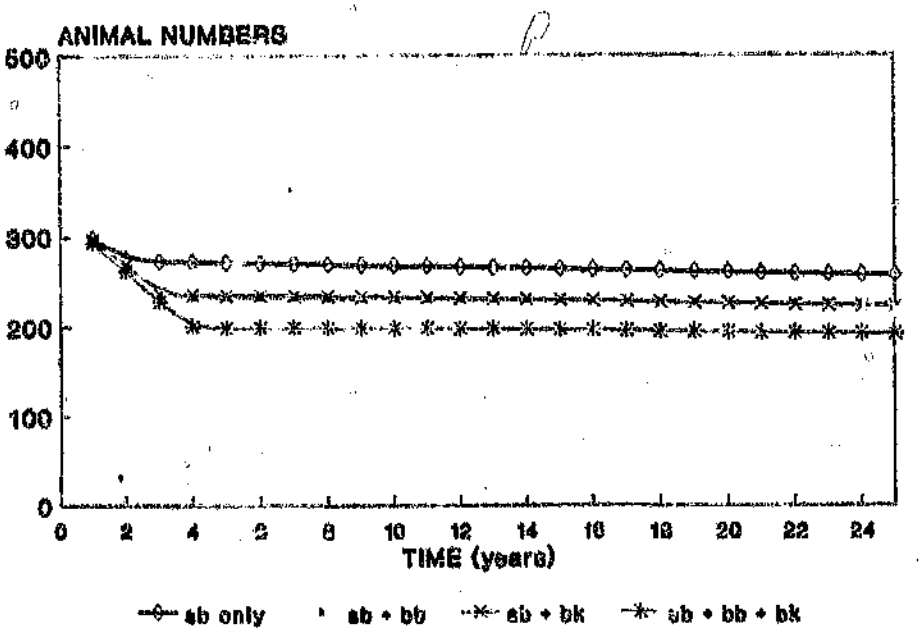


Figure 8.1 Springbok with and without blesbok and black wildebeest under low rainfall.

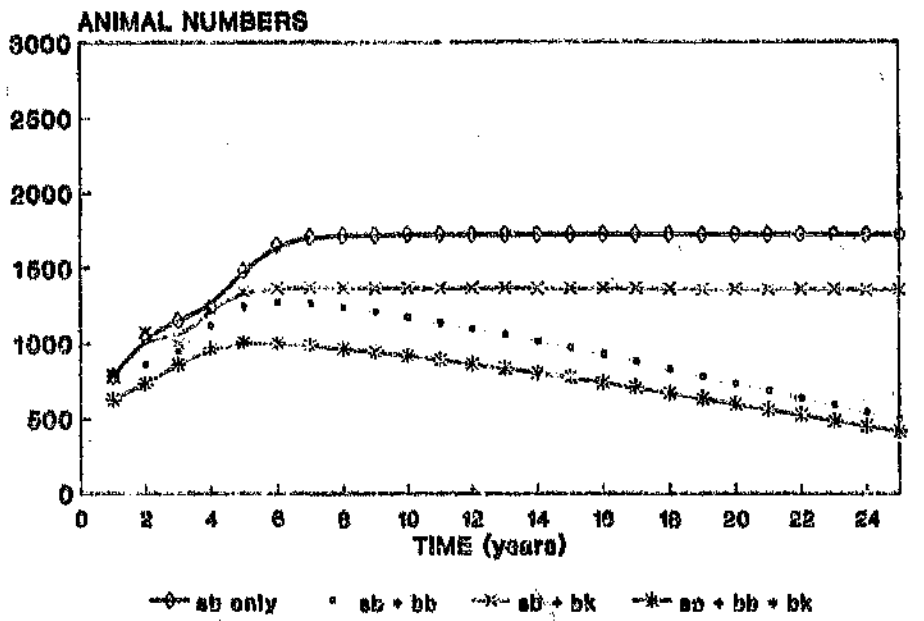


Figure 8.2 Springbok with and without blesbok and black wildebeest under medium rainfall.

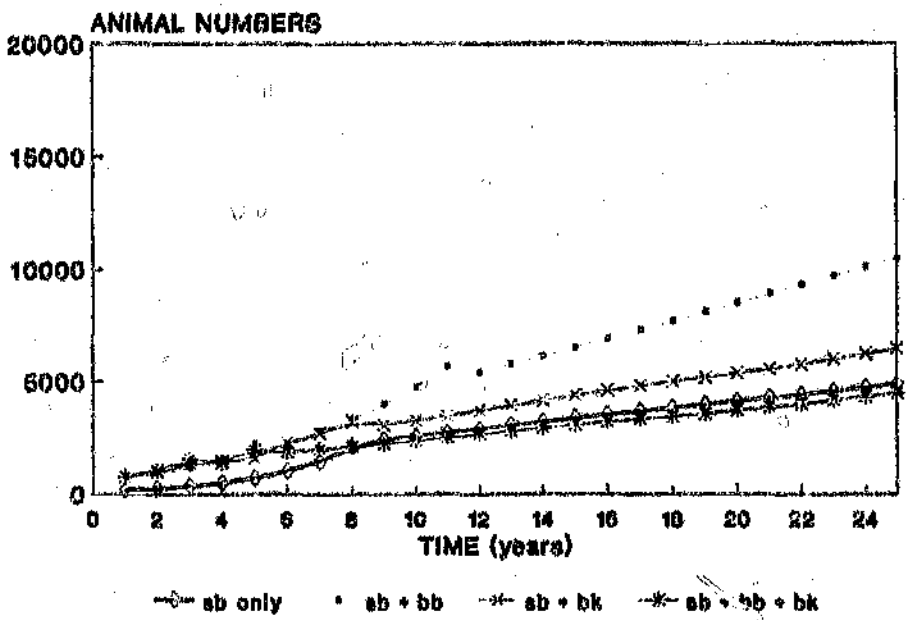


Figure 8.3 Springbok with and without blesbok and black wildebeest under high rainfall.

The outcomes suggested that under low rainfall the grass was too short for either blesbok or black wildebeest to crop. Under medium rainfall the grass was at a height that favoured blesbok and the species competed with springbok for the available resources. In this situation the grass was either too short due to insufficient moisture for black wildebeest to remove, or was kept short by both blesbok and springbok grazing.

Under high rainfall conditions the grass height favoured black wildebeest and was too long for springbok. However, grazing by either blesbok or black wildebeest reduced the vegetation canopy to a level which provided improved grazing for springbok. If both black wildebeest and blesbok were present together then the vegetation was depleted to such an extent that springbok numbers were reduced.

Several important management options were concluded from these results.

(i) Under low rainfall there was little to be gained by manipulating either blesbok or black wildebeest numbers.

(ii) Under medium rainfall springbok benefited most through control of blesbok.

(iii) Under high rainfall moderate numbers of blesbok and black wildebeest benefited springbok.

The outcomes were in accordance with the grazing theory of Allden & Whittaker (1982) relating to intake and plant height and that of Illius & Gordon (1987), where intake was controlled by bite dimension.

The model was also revealing with regard to facilitation and the establishment of grazing lawns that benefited springbok.

Conflicting results have been reported by several authors. McNaughton (1976) and Maddock (1979) found gazelles concentrated on areas previously grazed by wildebeest; Borner *et al.* (1987) found gazelle were limited by interspecific competition with other species and de Boer & Prins (1990, could find no evidence of facilitation as reported elsewhere (Gwynne & Bell 1968; McNaughton 1976).

In the light of the model output it was apparent that all these cases were possible but the outcome depended on plant height and climatic condition. This emphasized the complexity of plant-herbivore systems (Crawley 1983; McNaughton 1979) and predator-prey interaction (Noy-Meir 1975; Noy-Meir 1981).

8.3.2 Population management

The model output was then explored when blesbok and wildebeest populations were controlled. The best strategy was theoretically one that controlled blesbok and wildebeest numbers under medium rain but permitted them to increase under high rainfall. The unpredictability of rainfall made such a strategy impracticable.

Therefore, it was decided that, in the absence of prolonged droughts, blesbok would not be controlled below a population level of 150 and wildebeest not below 200. This would meet the other objectives of management that viable populations of these species be maintained and that the populations provide sufficient animals for a lucrative safari hunting enterprise. The results are given in Table 8.2.

Table 8.2 Population size and harvest for different rainfall regimes.

Rainfall	Population			Harvest	
	sb	bb	bk	bb	bk
dry	522	uncontrolled		0	0
medium	2806	150	200	13	1
medium	2554	200	250	17	1
wet	5293	150	200	33	74
wet	4783	200	250	43	92

Springbok numbers were higher, even under wet conditions, at the lower population levels of blesbok and black wildebeest than at the higher levels. This suggested that at the 200 blesbok and 250 wildebeest level competition rather than facilitation was taking place. The higher level of population control of blesbok and black wildebeest was therefore required to meet the objective of maximising springbok numbers.

Under continual dry conditions blesbok and black wildebeest numbers declined naturally. If dry conditions continued for 30 years the blesbok were reduced to some 60 animals and the black wildebeest to extinction. Natural (unmanaged) population levels from the model are given in Table 8.3 and would form the basis of

the recommended strategy during extended droughts.

Table 8.3 Model output of population declines of blesbok and black wildebeest under continual dry conditions

Drought period (yrs)	Blesbok	Black wildebeest
3	150	100
6	137	53
9	126	30

The yield of black wildebeest was too low under medium conditions to satisfy the hunting demand. However, under wet conditions there was an over supply (Table 8.2).

On average (dry, medium, wet) the annual harvest was 15 blesbok when the population was controlled at 150 and 20 blesbok when the population was controlled at 200. Similarly, the annual surplus of black wildebeest was 25 at the 200 level and 31 at the 250 level (Table 8.2).

The actual average annual harvest between 1982 and 1988 (Table 6.1) was 18.7 blesbok and 42.6 black wildebeest.

This suggested that the model was under-estimating the production of surplus black wildebeest and this could be attributed to either inadequacies in the model or under-counting in the field.

It was unrealistic to expect to control population numbers precisely. The unreliability of counting and the inability to accurately manipulate populations precluded this. In reality, population levels fell within a range that was practicable to maintain.

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It was unrealistic to expect to control population numbers precisely. The unreliability of counting and the inability to accurately manipulate populations precluded this. In reality, population levels fell within a range that was practicable to maintain.

The model suggested that population levels of 150 to 200 blesbok and 200 to 250 black wildebeest would best meet the objective of maximising springbok on The Pan under medium and high rainfall. This was the recommended strategy under these climatic conditions.

During extended periods of low rainfall the preferred strategy was that numbers of blesbok be reduced to below the 150 level and black wildebeest be reduced to below the 200 level in accordance with Table 8.3. This strategy was aimed and utilising surplus animals that would in any event die naturally.

Under fluctuating rainfall, the number of springbok on The Pan remained between one and two thousand when blesbok were kept below 200 (Fig 8.4). If blesbok were allowed to increase the springbok population tended to be depressed to around 1000 animals (Fig. 8.5). This again indicated that blesbok rather than black wildebeest were competing with springbok.

There was little difference in springbok numbers on The Pan under fluctuating rainfall when blesbok were maintained at 150 and black wildebeest at 200 (Fig. 8.6) compared with maintaining blesbok at 200 and black wildebeest at 250 (Fig. 8.7). This was useful for it meant that a rigorous culling strategy which was difficult to attain in practice was not essential.

The different culling strategies fluctuating rainfall are compared in Figure 8.8. Springbok numbers on The Pan were lowest in the absence of culling and highest when both blesbok and black wildebeest were culled.

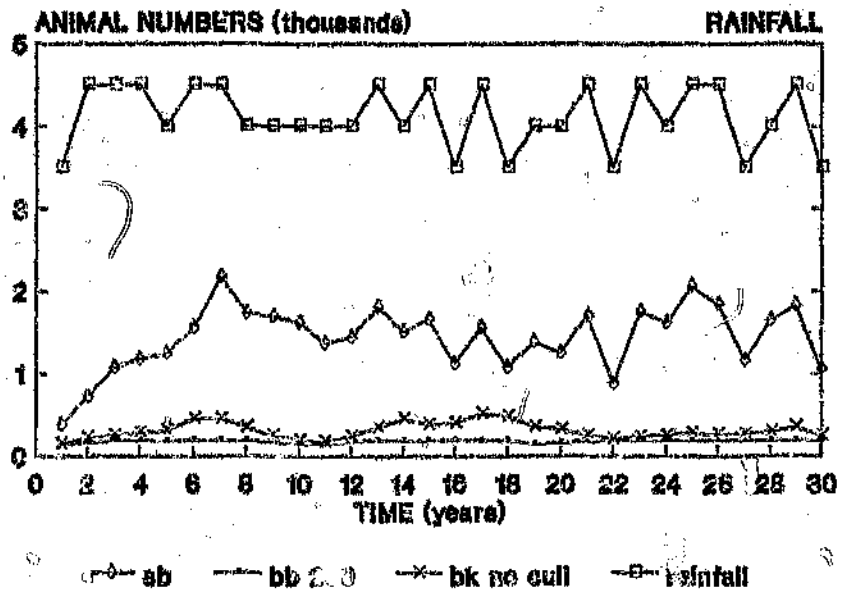


Figure 8.4 Springbok on The Pan under fluctuating rainfall when blesbok are maintained at 200.

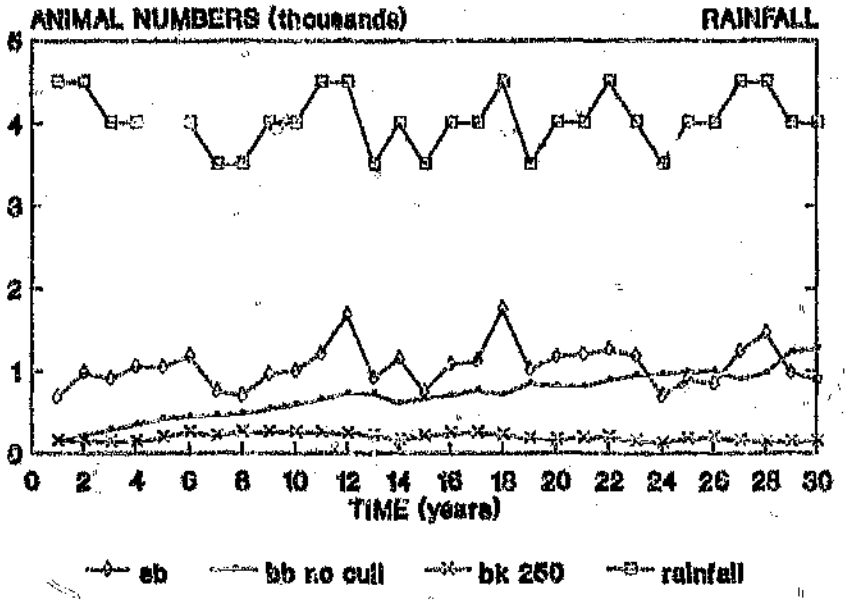


Figure 8.5 Springbok on The Pan under fluctuating rainfall when black wildbeest are maintained at 250.

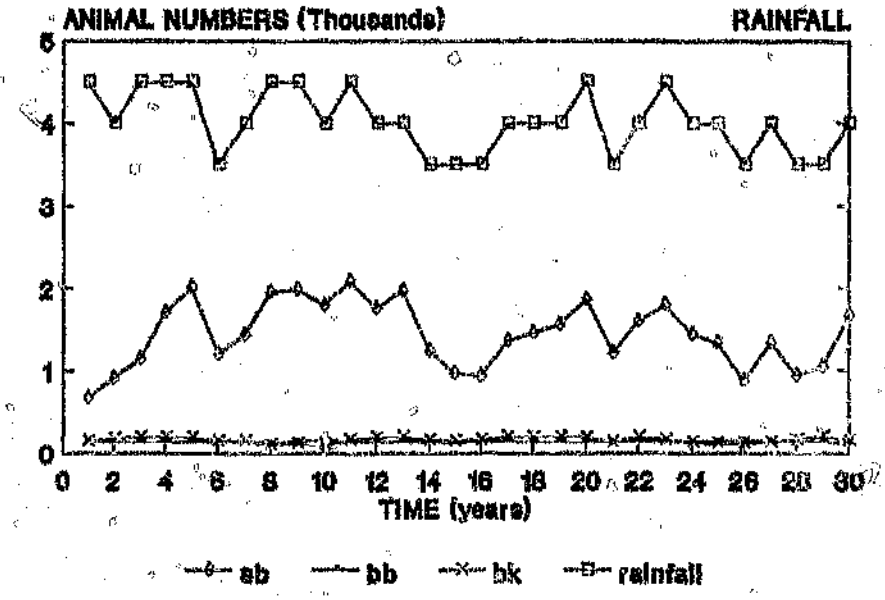


Figure . 8.6 Springbok on The Pan under fluctuating rainfall when blesbok are maintained at 150 and black wildebeest at 200.

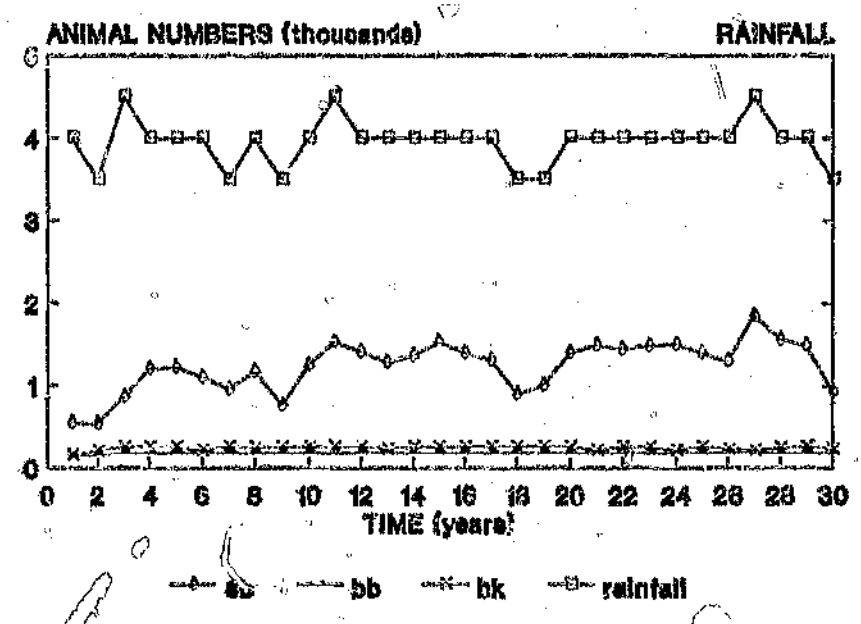


Figure 8.7 Springbok on The Pan under fluctuating rainfall when blesbok are maintained at 200 and black wildebeest at 250.

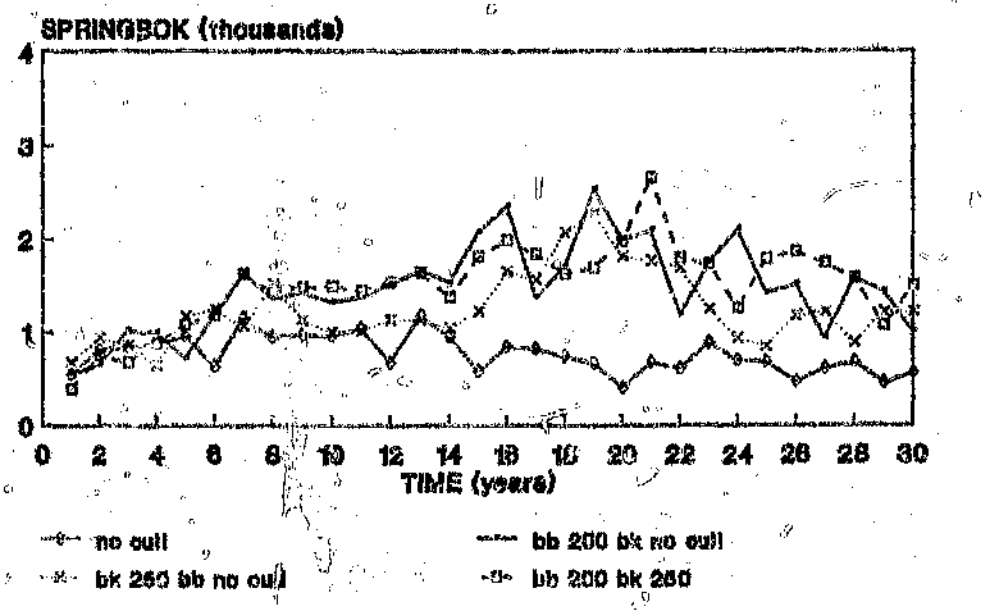


Figure 8.8 Springbok on The Pan under fluctuating rainfall and applying different management strategies.

There was little difference between the no cull black wildebeest and 250 black wildebeest strategies. This confirmed earlier findings that springbok numbers on The Pan were most influenced by blesbok. The proposed management strategy was robust under fluctuating rainfall.

In conclusion, a management strategy for maximising springbok has been formulated with the aid of the model and the objective of this study has been met.

The recommended tactic was not dissimilar to that employed in the recent past. This was largely co-incidental although a similar outcome was predictable given the confines in which the model was developed and the single data base. However, it was also important to note that, in the process, knowledge was advanced and understanding of this multi-herbivore system improved.

6.4 Summary

The overall objective of this study was to obtain the information and understanding of a vegetation-herbivore system that would allow a specific management goal to be attained. The problem was real and the strategy likewise was required to be practicable.

Supposedly simple single predator-single prey systems were themselves complex and their iteration has been theoretically explored. Multiplant-multiherbivore interactions have remained speculative due to the added complexity of such systems. However, despite this complexity and lack of understanding it was necessary to devise a management strategy that would meet the

overall objective within a multiherbivore system.

A analytical approach was used to evolve a model that was suited to the problem and that was appropriate for the data, the resolution required and for exploring the intricacies of multiherbivore interaction. The logistic equation which has remained the single most widely used model for studying predator-prey relations was found to be inappropriate. A discrete difference model was therefore adopted that was well suited to expressing interseasonal changes within an episodic arid system and to numerical solution.

The model was corroborated and sensitivity analyses were carried out. The important parameters were identified and the model performance was explored. Climatic factors were typically spatially and temporally highly variable and characteristically extreme. Vegetation growth was the single most sensitive parameter within the plant-herbivore system.

Vegetation production varied in response to climatic regime. Under favourable conditions production was relatively large. Similarly, under unfavorabl conditions vegetation biomass declined rapidly.

The concept of herbivore functional response, by and large, has remained theoretical, in the study of plant-animal interaction. Functional response was found to be an extremely useful means for expressing interspecific differences between herbivores and was practically applied.

The model performed plausibly and with refined data from the field the output was realistic. Vegetation production by the model was similar to that found in the field and was sensitive to both rainfall and season. Similarly herbivore populations were determined by seasonal vegetation biomass and species specific responses were elicited to changes in vegetation. The model was particularly useful in establishing long term population trends under different climatic regimes.

Under conditions of low rainfall herbivore populations were limited by vegetation availability and not interspecific competition. Under medium rainfall springbok were obliged to compete for the available resources and their numbers were limited primarily by blesbok. When conditions of high rainfall prevailed springbok benefited from low numbers of blesbok and black wildebeest as a result of facilitation but were limited at high population levels of competitors.

The model satisfactorily accounted for conflicting outcomes in plant-herbivore interactions and, depending on rainfall, demonstrated both competition and facilitation within the same vegetation-herbivore system. This had previously only been speculative and theoretical.

Finally the model was used to formulate a strategy that met both the objectives of the study and those of management. This involved a flexible approach geared to a rainfall driven system that was based on general principles rather than specific remedies.

It was unrealistic to expect a model that lacked precise detail to have evolved an infallible strategy. This was not the intention, but rather to discover general principles and highlight crucial elements of the vegetation-herbivore system. This was achieved. The results were not able to be proved but the modeling exercise had helped to define the objectives, identify important parameters, explore options and formulate broad decisions.

The model has advanced both understanding and knowledge of plant-herbivore interaction particularly under varying climatic regimes.

In conclusion, the model offers a practical approach to managing diverse multiherbivore systems. It has wide application and can be adapted to other herbivore guilds and multi-predator competitors to benefit conservation and improve wildlife management.

APPENDIX 1 : ANIMAL UNIT EQUIVALENTS

The purpose of this appendix was to derive the animal unit equivalents for the three herbivore species, black wildebeest, blesbok and springbok, in the study.

Animal unit equivalents (AU) provided a common unit by which animals of varying body mass could be compared and such a unit was required for the herbivore model.

Energy requirements of homeothermic animals were conventionally proportional to body mass raised to the three-quarter power (Moen 1973). Thus the animal unit equivalent of a herbivore could be determined provided its mass is known (Mentis 1977).

An animal unit (AU) was defined as a steer with a mass of 450 kg with an average daily gain (ADG) of 0.5 kg (Meissner, 1982).

Thus the metabolic equivalent (ME) was given by

$$ME = \frac{M^{0.75}}{450^{0.75}}$$

Where M was the mass of the animal.

Thonney *et al.* (1976 *in* van Soest 1982) have pointed out that this relationship was valid interspecifically. However, intraspecifically, when comparing animals of different sizes, it overestimated metabolic equivalent as a result of gastro-

intestinal differences which effected fill and therefore intake. On very short swards, where food intake declined, the relationship was reduced by as much as mass to the power of 0.36 (Illius & Gordon 1987). For the purpose of the model the animal unit equivalent given by mass to the three-quarter power was used.

A major difficulty was to determine what was the average mass for a single animal in the population and at best this estimate amounted to an intelligent guess (Mentis 1970). In order to accurately determine the average mass, the sex-age structure of the population and the mass of sex-age class must be known. Both these parameters changed from year to year, dependent on population size and veld condition. For example, in springbok the mean individual was found to vary by as much as 38 per cent between years of good and poor veld condition with in the same population and on the same property.

Young & Wagener (1968) and Young & Bronkhorst (1969) found that the average mass of an individual in the population varied from 0.75 (impala) to 0.80 (blue wildebeest) of the mean adult male mass. Du Plessis (1972) calculated the mean mass of a blesbok to be 52.6 kg and this was 82.7 per cent of adult male mass. A lower percentage was expected in species such as springbok with higher production rates (more young animals).

A determination of mean population mass for springbok, based on known mean mass for each age class and the sex-age structure of the population, gave a figure of 83.1 per cent of mean adult

mass. Thus the figure of 0.80 was used for springbok, blesbok and black wildebeest.

Dressing out percentages varied both inter- and intra-specifically. However, sixty per cent was an acceptable average figure (von la Chevallerie 1970).

Therefore

$$\text{live mass} = \text{dressed carcass mass} / 0.6$$

and

$$\text{mean animal mass (M)} = \text{live mass} \times 0.8$$

The derived values for each species are given in Appendix Table 1.1.

Appendix Table 1.1 Derivation of AU equivalent.

species	n	carcass mass (kg)	calculated live mass	mean mass	AU equiv
black wbeest	23	76.0	126.7	101.3	3.1
blesbok	16	38.6	64.3	51.5	5.1
springbok	23	22.3	37.2	29.7	7.7

The AU equivalents for back wildebeest and blesbok were marginally higher and, that for springbok marginally lower, than those given by Mentis & Duke (1976) of 2.9, 4.9 and 8.1 respectively. This was a result of these authors using a higher mean body mass for black wildebeest and blesbok and a lower body

mass for springbok. Meissner (1982) derived AU equivalents from growth curves and assumed growth was proportional to intake. The AU equivalents thus derived were also higher than those used in this study.

APPENDIX 2 : FUNCTIONAL RESPONSE

The aims of this appendix were to

(i) introduce the concept of functional response
(ii) examine the various functional response types, and
(iii) use the concept to modify population parameters.

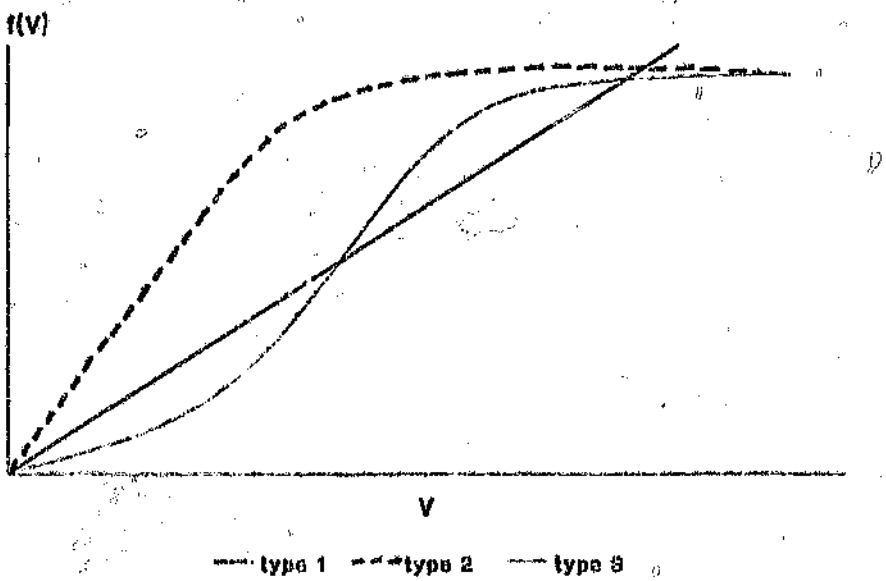
A means was required with which to separate the response of each herbivore type to the state of the vegetation. In this way the population parameters of each species could be individually manipulated. The concept of "functional response" provided such a means.

Overview

The functional response f(V) (Crawley 1983; Starfield & Bleloch 1986) is the ability of a herbivore to meet its consumption requirements. It is also referred to as "grazing efficiency" (Noy-Meir 1975) and varies with the herbivore type.

The functional response of herbivores to changes in plant abundance takes many forms. Three types of curves (Appendix Fig. 2.1) are generally recognised (Crawley 1983) and these are linear (Type 1), asymptotic (Type 2) or sigmoid (Type 3).

In Type I response, there is increasing intake with increasing availability. In Type 2 response, intake increases until the herbivore is satiated due to limited gut capacity or limited



Appendix Figure 2.1 Types of herbivore functional response.

time for food handling and processing. A Type 3 response occurs when a herbivore changes its grazing preference in response to plant abundance, e.g. when plant biomass falls below the minimum grazing threshold.

It is difficult to determine the functional response of herbivores in the field (Crawley 1983). The majority of herbivores are thought to have an initial linear response that levels off as animals become satiated (Type 2 response). Type 3 responses have not been reported for herbivores on a single food source. Crawley (1983) has shown that under most conditions a Type 3 functional response model behaves exactly as a Type 2.

Species specific response

The functional response of black wildebeest, blesbok and springbok was determined by the amount of vegetation on The Pan. Mentis & Duke (1976) classified all three species small bulk and roughage eaters. However, the intermediate diet of springbok and preference for green nutritious shoots (Bigalke 1972; Schijf 1978) suggested this species was a concentrate selector.

The small mouth of the springbok enables this species to be more selective and it is better able to utilise short grass. Similarly, blesbok are more efficient than black wildebeest in meeting their intake requirements at low plant biomass.

In grazing ruminants there is an inverse relationship between live mass and quality of intake (van Soest 1982). Thus in order

to maintain intake quality there is an increase in feeding selectivity with decrease in body size.

A minimum above ground vegetation biomass is necessary before a species is able feed. This is termed the minimum grazing threshold.

Above the minimum grazing threshold intake increases with increasing plant biomass. Ultimately the biomass reaches the point where it becomes too coarse and fibrous to satisfy the demands of both concentrate selectors (springbok) and selective feeders (blesbok and black wildebeest). At this point consumption peaks and thereafter declines.

It was therefore assumed that each species has a curved functional response. The curve is expressed schematically in Appendix Fig. 2.2.

The shape of the curve was given by

$$f(V) = 0 \text{ when } V < Vmin \text{ or } > Vmax$$

between Vmin and Vopt by

$$f(V) = (V - Vmin)/(Vopt - Vmin)$$

and between Vopt and Vmax by

$$f(V) = (Vmax - V)/(Vmax - Vopt)$$

All f(V) values lie between 0 (low) and 1 (high).

Population functional response f(P)

It was assumed that The Pan was the preferred habitat for all three species. The number of animals on The Pan was determined by how many were able to meet their nutritional requirements on The Pan. Thus, the higher f(V) for the species the greater the number of that species that would be found on the Pan. This was termed the "population functional response" or f(P) and was similar to the "attractiveness" employed by Starfield *et al.* (1982b). The f(P) was expressed as a linear relationship that peaked at a given f(V) value and was similar to a Type 2 response (Appendix Fig. 2.3).

The slope of the line is given by

$$f(P) = 0 \quad \text{when } f(V) < f(V)min$$

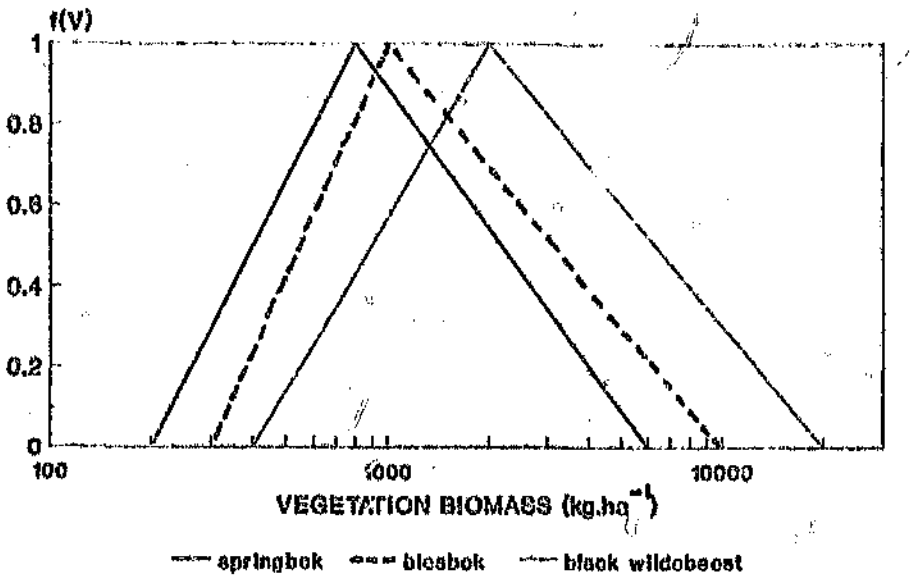
and

$$f(P) = 1 \quad \text{when } f(V) > f(V)max$$

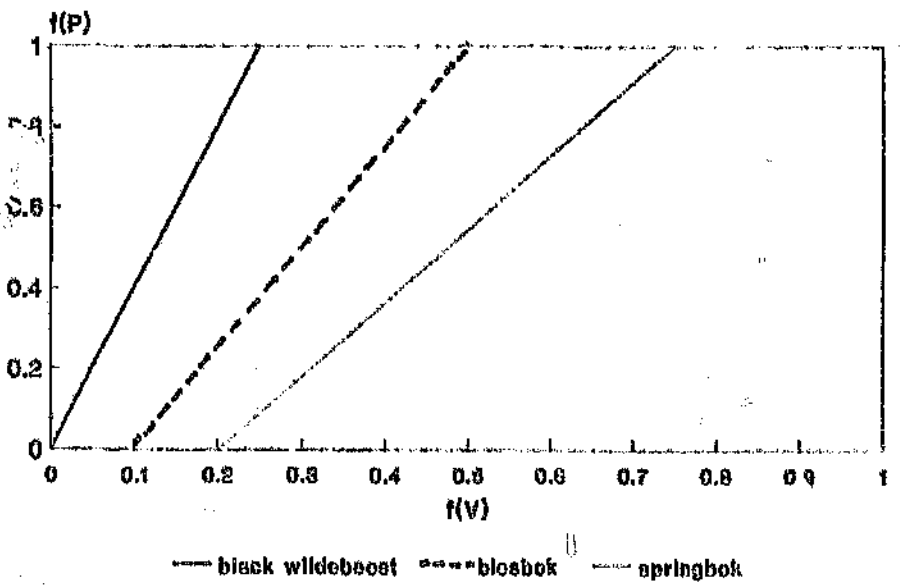
between these values

$$f(P) = f(V)/f(V)max$$

The correlation of species biomass on The Pan and rainfall indicated that the minimum grazing threshold for blesbok was less than that of springbok and that of black wildebeest was less than that of blesbok. Black wildebeest were found to occupy The Pan irrespective of grazing conditions and therefore were present even at a value of f(V) = 0. Black wildebeest were less selective than springbok and all available black wildebeest habitat on The Pan was occupied at a lower f(V) value than that of springbok. The grazing thresholds of blesbok lay intermediate between those of springbok and black wildebeest.



Appendix Figure 2.2 Herbivore functional response f(V).



Appendix Figure 2.3 Herbivore population functional response f(P).

Birth functional response f(w)

The rate of increase f(w) is determined by body mass and the plane of nutrition (Clutton-Brock et al. 1982; Crawley 1983; Sinclair 1979).

A minimum body condition which depended on f(V) was necessary for births to occur. As the functional response for vegetation improved so did the birth rate and above a given f(V) value the birth rate peaked and was maintained.

Thus $f(w) = 0$ when $f(V) < f(V)min$

and $f(w) = 1$ when $f(V) > f(V)max$

between these values

$$f(w) = (f(V) - f(V)min)/(f(V)max - f(V)min)$$

The relationship between f(V) and f(w) is given in Appendix Fig. 2.4.

Black wildebeest were the least selective and were able to meet their metabolic requirements at lower f(V) values than both blesbok and springbok. As the f(V) value increased black wildebeest attained maximum birth rate first, followed by blesbok and springbok. Conversely, springbok were the most selective and only had a high birth rate at a high f(V) value. Black wildebeest were the least selective feeders continued to breed after blesbok and springbok had ceased breeding.

Mortality functional response f(m)

Mortality is a function of body condition and therefore nutrition and f(V).

Mortality decreased with increasing values of f(V).

Thus

$$f(m) = 1 \quad \text{when} \quad f(V) > f(V)min$$

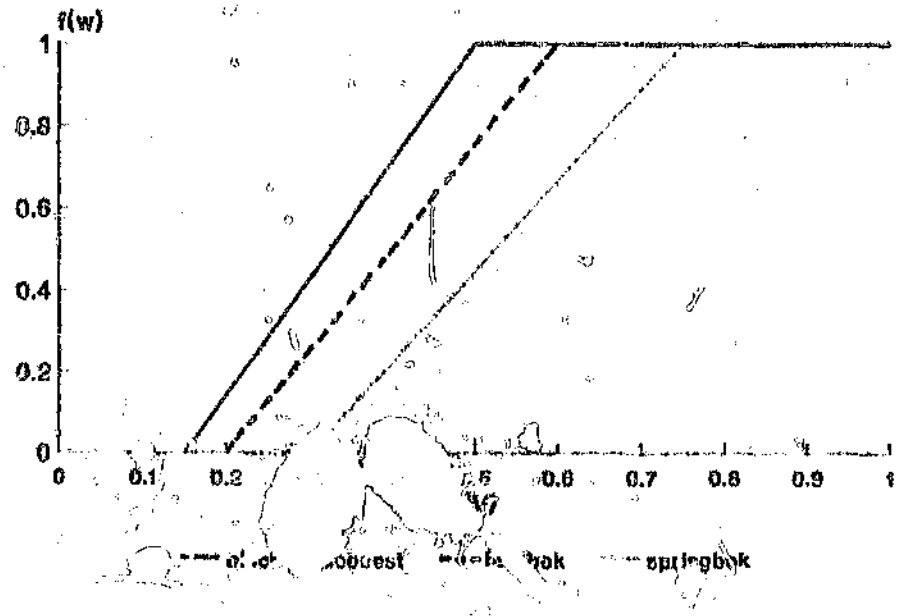
and when $f(V) < f(V)min$

$$f(m) = f(V)/f(V)min$$

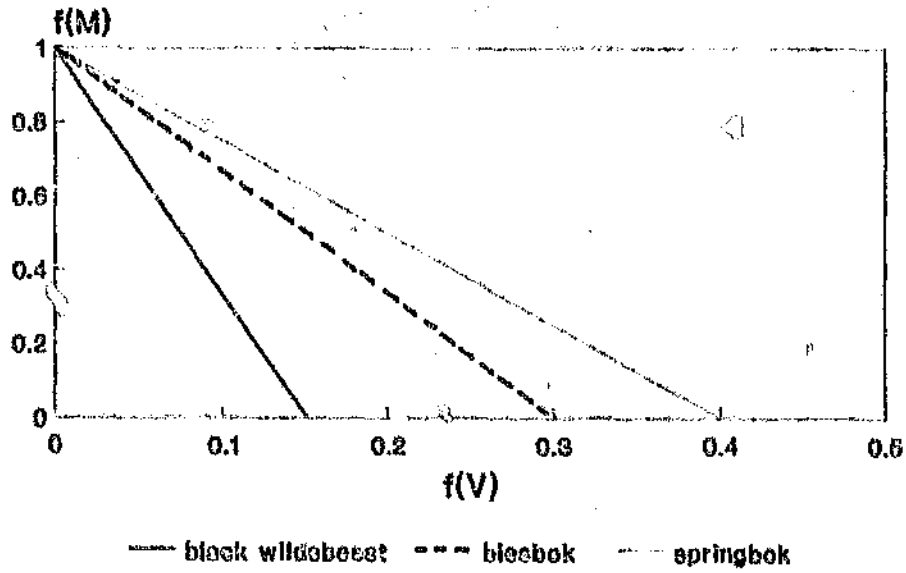
At lower f(V) values black wildebeest were more able than the other two species to meet their consumption requirements. Similarly, blesbok had a lower mortality threshold than springbok. As vegetation conditions improved so mortality declined (Appendix Fig. 2.5).

Conclusion

The use of functional response was convenient tool for regulating herbivore performance in a plant-herbivore relationship. In this way the numbers of herbivores and the population determinants of birth and death were geared to the state of the vegetation.



Appendix Figure 2.4 Herbivore birth functional response f(w).



Appendix Figure 2.5 Herbivore mortality functional response f(M).

```
B1: 'Season          B2: 1
C1: 'Rainfall        C2: 'DRY
D1: 'SEASON          D2: 'WINTER
E1: 'VEG START       E2: 500
F1: 'PRODN           F2: +E2+J2
G1: 'Springbok       G2: 1100
H1: 'Blesbok         H2: 170
I1: 'Gnu             I2: 200
J1: 'Veg growth      J2: 1*@VLOOKUP(C2,$PEAKS,@VLOOKUP(D2,$SEASON,1))
K1: 'f(V)sb          K2: (@VLOOKUP($C2,$PEAKS,1)*(@IF($F2>800,@IF($F2>6000,0,(6000-$F2)/5200),$F2/1000)))
L1: 'f(V)bb          L2: (@VLOOKUP($C2,$PEAKS,6)*(@IF($F2>1000,@IF($F2>8000,0,(8000-$F2)/7000),$F2/1000)))
M1: 'f(V)gn          M2: (@VLOOKUP($C2,$PEAKS,7)*(@IF($F2>2000,@IF($F2>20000,0,(20000-$F2)/18000),$F2/2000)))
N1: 'F(P)SB          N2: @IF(K2>0.75,1,@IF(K2<0.2,0,K2/0.75))
O1: 'F(P)BB          O2: @IF(L2>0.5,1,@IF(L2<0.1,0,L2/0.5))
P1: 'F(P)BK          P2: @IF(M2>0.25,1,M2/0.25)
Q1: 'PANSB           Q2: +G2*N2
R1: 'PANBB           R2: +H2*O2
S1: 'PANGN           S2: +I2*P2
T1: 'TOTAL VEG       T2: 600*F2
U1: 'VEG REMOVED     U2: (Q2/7.7*N2*900)+(R2/5.1*L2*900)+(S2/3.1*M2*900)
V1: 'VEG END SEAS    V2: (+T2-U2)*@VLOOKUP($C2,$PEAKS,8)*@VLOOKUP($D2,$SEASON,2)-U2
W1: 'SB BORN         W2: @IF($D2="SPRING",AL2,@IF($D2="AUTUMN",AL2*0.32,0))*(@IF(K2<0.2,0,@IF(K2>0.6,1,(K2-0.2)/0.4))*Q2)+@IF($D2="SPRING",AL2,0)*(G2-Q2)*0.4
X1: 'BB BORN         X2: @IF($D2="SPRING",AM2,0)*(@IF(L2<0.2,0,@IF(L2>0.6,1,(L2-0.2)/0.4))*R2)+@IF($D2="SPRING",AM2,0)*(H2-R2)*0.4
Y1: 'GN BORN         Y2: @IF($D2="SUMMER",AN2,0)*(@IF(M2<0.2,0,@IF(M2>0.6,1,(M2-0.2)/0.4))*S2)+@IF($D2="SUMMER",AN2,0)*(I2-S2)*0.4
Z1: 'SB TOT          Z2: +W2+G2
AA1: 'BB TOT         AA2: +X2+H2
AB1: 'GNU TOT        AB2: +Y2+I2
AC1: 'SB PM          AC2: @IF($D2="WINTER",@IF(K2>0.4,1,K2/0.4)*Q2+0.75*(Z2-Q2),Z2)
AD1: 'BB PM          AD2: U @IF($D2="WINTER",@IF(L2>0.2,1,L2/0.2)*R2+(AA2-R2)*0.75,AA2)
AE1: 'GNU PM         AE2: @IF($D2="WINTER",@IF(M2>0.15,1,M2/0.15)*S2+(AB2-S2)*0.75,AB2)
AF1: 'CULL SB        AF2: 0
AG1: 'CULL BB        AG2: @IF($D2="WINTER",@IF(AD2>200,(AD2-200),0),0)
AH1: 'CULL GN        AH2: @IF($D2="WINTER",@IF(AE2>250,(AE2-250),0),0)
AI1: 'P CULL SB      AI2: +AC2-AF2
AJ1: 'P CULL BB      AJ2: +AD2-AG2
AK1: 'P CULL GNU     AK2: +AE2-AH2
AL1: 'SB BIRTH       AL2: @VLOOKUP($C2,$A0$4..$AX$5,9)
AM1: 'BB BIRTH       AM2: @VLOOKUP($C2,$A0$4..$A$6,10)
AN1: 'GK BIRTH       AN2: @VLOOKUP($C2,$A0$4..$A$6,11)
```

APPENDIX 4 : RAINFALL

APPENDIX TABLE 4.1 ROOIPOORT RAINFALL (mm) 1981 TO 1988.

	SEP	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG
1981/82	0	2	10	94	40	41	66	35	7	0	26	0
1982/83	0	33	13	59	0	12	43	5	11	17	3	0
1983/84	11	32	72	34	13	15	66	11	22	0	0	0
1984/85	5	49	40	33	8	55	34	5	0	0	0	0
1985/86	9	33	64	71	48	15	3	9	0	13	0	2
1986/87	19	33	29	0	55	67	33	25	0	0	16	2
1987/88	64	10	61	47	9	288	50	18	0	0	1	0
MEAN	15.3	27.4	41.8	48.1	24.6	70.3	41.9	38.9	5.7	4.3	6.5	0.6

APPENDIX TABLE 4.2 KIMBERLEY RAINFALL (mm) 1981 TO 1988.

	SEP	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG
1981/82	0	24	47	137	23	45	51	69	0	26	36	0
1982/83	8	50	18	18	18	14	27	13	23	20	9	0
1983/84	16	15	64	24	14	70	73	11	32	1	0	2
1984/85	0	45	42	28	54	110	47	4	0	0	0	0
1985/86	3	60	19	95	65	66	43	9	0	10	0	15
1986/87	16	28	26	19	31	63	42	50	0	0	18	5
1987/88	70	22	45	53	7	332	93	106	0	6	1	0
MEAN	16.0	34.7	37.3	53.5	30.1	99.9	53.7	37.3	7.9	8.9	9.1	3.2

GLOSSARY

V	vegetation biomass (above ground standing crop) ($kg.ha^{-1}$)
Vo	vegetation biomass at time t ($kg.ha^{-1}$)
Vi	vegetation biomass at time t + 1 ($kg.ha^{-1}$)
t	time at start of period (season)
t + 1	time after a given period
a	vegetation growth ($kg.ha^{-1}$)
p	senescence (fraction of V remaining)
kVo	proportion of vegetation remaining after senescence
H	herbivore population ($AU.ha^{-1}$)
Ho	herbivore population at time t ($AU.ha^{-1}$)
Hi	herbivore population at time t + 1 ($AU.ha^{-1}$)
C	total consumption by herbivore population ($kg.ha^{-1}.AU^{-1}$)
c	intake of each herbivore ($kg.ha^{-1}.AU^{-1}$)
f(V)	functional response (ability to meet intake requirement) related to V or Vo
b	herbivore birth rate
m	herbivore mortality rate
f(P)	herbivore population functional response (f(V) which determines the number of herbivores on The Pan
f(w)	birth rate functional response (f(V) which determines the number of herbivores that give birth)
f(m)	mortality functional response (f(V) which determines the degree of herbivore mortality)
r	recruitment rate of herbivores
j	number of juveniles in herbivore population
P	size of herbivore population

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