

A MODELLING APPROACH TO ELEPHANT  
AND TREE POPULATION DYNAMICS  
FOR A SMALL GAME FARM

*BY*

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## **ABSTRACT**

Throughout Africa, growing human populations and resulting loss of wildlife habitat is a critical issue for most animal species. It is more and more common for privately owned small or medium sized farms to reintroduce wildlife on their land and such protected areas are fast becoming the only refuges available to wild animals. However a comprehensive understanding of the complex ecological processes taking place is vital for the effective management of restricted areas and the conservation of biodiversity. Due to the enormous complexity of an ecological system and the long periods of the related dynamics, it is very difficult to analyse the interaction between animals and plant populations without suitable computer models. In this thesis, the dynamics between elephant and trees (a major food source) are considered using computer simulations. A small game farm with recently introduced elephant is used as an example for comparing field data and the results of model simulations. To simulate elephant and tree dynamics, it is essential to utilise the underlying topography of the environment in which they live. A detailed terrain and vegetation map is developed to that effect. Field data is considered for parameterisation and validation of the models. Results indicate that what might appear as discrepancies in the field data can be understood with the help of simulation models which provide some possible explanation.

## **PREFACE**

The work described in this thesis was conducted under the supervision of Prof. Kevin J. Duffy of the Center for Systems Research , Durban Institute of Technology

These studies present original work by the author and have not otherwise been submitted in any form to another academic institution. Where use has been made of the work of others, it is duly acknowledged in the text.

## **ACKNOWLEDGEMENTS**

I would like to thank Prof. Kevin Duffy, my supervisor, for his direction, advice and encouragement throughout the project. It has been a privilege to work with him.

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# **CHAPTER ONE**

## **BACKGROUND TO THE STUDY**

### **1.1. INTRODUCTION**

Centuries ago, the African elephant (*Loxodonta africana*) inhabited most of the African continent, from the Mediterranean Sea to the Cape of Good Hope and was absent only in parts of the Sahara and other desert regions. Today, elephants are found only south of the Sahara Desert and are an endangered species with declining numbers in many parts of Africa (Said *et al.*, 1995). Elephants occupy a variety of habitats, including savannah, rainforests, swamps, seashores and mountains but their range is fragmented and discontinuous. Elephant numbers across the continent have declined as a result of loss of habitat and poaching for ivory. Between 1979 and 1989, the worldwide demand for ivory caused elephant populations to decline to dangerously low levels. During this time period, poaching fuelled by ivory sales cut Africa's elephant population in half. In 1977, 1.3 million elephants lived in Africa; by 1997, only 600,000 remained. In Kenya alone, the elephant population plummeted from 130,000 in 1973 to less than 20,000 in 1989, a loss of 85%. Recently, that number has stabilized, due in large part to the 1990 Convention on International Trade in Endangered Species (CITES) ban on international ivory sales. There has even been a substantial recovery of elephant populations over much of Eastern and Southern Africa. In Botswana, Namibia, Angola and South Africa, less poaching and better management have led to high elephant densities and in some cases overpopulation, as National Parks and privately owned reserves are fast becoming the only refuges available to them.

Culling programmes were introduced in some areas to prevent habitat damage and human-elephant conflicts. As a management option, elephant culling is very controversial and appears inconsistent with the role of conservation (Maas, 1995). It is also not clear that culling is the best answer (Van Aarde *et al.*, 1999). Another management option becoming an increasingly common tool, is the translocation of elephants. However, moving elephants is

a complex operation that requires a great deal of expertise, planning and resources. In South Africa, elephant are mostly translocated from Kruger National Park to other National Parks or to small private reserves and conservancies such as the Pongola Biosphere where this study took place. It is of great importance to the managers of these reserves to understand the impact elephant will have on previously undisturbed vegetation and biodiversity. Realistic solutions to the problems facing Africa's elephant can only be developed with the help of comprehensive long-term research studies. Monitoring elephant ranges and numbers provides wildlife managers with invaluable data for the effective conservation and management of remaining populations and decision-makers with information on which to base national and international policies relevant to elephant conservation.

Because of the restriction of movement through fencing and limited areas, elephant can drastically alter their environment by destroying trees and possibly decreasing biological diversity (Hall-Martin, 1992, Cumming *et al.*, 1997). As the largest living terrestrial mammal (shoulder height up to 290cm; weight up to 7,500 kg), a single elephant can consume up to 300kg of vegetation a day (Owen-Smith 1988). The diet of elephant consists mainly of leaves and branches of bushes and trees, but elephant also eat grasses and fruit, and often exhibit feeding habits such as debarking and killing mature trees. It is generally accepted that wherever elephant occur in large numbers, they have a substantial impact on their habitat which can lead to the destruction and possible extinction of rare trees (Hanks 1979, Anderson and Walker 1974). Elephant are known to be destructive foragers and trees are especially vulnerable to elephant damage (Barnes *et al.*, 1994; Cumming *et al.*, 1997; Hall-Martin, 1992). However, situations where elephant at high densities do not threaten tree species survival are also recorded (Ben-Shahar, 1996). As with all foragers, impact can also be positive by providing a mechanism for vegetative succession dynamics (Du Toit, 1991; Viljoen, 1991). In certain circumstances, this might eventually shift the equilibrium from woodland to grassland. The shift to grassland can benefit 'smaller' herbivores like the Blue Wildebeest (*Connochaetes taurinus*) and the Nyala (*Tragelaphus angasii*) (Van de Koppel and Prins., 1998). For relatively small game farms, the need to balance the tourism potential



offered by elephant against the tourism potential of a certain vegetation physiognomy (e.g. trees) is not always easy.

## **1.2. SIMULATION APPROACH**

It is rather difficult to fully grasp all the components and workings of an ecosystem, partly because the time periods involved are very long (Duffy, 1999) and the dynamics between elephant and trees are poorly understood hence the use of simulation models. It is necessary to understand that any attempt to simulate a system depends on the theoretical approach taken. For a number of decades, the equilibrium paradigm approach underpinned much of theoretical ecology. The equilibrium paradigm is founded on the assumption that ecosystems have the capability to regulate internally through negative feedback. Mechanisms for this type of regulation include intra-specific and inter-specific competition and plant-animal interactions. External effects due to the environment are considered as disturbances to these internal dynamics. Recently these assumptions have been severely criticized by a new non-equilibrium paradigm. The non-equilibrium paradigm is founded on the assumption that ecosystems possess a limited capacity for internal regulation (Ellis & Swift, 1988). Thus, non-equilibrium systems are those more vulnerable to external disturbances and equilibrium systems are less vulnerable to external disturbances.

Briske *et al.*, (2003) use theoretical evidence to show that both equilibrium and non-equilibrium dynamics may operate in ecosystems, at different spatial and temporal scales, to influence vegetation dynamics. This explanation backs up the initial assessment of Wiens (1984) that individual ecosystems exist on a continuum between equilibrium and non-equilibrium. In this thesis, the equilibrium paradigm is used in the simulations. Thus, the results describe the possible dynamics of the system on the equilibrium side of the paradigm continuum. It is important to realize that the results are relevant within the context of modest environmental variability. Further work will be needed to establish how useful this will be for practical predictions.

Caughley (1976) was the first person to suggest the use of a predator-prey ordinary differential equation model to describe the dynamics between elephant and trees. Caughley (1976) suggested that limit cycles in the dynamics between elephant and trees were possible. Duffy *et al.* (1999) showed that this claim is unlikely but that these types of equations can be used to consider the global dynamics of the system. Duffy *et al.* (1999) used parameter estimates from studies of elephant and trees in their model and the results were realistic. Their model ignores temporal and spatial variations in environmental conditions but these variations can be considered with grid based models (Duffy and Page, 2002) or a combination of grid based models and differential equations (Duffy, 2002). Similar approaches are used here.

### **1.3. STUDY AREA**

The Pongola Game Reserve in Northern KwaZulu Natal has been chosen as the study site for this project. It is a perfect example of a small privately owned reserve with recently introduced elephant (1997) where management is trying to understand the impact elephant will have on the vegetation and prevent unacceptable landscape transformation.

In 1894, the strip of land between KwaZulu-Natal and Swaziland was proclaimed a protected nature reserve: Pongola. It was the first proclaimed nature reserve in Africa. However during the following turbulent years, it was disbanded and many animals were killed as people believed game carried Nagana and Tsetse fly diseases. The Tsetse flies were eradicated in 1948 and farmers returned. The area originally consisted mainly of grassland but bush encroachment has occurred in the last 20 years.

In 1993, the separate farms covering a large portion of the original area, agreed to common management as a biosphere. Today, this area is called the Pongola Game Reserve and encompasses land from KZN Wildlife and private landowners. One of the objectives of the

Pongola Game Reserve is the reintroduction of game to establish and maintain viable populations of animal species which historically occurred in the area.

The Pongola Game Reserve is located in the Maputoland district of Northern KwaZulu Natal, South Africa (27.35 °, 27.55° S and 31.86°, 32.02° E). It is approximately 8000 ha and surrounds part of the Jozini dam (also called Pongolapoort). The Pongola Game Reserve consists of 7 private properties with no internal fences. The climate is arid and hot, with an average temperature of 21° C and limited rainfall averaging 500mm per annum, predominantly from September to December (Goodman, 1997). The Pongolapoort dam provides however more humidity and less dehydration than further inland. The four major soil types occurring are: eroded dolomite, turf, black soil (found along the lakeshore) and red soil.

In June 1997, a group of 17 African elephant (*Loxodonta africana*) from two family groups, were relocated from the Kruger National Park, followed by a group of 4 elephant bulls in 1998. In January 1999, one bull was culled after breaking out of the reserve and a train killed another bull in September 1999. Early in 2001, a sub-adult orphan group of 3 females and 2 bulls broke into the reserve. Later that same year, 3 mature bulls also broke into the reserve. At the time of this study, the population stood at 48. It can be divided into three groups: a family herd consisting of females with young, the sub-adult orphan group and a group of 3 mature bulls. A 20km railway line splits the reserve, forming a psychological barrier for the family group which stay in an area of 3400 ha on the Eastern side adjacent to the dam. The orphans and mature bulls use the entire area of 7500ha and often cross the railway line although collisions with freight trains have occurred several times.

Pongola Game Reserve provides a unique case study where bulls and family group, are naturally separated. It is however, still quite typical of the small game farms of Northern KwaZulu Natal.

#### 1.4. THESIS OUTLINE

As the largest living terrestrial animal, the African elephant (*Loxodonta africana*) has a considerable impact on its environment. This study will focus on methods which can be used to assess its vegetation usage in order to begin understanding how large a home range should be to support a particular population without permanently altering the vegetation composition.

Due to the enormous complexity of an ecological system and the long periods of the dynamics, it is very difficult to analyse the interaction between elephant and tree populations solely by conducting field studies. However, modelling has been found to be an effective tool to investigate and reveal important aspects of the system dynamics. The development of suitable computer models allows for scenario planning and prediction and can help with the effective management of elephant and the ecological systems in which they live.

This research investigates a specific situation where elephant have been reintroduced to a region and there is concern as to the damage they might cause. In the first step, sufficient field data is collected to map the vegetation and assess damage. Predictive computer models studying the interaction between elephant and their food source are then developed using field data as parameters and for validation. Modelling methods for understanding global scale changes and local scale changes are applied.

To try and appraise to what extent the impact on the vegetation is predictable given a particular region and group of elephant, the following is undertaken:

- Build a GIS (Geographic Information System) vegetation map of the area in question
- Consider field studies to provide a better assessment of the existing vegetation and random sampling to give an estimate of damage to date.

- Investigate the global dynamics of the elephant / tree system with a set of ordinary differential equations
- Investigate local dynamics of the elephant / tree system using a grid based model
- Investigate local and global dynamics of the elephant / tree system using a combination of ode's and grid based models

## **CHAPTER TWO**

### **VEGETATION STRUCTURE OF THE PONGOLA GAME RESERVE**

#### **2.1. INTRODUCTION**

The first step towards understanding the impact of elephant on a particular reserve, is to establish the topography of their environment. For this, a detailed terrain and vegetation map is important. In the Pongola Game Reserve, we are faced with largely uniform terrain, so vegetation becomes the crucial element. In this case, a vegetation map is created from aerial photographs and checked on the ground for accuracy. The map is then used for first estimates of elephant impact and serves as a basis for habitat utilisation analysis. It is also used in spatially explicit simulation models.

#### **2.2. METHODS**

Aerial photographs from the Office of the Surveyor General were digitised with Mapinfo PC based mapping software to produce a GIS (Geographic Information System) map of the reserve combining layers of information such as roads, rivers, dwellings and different vegetation types.

##### **2.2.1. Transects**

Fifty-two transects were distributed randomly throughout the study area. They were sampled for woody plants over 0.5 m. Species and height classes were recorded. An assessment of canopy cover for each area sampled was also made. Furthermore, a study of vegetation dynamics and browser utilisation was conducted using forty-three additional transects distributed randomly throughout the study area and independent of the original sample transects. These transects were 50 meters in length and up to 5 meters wide. The width was chosen according to plant density. Relatively rare plants outside transects were recorded using a nest method. The direction of each transect was chosen at a 90° angle to the slope or

in the absence of elevation, parallel to the direction of waterways such as rivers or the dam. This ruled out differences in abundance or composition within transects caused by elevation or cross over to a different vegetation type. For each tree, the following was recorded: species, number of stems (live and dead) with their diameter, height, canopy dimensions, state, utilisation (age, agent and growth response). A herbarium was developed to facilitate tree and shrub identification within the Pongola Game Reserve.

The presence/absence of 62 species of trees in the Pongola Game Reserve was analysed by **Two-Way Indicator Species Analysis**, to establish the major species assemblages and to examine the spatial distribution of woody plant communities.

### **2.2.2. TWINSPAN**

**Two-Way Indicator Species Analysis**, or TWINSPAN, is a FORTRAN program widely used by ecologists for classifying species and samples, producing an ordered two-way table of their occurrence. This numerical classification technique developed specifically for hierarchical classification of community data was originally devised by Hill (1979) for vegetation analysis. It is best envisaged in terms of samples characterised by species' abundances. The technique is based on the concept that a group of samples which constitute a community type will have a corresponding group of species that characterise that type (indicator species). The technique begins with an ordination produced by reciprocal averaging (RA). Ordination is a widely-used family of methods which attempts to reveal the relationships between ecological communities. The use of a reciprocal averaging algorithm provides a solution to the task of discovering appropriate weights for species and samples. The ordination is divided at its centroid. Each sample is then classified into one of two groups, and a discriminant function analysis is used to refine the classification. Essentially, species are scored according to their degree of preference for one side or the other. Highly preferential species are those that are at least 3 times more common on one side. These species scores are applied back to the samples, using a weighting algorithm. This is now the first division.

The process is hierarchical, and each of the new groups undergoes the same process until either a certain number of divisions has been reached or a group is too small to subdivide further. Once all the samples have thus been classified, the species are classified according to their overall fidelity to the groups and a sorted table is produced.

The final product of a TWINSpan run is called a two-way table. The two-way table is one of the most powerful tools available for vegetation analysis. In it, stands are arrayed according to dissimilarity in species composition (the less dissimilar, the closer they are; the more dissimilar, the farther apart they are). So the species list in the two-way table proceeds from a single species on one end, through progressively less similar species, to a species on the other end of the list that likely occurs in a different environment, and never in the same place as the first species.

The steps in TWINSpan are as follow:

1. Ordinate the samples by RA.
2. Find the best place ("centre of gravity") at which to split the data set into two.
3. Identify the species showing most difference in occurrence on the two sides (+ve and -ve) of the split - these are termed Indicator Species.
4. Use these species to do a "refined ordination" and verify the best split.
5. Calculate indicator scores for the samples (adding +1 for each +ve indicator species present and -1 for each -ve indicator species).

Repeat steps 1 to 5 for each of the sub-groups until the required number of classes is obtained. The splits between classes can be described in terms of (a) how "good" they are, i.e. how different are the resultant groups, and (b) indicator species.

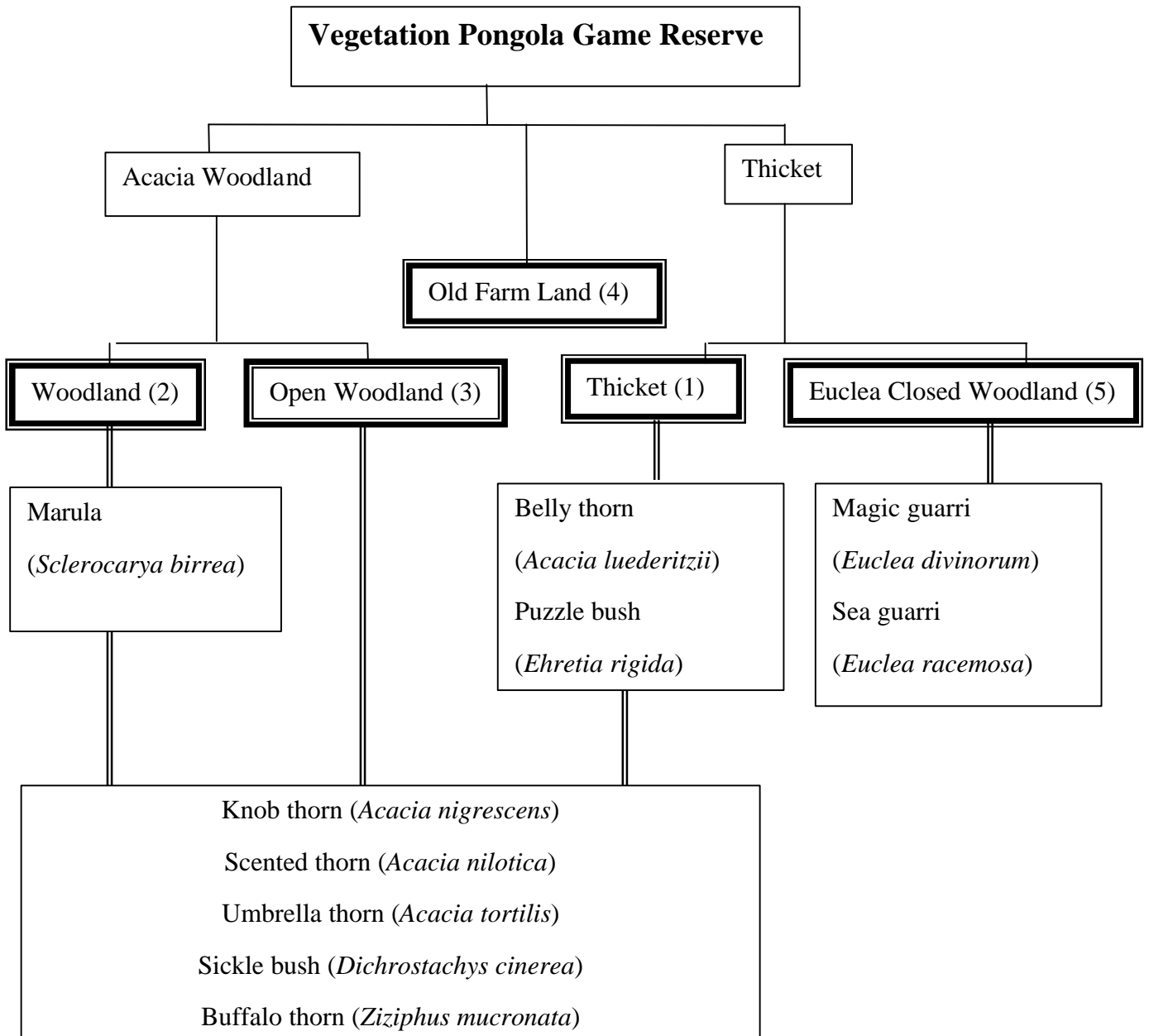
The results of the TWINSpan analysis were used together with estimates of cover to define broad woody vegetation types in terms of species composition and abundance. This analysis helped to refine the vegetation regions digitised from the aerial photographs.



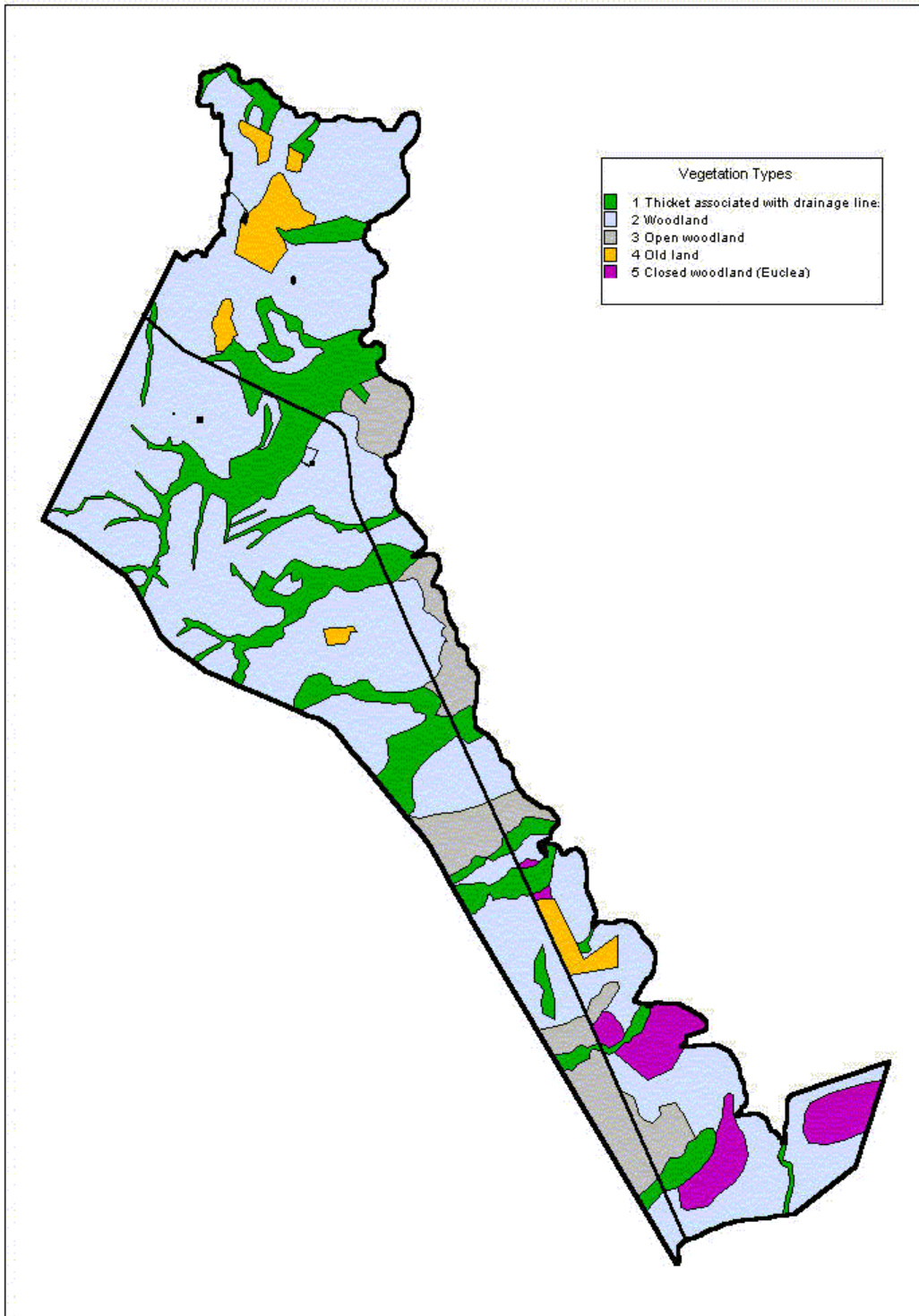
### 2.3. VEGETATION TYPES

Five major vegetation types were identified based on extent of cover and species composition : Thicket (1), Woodland (2), Open woodland (3), Old farm land (4) and Euclea closed woodland (5). Key species in each group can be seen in Fig. 2.1. Knob thorn (*Acacia nigrescens*), Scented thorn (*Acacia nilotica*), Umbrella thorn (*Acacia tortilis*), Sickle bush (*Dichrostachys cinerea*) and Buffalo thorn (*Ziziphus mucronata*) provide the major split between the Acacia dominated communities and the Euclea closed woodland. The difference between Woodland and Open woodland is based on cover: 0.25-0.6 and 0.1-0.25 respectively. Analysis of species composition based on transect data revealed that Marula (*Sclerocarya birrea*) is almost exclusively found in the Woodland vegetation type (2). This is an interesting fact in itself since Marula is a relatively rare tree and enjoys a high profile with the landowners.

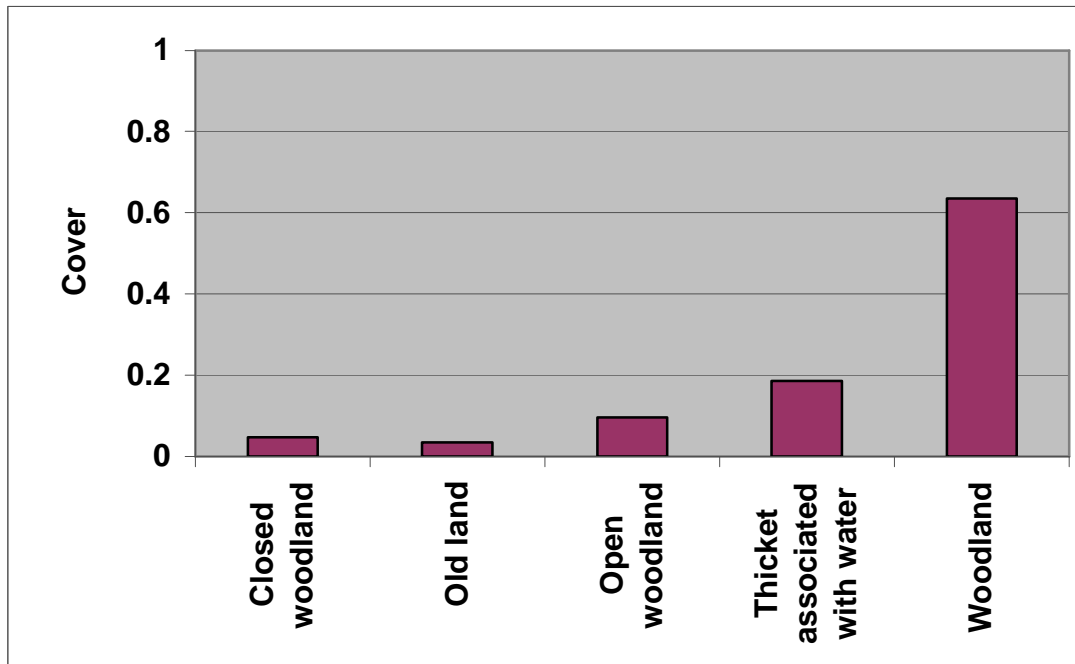
A map of the Pongola Game Reserve with the vegetation types is given in Fig. 2.2. The amount of land covered by each vegetation type as a percentage of the whole is given in Fig. 2.3. It is evident that Woodland is by far the most extensive vegetation type but as will be seen further in this thesis, Thicket associated with drainage lines is very significant because of its high tree density (i.e. excellent source of food).



**Fig. 2.1** Flow Diagram of Vegetation Types



**Fig 2.2** Vegetation Types for the Pongola Game Reserve



**Fig. 2.3** Cover for each vegetation type as a percentage of the whole of the Pongola Game Reserve

Table 2.1 gives the list of woody species recorded (> 0.5m) with average densities per ha. The most abundant species, in descending order, are Sickle bush (*Dichrostachys cinerea*), Knob thorn (*Acacia nigrescens*), Mallow raisin (*Grewia villosa*), Umbrella thorn (*Acacia tortilis*), Puzzle bush (*Ehretia rigida*) and Scented thorn (*Acacia nilotica*). The abundance of Sickle bush gives further evidence of bush encroachment after livestock farming.

Genus	Species	Average Density per ha (>0.5m)
<i>Acacia</i>	<i>Borleae</i>	0.78
<i>Acacia</i>	<i>Caffra</i>	0.31
<i>Acacia</i>	<i>Luederitzii</i>	no data
<i>Acacia</i>	<i>Nigrescens</i>	108.81
<i>Acacia</i>	<i>Nilotica</i>	77.72
<i>Acacia</i>	<i>Robusta</i>	5.99
<i>Acacia</i>	<i>Senegal</i>	8.85
<i>Acacia</i>	<i>Tortilis</i>	87.77
<i>Acacia</i>	<i>Xanthophloea</i>	no data

<i>Aloe</i>	<i>Marlothii</i>	0.06
<i>Azima</i>	<i>Tetracantha</i>	4.98
<i>Berchemia</i>	<i>Zeyheri</i>	4.19
<i>Bolusanthus</i>	<i>Speciosus</i>	6.64
<i>Cadaba</i>	<i>Natalensis</i>	0.47
<i>Canthium</i>	<i>Inerme</i>	0.23
<i>Canthium</i>	<i>Spinosum</i>	1.16
<i>Capparis</i>	<i>Tomentosa</i>	23.26
<i>Cassine</i>	<i>Transvaalensis</i>	5.58
<i>Catunaregum</i>	<i>Spinosa</i>	0.93
<i>Combretum</i>	<i>Apiculatum</i>	3.72
<i>Combretum</i>	<i>Erythrophyllum</i>	0.93
<i>Commiphora</i>	<i>Africana</i>	3.76
<i>Commiphora</i>	<i>Pyracanthoides</i>	3.02
<i>Cordia</i>	<i>Monoica</i>	0.78
<i>Crotalaria</i>	<i>Capensis</i>	1.86
<i>Dichrostachys</i>	<i>Cinerea</i>	352.50
<i>Dovyalis</i>	<i>Caffra</i>	0.09
<i>Ehretia</i>	<i>Amoena</i>	2.00
<i>Ehretia</i>	<i>Rigida</i>	86.54
<i>Euclea</i>	<i>Divinorum</i>	31.63
<i>Euclea</i>	<i>Natalensis</i>	5.12
<i>Euclea</i>	<i>Racemosa</i>	20.13
<i>Euclea</i>	<i>Undulata</i>	2.79
<i>Gardenia</i>	<i>Volkensii</i>	9.50
<i>Grewia</i>	<i>Bicolor</i>	5.12
<i>Grewia</i>	<i>Caffra</i>	3.72
<i>Grewia</i>	<i>Flava</i>	17.79
<i>Grewia</i>	<i>Hexamita</i>	23.91
<i>Grewia</i>	<i>Monticola</i>	0.19
<i>Grewia</i>	<i>Occidentalis</i>	3.72
<i>Grewia</i>	<i>Villosa</i>	105.96
<i>Gymnosporia</i>	<i>Buxifolia</i>	49.84
<i>Harpephyllum</i>	<i>Caffrum</i>	9.30
<i>Hippobromus</i>	<i>Pauciflorus</i>	0.16
<i>Maerua</i>	<i>Angolensis</i>	4.65
<i>Myrica</i>	<i>Serrata</i>	0.16
<i>Ormocarpum</i>	<i>Trrichocarpum</i>	0.93

<i>Ozoroa</i>	<i>Engleri</i>	1.20
<i>Pappea</i>	<i>Capensis</i>	16.43
<i>Pavetta</i>	<i>Lanceolata</i>	0.98
<i>Peltophorum</i>	<i>Africanum</i>	0.31
<i>Pyrostria</i>	<i>Hystrix</i>	4.65
<i>Rhoicissus</i>	<i>Digitata</i>	0.47
<i>Rhoicissus</i>	<i>Tridentata</i>	1.86
<i>Rhus</i>	<i>Dentata</i>	6.51
<i>Schotia</i>	<i>Brachypetala</i>	15.43
<i>Schotia</i>	<i>Capitata</i>	7.44
<i>Sclerocarya</i>	<i>Birrea</i>	12.48
<i>Sideroxylon</i>	<i>Inerme</i>	0.93
<i>Spirostachys</i>	<i>Africana</i>	31.26
<i>Ximenia</i>	<i>Caffra</i>	0.27
<i>Ziziphus</i>	<i>Mucronata</i>	23.73

**Table 2.1 Species list with estimated densities**

## **2.4. PRELIMINARY ANALYSIS AND DISCUSSION**

An indication of the overall woody abundance for each vegetation type is given in Table 2.2. Closed woodland is the densest, followed by Thicket, Woodland, Open woodland and Old farm land. The accuracy of the vegetation type classifications is therefore strengthened. Densities of trees under 0.5m were divided into densities of trees over 0.5m to provide a crude estimate of recruitment. One needs to emphasise that this method does not give the actual recruitment but is used to compare the rate of regeneration in the different types of vegetation. Recruitment appears to be very good in all vegetation types. In Acacia dominated regions (types 1, 2, 3 and 4), the higher the density, the lower the recruitment. This would be expected since the slope of a typical density growth curve will decrease with density. High recruitment in the Closed woodland might be explained by the difference in species composition (mainly Eucleas are found in type 5).

Vegetation type	Thicket (1)	Woodland (2)	Open woodland (3)	Old land (4)	Closed woodland (5)
> 0.5 m	1516	1311	949	49	2567
< 0.5 m	456	820	748	130	1727
Recruitment	0.30	0.63	0.79	2.68	0.67

**Table 2.2 Overall density of woody trees per ha by vegetation type**

Table 2.3 provides an indication of the extent of elephant damage. However, many of the trees with over 50% canopy removed can still survive so Table 2.3 gives an upper estimate of trees killed by elephant. The values in Table 2.3 are much lower than the estimates for recruitment in Table 2.2. Thus, overall tree survival appears good but individual tree species could still be threatened.

Vegetation type	Thicket (1)	Woodland (2)	Open woodland (3)	Old land (4)	Closed woodland (5)
> 0.5 m	0.05	0.05	0.09	0.00	0.06
< 0.5 m	0.09	0.15	0.01	0.00	0.07

**Table 2.3 Proportion of woody trees per vegetation type with at least 50% of the canopy removed by elephant**

It is essential to note that while destruction of mature trees is obvious and tends to attract attention, the status and fate of seedlings and other regenerating growth is much more difficult to assess. In the Pongola Game Reserve, the overall tree recruitment does not appear to be significantly affected by elephant (see also Duffy *et al.*, 2002). However, further analysis must be done on a species basis as some species might be more vulnerable than others. In the next chapter, we will select a number of species which seem to be favoured by elephant and analyse their utilisation.

# **CHAPTER THREE**

## **ANALYSIS OF DATA ON VEGETATION UTILISATION**

### **3.1. INTRODUCTION**

Understanding the impact of elephant on a particular area requires an on-going monitoring of the vegetation. As seen in Chapter 2, a vegetation map together with a list of species, are the corner stones of any study. Transects can then be set-up and detailed data on vegetation utilisation can be collected.

The subsequent analysis of the data will show to what extent elephant alter their environment in the short and long term. A number of studies have adopted similar approaches (see Hiscocks (1998), Bowland and Yeaton (1997)). However in the latter, the elephant had been tamed and difference in results could be explained by behavioural patterns.

### **3.2. METHODS**

This chapter deals with the first transect data ever collected in the Pongola Game Reserve, showing tree utilisation by elephant. The recording was the work of undergraduate students from Holland (Duffy *et al.*, 1999) and took place between October and November 1999. At this point in time, elephant would have been in the reserve for approximately 28 months. Data was recorded in 20 transects of 1000m by 20m (2 ha) located throughout the reserve along dirt roads. Each transect was made up of 10 meters on each side of the road. Trees in each transect were divided into two categories. The first category comprises tree species thought to be important in the elephant diet (see Table 3.1).



Genus	Species	Common Name
<i>Acacia</i>	<i>Nigrescens</i>	Knob Thorn
<i>Acacia</i>	<i>Nilotica</i>	Scented Thorn
<i>Acacia</i>	<i>Robusta</i>	Splendid Thorn
<i>Acacia</i>	<i>Senegal</i>	Three-hook Thorn
<i>Acacia</i>	<i>Tortilis</i>	Umbrella Thorn
<i>Acacia</i>	<i>Xanthophloea</i>	Fever Tree
<i>Combretum</i>	<i>Apiculatum</i>	Red Bushwillow
<i>Sclerocarya</i>	<i>Birrea</i>	Marula
<i>Ziziphus</i>	<i>Mucronata</i>	Buffalo Thorn

**Table 3.1 Tree species for which utilisation data was collected**

For each of the above trees the following information was recorded:

- 1- Size relative to the species (large, medium, small)
- 2- Status (alive, dead, sick or destroyed by elephant)
- 3- Type of elephant utilisation:
  - Pushed (percentage pushed towards the ground)
  - Debarked (percentage of circumference debarked)
  - Browsed (percentage of canopy removed by elephant)

The second category comprises all other trees. Trees in the second category identified as utilised, represented only 0.61% of the total. This reinforces the assumption that the first category (Table 3.1) is representative of the species utilised by elephant. Transect data standardised to 1 ha and averaged for the region is presented in Fig 3.1 in the form of bar charts.

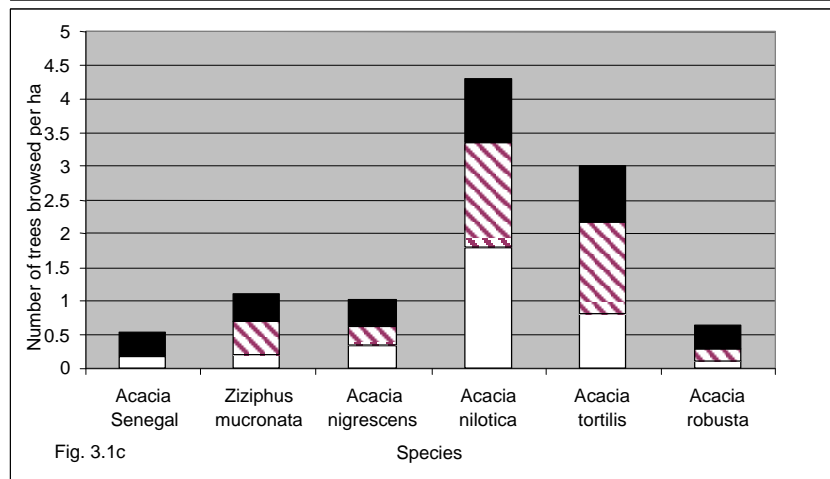
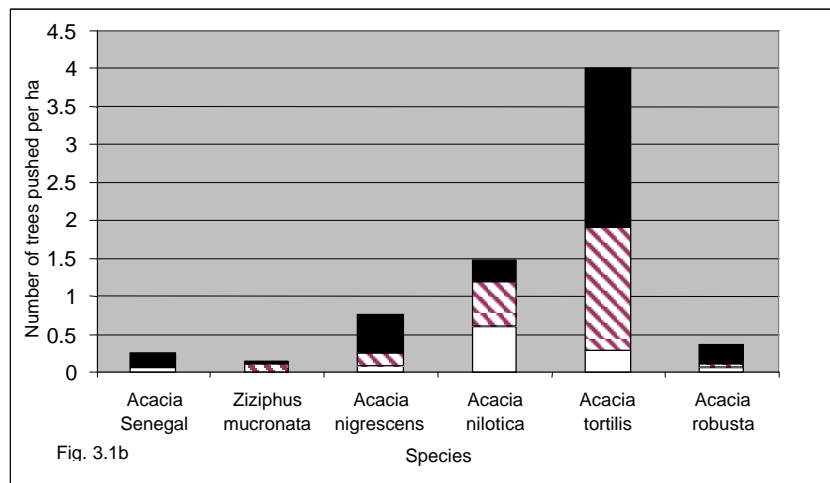
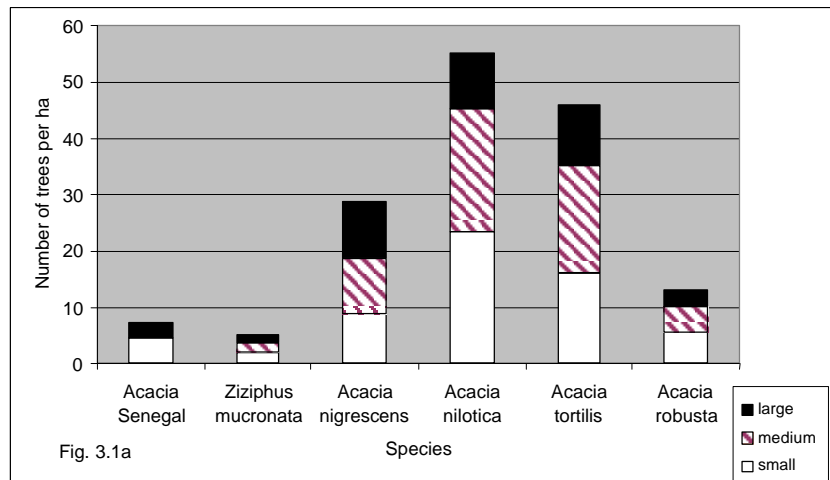
During the 28 month period following the reintroduction of elephant in the reserve, their position was recorded once a day on 302 days for the female herd and on 237 days for the bulls. The reserve was divided into 14 different regions and sightings were recorded as belonging to one of those 14 regions. This method gives an indication of elephant range but is not an exact measure of the length of time elephant are found in a particular region.

### **3.3. ANALYSIS OF TREE UTILISATION**

The trees in Fig. 3.1 are divided into three size classes: large, medium and small as defined in Table 3.2. The densities of the most abundant tree species per hectare are given in Fig. 3.1a (tree densities > 1/ha). Trees killed by elephant are included. Therefore Fig. 3.1a is a representation of the densities of trees available at the time of reintroduction. It can be seen that the most abundant species are *Acacia tortilis*, *Acacia nilotica* and *Acacia nigrescens* which all occur throughout the reserve.

Fig. 3.1b gives the number of trees per ha pushed over by elephant (at least 67.5 % toward the ground).

Fig. 3.1c gives the number of trees browsed but not pushed over. *Acacia tortilis* and *Acacia nilotica* are the most utilised trees. Of the two, *Acacia nilotica* is more browsed but more *Acacia tortilis* are pushed over. *Acacia tortilis* is on average larger and has a flatter crown than *Acacia nilotica* and one possible explanation for this difference in utilisation is that elephant push over *Acacia tortilis* to get at the inaccessible leaves.



**Fig. 3.1** Trees per hectare with densities > 1/ha (size classes indicated). Total density is the sum of the three size class densities for each species.

**(3.1a)** Number of trees per hectare available to the reintroduced elephant (trees currently alive and killed by elephant).

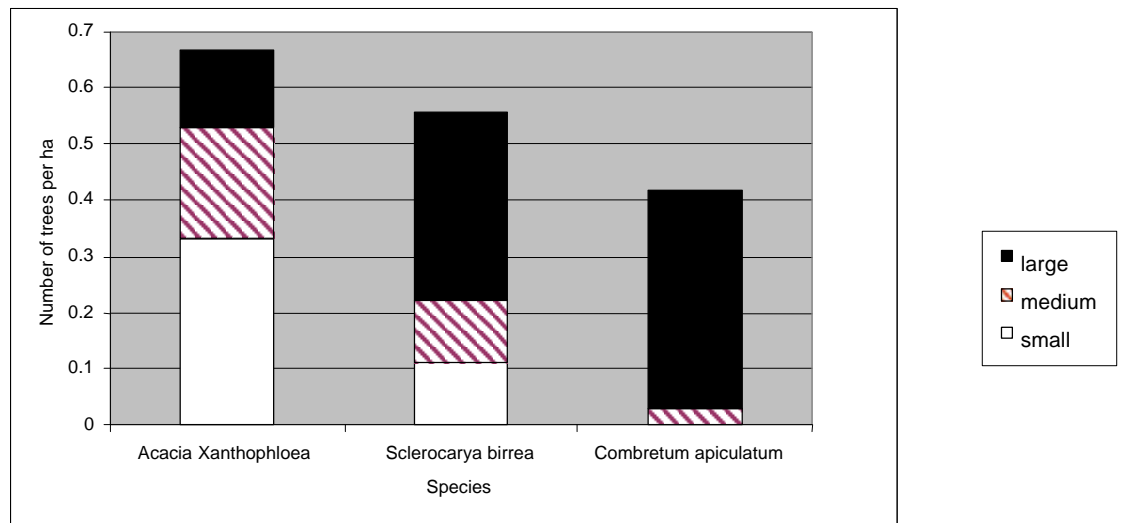
**(3.1b)** Number of trees per hectare pushed over by elephant.

**(3.1c)** Number of trees per hectare browsed but not pushed over.

Species	large	medium	small
<b><i>Acacia Nigrescens</i></b> height stem circumference	>3 m >20 cm	>2 m >15 cm	>1,5 m >10 cm
<b><i>Combretum Apiculatum</i></b> height stem circumference	>3 m >20 cm	>2 m >15 cm	>1,5 m >10 cm
<b><i>Acacia Tortilis</i></b> height stem circumference	>2,5 m >25 cm	>2 m >15 cm	>1,5 m >5 cm
<b><i>Ziziphus Mucronata</i></b> height stem circumference	>2,5 m >20 cm	>2 m >10 cm	>1,5 m >5 cm
<b><i>Acacia Nilotica</i></b> height stem circumference	>2 m >20 cm	>1,5 m >10 cm	>1 m >5 cm
<b><i>Acacia Senegal</i></b> height stem circumference	>2 m	none	>1 m
<b><i>Sclerocarya Birrea</i></b> height stem circumference	>3 m >30 cm	>2,5 m >20 cm	>2 m >10 cm
<b><i>Acacia Xanthophloea</i></b> height stem circumference	>8 m >25 cm	>5 m >15 cm	>2,5 m >10 cm
<b><i>Acacia Robusta</i></b> height stem circumference	>3 m >30 cm	>2 m >20 cm	>1,5 m >10 cm

**Table 3.2 Definition of size classes for selected species**

The three rarest species considered are *Sclerocarya birrea*, *Acacia xanthophloea* and *Combretum apiculatum* (tree densities < 1/ha in Fig. 3.2). It can be seen that no *Combretum apiculatum* was recorded in the small size class. This is a concern and should be considered further (the extent and design of this study is not detailed enough to make firm conclusions about such rare trees since they are likely to occur in patchy distributions).

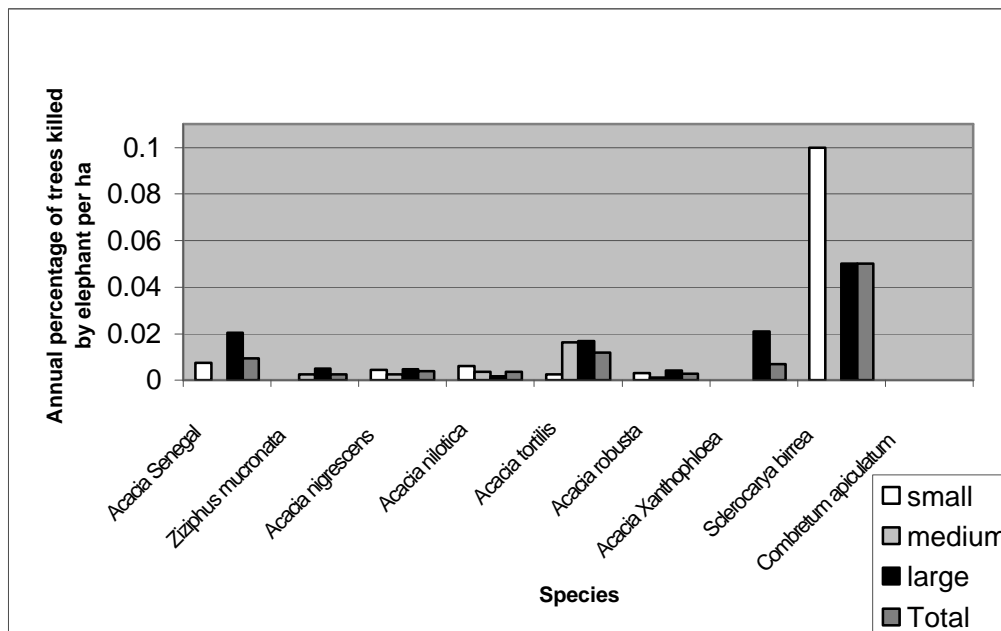


**Fig 3.2** Number of trees per hectare (with densities < 1/ha), available to the reintroduced elephant (trees currently alive and killed by elephant).

Fig. 3.3 gives the annual rate of trees judged to be destroyed by elephant as a percentage of those that were available to the reintroduced elephant. The number of years that elephant were present is taken as two (the totality of the group was present for 28 months). Annual regeneration of trees will vary by species and region but is likely to be in the range 0.01 to 0.04 (Duffy *et al.*, 1999). Thus, any species being removed at a rate greater than 0.04 per year could eventually be decimated. It appears from Fig. 3.3 that *Sclerocarya birrea* (Marula) is threatened. The greatest concern is for the small size class with 0.1 removal. However, as *Sclerocarya birrea* is relatively rare (Fig. 3.2), more widely distributed data of elephant impact on that particular species is needed. Other species do not appear to be under threat. *Acacia tortilis* for example is liked by elephant (Fig. 3.1) but total destruction (dead)

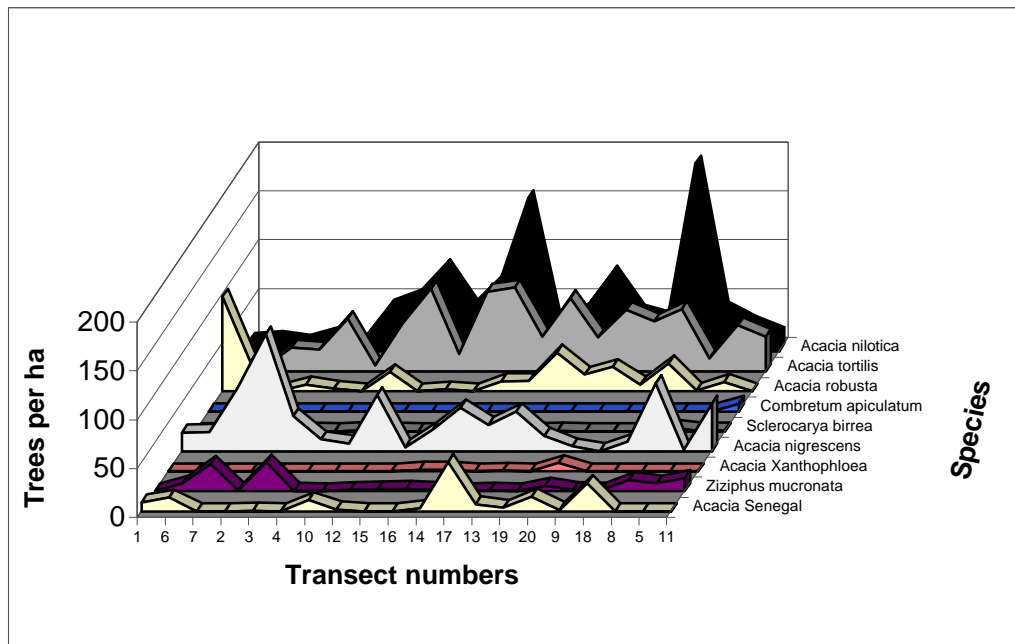
is low. Moreover, the small size class is well represented for the species (Fig. 3.1a) but relatively untouched compared to the small size class of *Sclerocarya birrea* (see Fig. 3.3) and it appears that the recruitment of *Acacia tortilis* is not under severe threat.

It should be noted that for some species, the number of trees pushed over (at least 67.5° toward the ground) plus the number of trees debarked (at least 50% of the circumference) is higher than the number of dead trees but those trees could still die. The largest discrepancy is for *Acacia xanthophloea* (over 0.1 per annum pushed and debarked). However, *Acacia xanthophloea* is a very supple tree and does not always die when pushed over. As with *Sclerocarya birrea*, its distribution is likely to be patchy and more detailed data is needed.

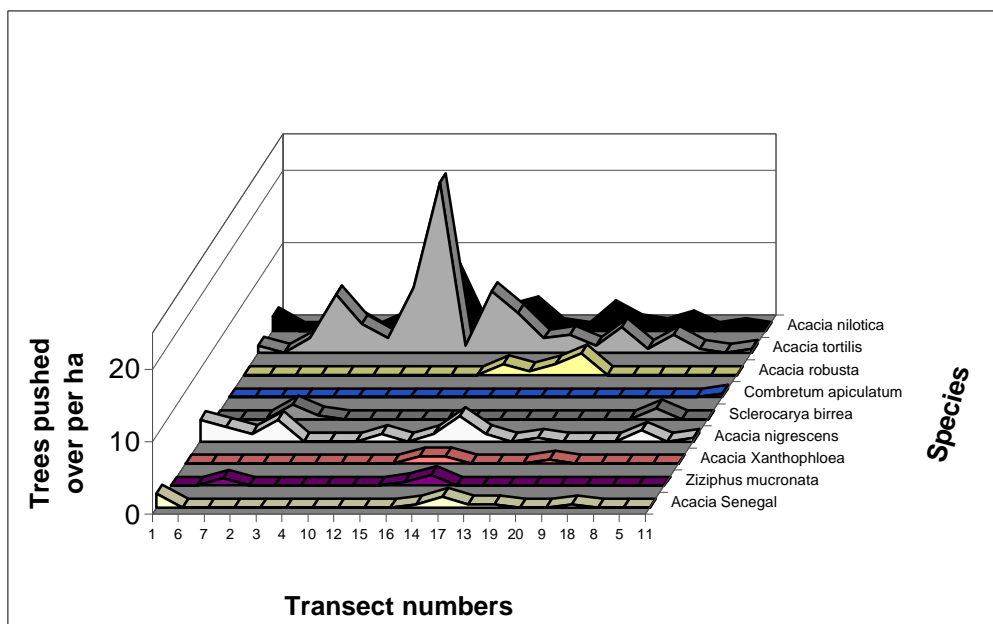


**Fig. 3.3** Annual percentage of trees per hectare killed by elephant for all species in the first category, averaged over all transects.

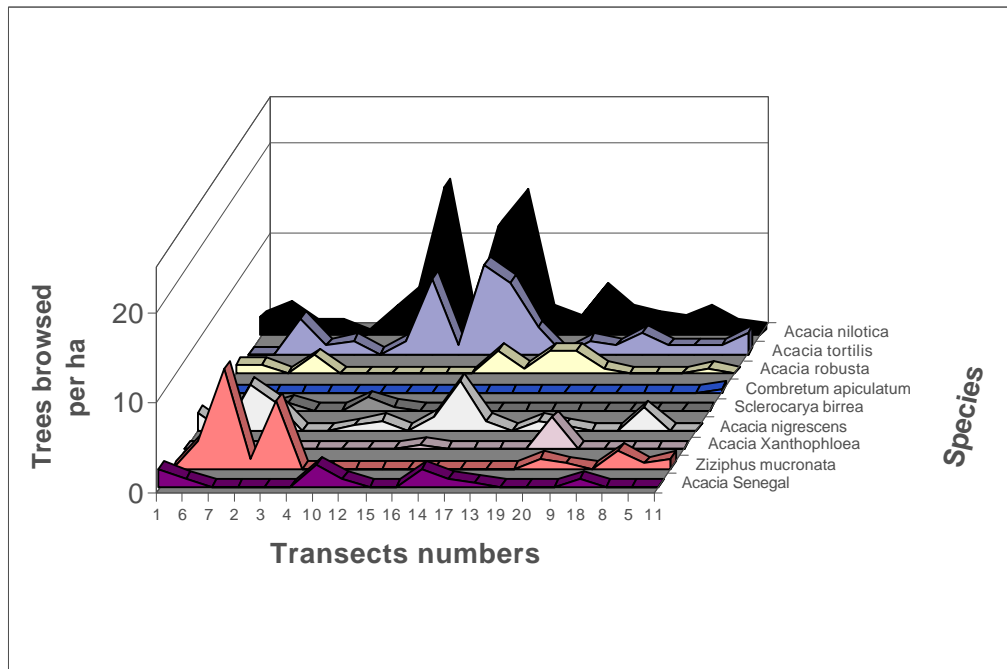
Tree density data by region is shown in Fig. 3.4a, Fig. 3.4b and Fig. 3.4c. The transect numbers on the x-axes are in order of adjacency. Transects only accessed by bulls are separated and placed at the end (13 to 11).



**Fig. 3.4a** Densities of trees available to the reintroduced elephant for the 9 selected species. The transects are given in order of adjacency. Transects only accessed by bulls are separated and placed at the end (transects 13 to 11).



**Fig. 3.4b** Densities of trees pushed over for the 9 selected species. The transects are given in order of adjacency. Transects only accessed by bulls are separated and placed at the end (transects 13 to 11).



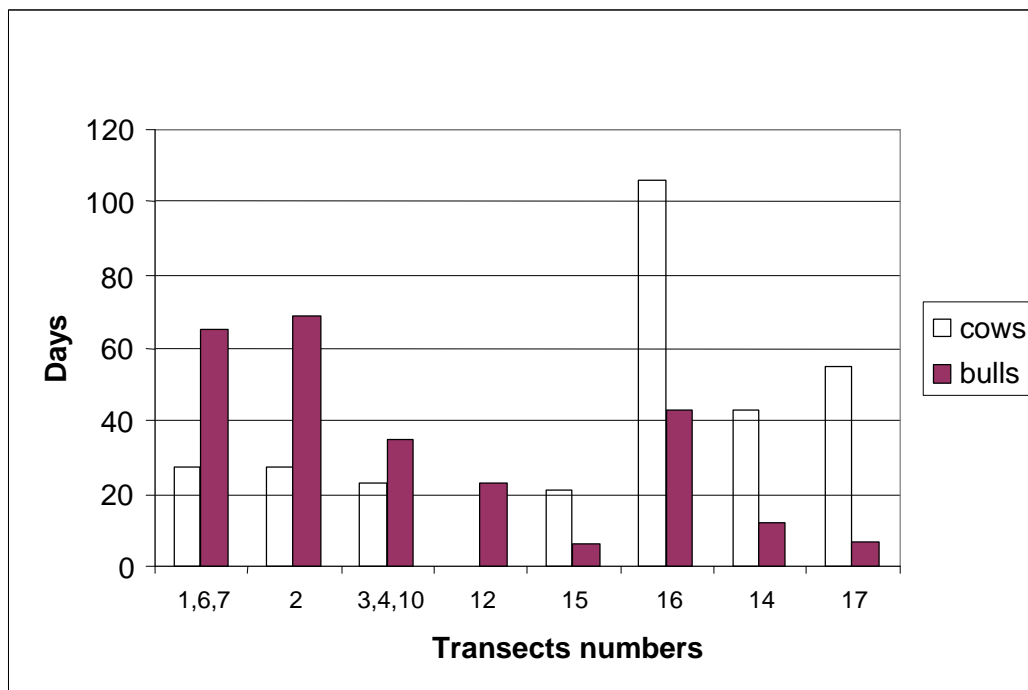
**Fig. 3.4c** Densities of trees browsed but not pushed over for the 9 selected species. The transects are given in order of adjacency. Transects only accessed by bulls are separated and placed at the end (transects 13 to 11).

Tree densities available to the reintroduced elephant are presented in Fig. 3.4a. Tree utilisation is given in terms of trees pushed over in Fig. 3.4b and trees browsed in Fig. 3.4c. The densities of trees available, pushed over and browsed vary considerably from region to region. As in Fig. 3.1, it is evident that elephant heavily select *Acacia tortilis* and *Acacia nilotica*. One should note that the actual distribution of trees available and impacted do not match: *Acacia tortilis* and *Acacia nilotica* are abundant in most of the transects (Fig. 3.4a) but are not pushed over or browsed to the same extent in all transects (Fig. 3.4b and Fig. 3.4c). If one excludes the transects only frequented by bulls (transects 13 to 11), then the match between Fig. 3.4a and Fig. 3.4b or Fig. 3.4c is better. If all 9 tree species are averaged for all transects, the correlations between trees available and trees pushed or browsed are 0.54 and 0.51. For the family group transects only, these correlations are much higher with values of 0.78 and 0.86. Thus, in the female range, the abundance of trees appears to be linked to utilisation (i.e. the more trees, the more utilisation). However, this is not the case for transects frequented by bulls. Other factors must influence bull foraging.



### 3.4. SPATIAL DISTRIBUTION OF ELEPHANT IN RELATION TO UTILISATION DATA

Utilisation is much lower in the regions only frequented by the bulls (i.e. the other side of the railway line). This could be explained by the difference in the number of elephant : 3 bulls as opposed to 17 elephant in the family group. Utilisation in terms of browsing is likely to be lower. On the other hand, bulls push over trees significantly more than females (Barnes *et al.*, 1994). The higher numbers of trees pushed over in the female territory might indicate that the bulls spend more time in the territory of the family group. This conclusion is strengthened by data on daily positions in which bulls spend 67% of their time in the family group territory (237 days out of 354 days recorded). It would seem that bulls keep close to the females but are not necessarily with them (see Fig. 3.5).



**Fig. 3.5** Regions where elephant were found within the family group range (regions encompassing transects 13 to 11 are excluded). Data was taken on 354 days over a 2 year period.

The region near transect 16 is the one most frequented by the family group (Fig. 3.5). This particular region is very dense (mainly with non-palatable tree species) and the family group was observed to congregate there when agitated, possibly because after relocation, the matriarch being very nervous, stuck to dense areas that provided cover. This behaviour was recorded for the family group more than for the bulls probably because the females were protecting calves. Nervous behaviour is likely to have been reinforced by the sounds of hunting in nearby territories.

Elephant impact is much greater in the areas frequented by the family group (Fig. 3.4) but there are also variations within each region. Impact varies for areas with similar elevation, species composition and distance from water. For example transects 12 and 14 are very similar. They are both adjacent to the dam, of similar elevation and with similar species composition (Fig. 3.4a). The overall number of trees available when elephant were reintroduced was 233 per ha for transects 12 and 304 trees per ha for transect 14. But impact for transects 12 and 14 is very different. For these two transects, the number of trees only browsed is similar (28 trees per ha and 34 trees per ha) but the number of trees pushed over is much higher for transect 12 (33 trees per ha as opposed to 17 trees per ha). The bulls spend almost twice as much time near transect 12 than near transect 14 (Fig. 3.5). Considering Fig. 3.5, the females spend very little time near transect 12. This strengthens the argument that bulls push over more trees.

### **3.5. DISCUSSION**

As expected, the Pongola Game Reserve has been impacted by the reintroduction of elephant. Tree utilisation recorded included trees debarked, pushed over, browsed and dead. From the data, it becomes apparent that *Sclerocarya birrea* is the most threatened species in the park but the long-term survival of other tree species appears good. At the time of the study, the density of elephant did not appear to have reach a critical point since the rate of

tree regeneration was higher than the destruction rate. However, detailed studies on the actual tree recruitment rates for the region are necessary as well as monitoring of the elephant population. More detailed work is also needed on all rare trees because of their patchy distributions. An interesting result of this field study is that elephant impact appears non-homogeneous even in regions with very similar characteristics. Areas of the reserve with similar elevation, species composition and distance from water are impacted differently. The reasons for this could be social and behavioural. For example, bulls and the family group will impact the vegetation in different ways with bulls removing more trees than females. Thus, while elephant population growth must be factored, it appears that the population dynamics of mature bulls is also an essential component affecting the survival of trees. We will see in the following chapters that simulations give another possible explanation to the non-homogeneous impact: foraging behaviour could be the reason.

It also appears from this study that the reintroduced elephant remain in areas with dense cover even if those areas do not provide a good source of food (i.e. the females, in protecting their young, hide in those dense regions). Reintroduced elephant can be expected to be nervous. How long this particular forced behavioural pattern will last and what will be the long-term effects on tree species distributions, are some of the remaining questions.

The emphasis of this chapter was on the possibility of assessing the impact of reintroduced elephant using transect data. The method is relatively cheap to implement and the results are informative. Tree species under potential threat are highlighted. In this case, the work also gives an indication of the role of bulls and family groups in the reduction of tree biodiversity but additional work is warranted to compliment and validate these findings.

One way to analyse further the interaction between elephant and their food source is to develop suitable computer models using the collected field data as parameters and for validation. This will be the focus of the next chapters of this thesis.

## **CHAPTER FOUR**

### **UNDERSTANDING ELEPHANT AND TREE GLOBAL DYNAMICS WITH ODE'S**

#### **4.1. INTRODUCTION**

In this chapter, a simple model describing the global characteristics of an ecosystem inhabited by elephant is considered. Since a single elephant can consume up to 300 kg of vegetation - tree and grass - per day (Owen-Smith, 1988), elephant will have a significant impact on such a system. To further our understanding, we will investigate the global dynamics of an elephant / tree system with a simple set of ordinary differential equations.

As previously mentioned, Caughley (1976) was the first person to suggest the use of a predator-prey ordinary differential equation model to describe the dynamics between elephant and trees. The elephant / tree system can also be described by a variation of the predator-prey model first suggested by Holling (1959). This chapter indicates that this version of a predator-prey model appears applicable to elephant / tree dynamics. The stability properties of the system are investigated and the importance of those properties for an understanding of the global system dynamics are discussed. Actual solutions to the equations are found using the software package *Matlab* and the Runge-Kutta numerical routine.

#### **4.2. THE MODEL**

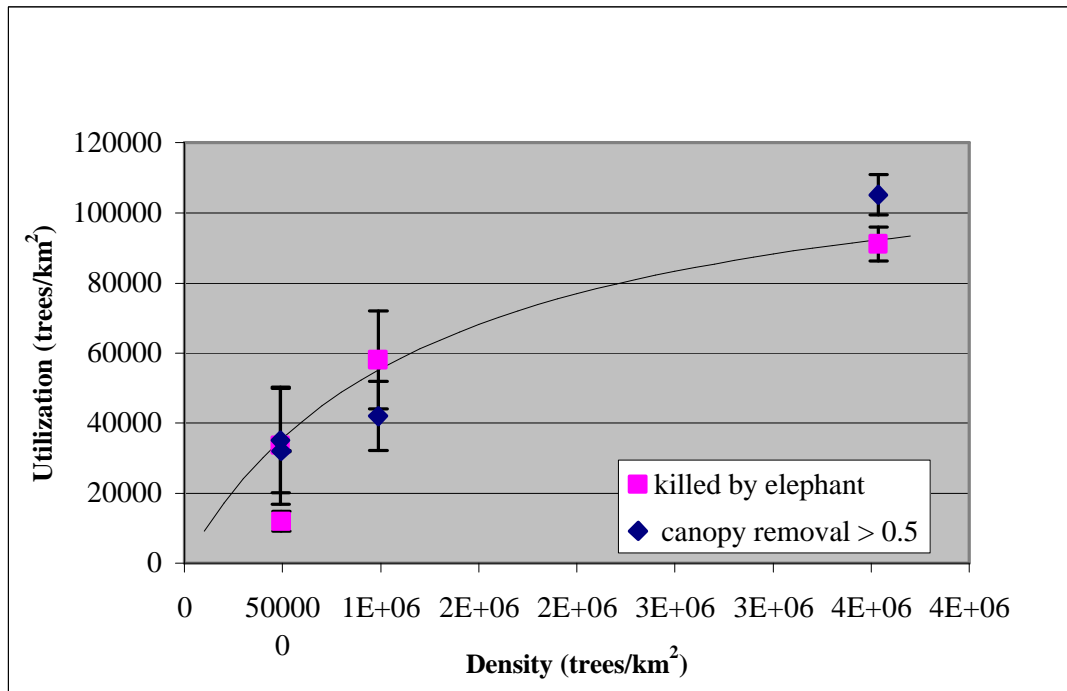
Basic predator-prey models were first proposed by Lotka in 1925 and then independently by Volterra in 1927. The approach is based on the logistic model for single species population growth given by the following equation:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) \quad (4.1)$$

where  $N$  denotes population density at time  $t$ ,  $r$  is the intrinsic relative growth rate and  $K$  is the carrying capacity of the environment for the species. A version of the original model for two interacting species from Holling (1959) is used here for the interaction between elephant and trees and is given by :

$$\begin{aligned} \frac{dT}{dt} &= r_T T \left(1 - \frac{T}{K}\right) - fr(T)E \\ \frac{dE}{dt} &= r_E E \left(1 - \frac{gE}{T}\right) \end{aligned} \quad (4.2)$$

where now  $T$  and  $E$  denote the respective densities of the tree and elephant populations at time  $t$ ;  $r_T$  and  $r_E$  are the respective growth rates and  $K$  is the carrying capacity for the trees in the absence of elephant. The parameter  $g$  is the density of trees per elephant required for elephant equilibrium. It is expected that tree removal will be a function of tree density. However, elephant can only remove a certain number of trees, so this function is expected to level out at a particular tree density. The relationship between prey removal and prey density is called the functional response and is given by  $fr(T)$  in (4.2). Functional response in predator-prey models, was considered in detail by Holling (1959), who described three broad categories of responses (Type I, Type II, Type III). Type I shows a linear increase to a plateau. In Type II, the increase in predation rate drops with increasing prey. In Type III, the predation rate is sigmoidal with an increase in prey density. A good description of the introduction of functional response by Holling can be found in Brown and Rothery (1994). Data from the Pongola Game Reserve would tend to suggest a type II functional response (Fig. 4.0).



**Fig. 4.0** The densities of trees removed (killed) or browsed by elephant as a function of overall tree density in the Pongola Game Reserve, The data is fit with the functional response equation  $fr(T)$  given in the text (full line).

Holling (1959) proposed a rectangular hyperbola to describe the Type II functional response given here for elephant and trees as :

$$fr(T) = \frac{d_T T}{1 + d_T T h} \quad (4.3)$$

where  $d_T$  is the death rate of trees due to elephant and  $h$  is the time spent by each elephant on each tree.

### 4.3. PARAMETER ESTIMATES

Units chosen for model variables are trees/km<sup>2</sup> ( $T$ ) and elephant/km<sup>2</sup> ( $E$ ). The unit of time is one year. Thus, the units of system (4.2) are trees/km<sup>2</sup>/year and elephant/km<sup>2</sup>/year, which fixes the units of each parameter. Knowledge of parameter units allows one to estimate parameter values from previous studies on elephant and trees.

Van Wijngaarden (1985) measured the change in total woody cover for the Tsavo region in Kenya where the vegetation is dominated by *Commiphora* and *Acacia* species, from 1971 to 1978. The increase ranged from 1% to 3.5% per annum. For system (4.2),  $r_T$  is assumed to vary from 0.01 to 0.04. This range is likely to be applicable to trees in the Pongola Game Reserve.

From 1967 to 1968, Kruger National Park in South Africa had its first two reliable elephant censuses. The population went from 6586 to 7701, an increase of 1115 animals for a 19 485 km<sup>2</sup> region which translates to 0.16 /year (Hall-Martin 1992). Elephant in the Pongola Game Reserve are increasing at a rate of 0.18 /year (Mackey, et al., unpublished data) and 0.02/year is taken from Duffy *et al.* (1999) as the lower limit value. Elephant recruitment  $r_E$  in a range of 0.02 to 0.18 will therefore be considered.

We can see from Chapter 3 that tree densities in the Pongola Game Reserve ranged from 6000 trees/km<sup>2</sup> to 32 000 trees/km<sup>2</sup> before the reintroduction of elephant. However it seems unlikely that the upper number is anywhere near the carrying capacity. Some regions of the Kruger National Park have average tree densities in the range of 100 000 trees/km<sup>2</sup> to 250 000 trees/km<sup>2</sup> (VanWyk & Fairall, 1969). Mopane woodlands in southern Africa have recorded densities as high as 455 000 trees/km<sup>2</sup> (Henning, 1976). For this model, the carrying capacity ( $K$ ) is set in a range of 50 000 to 500 000 trees/km<sup>2</sup>.

Based on data from VanWyk & Fairall (1969) for the proportion of trees destroyed by elephant in the Kruger National Park,  $d_T$  is in the range 0.05 km<sup>2</sup>/elephant/year to 0.3 km<sup>2</sup>/elephant/year.

It can take an elephant as little as 10 minutes to destroy a tree (a big bull can push over a medium size tree very quickly). Elephant also ringbark trees. They remove the bark with their tusks and when more than half of the circumference is taken off, the tree will most probably die. Elephant can spend hours browsing on a particular tree and in some extreme cases the tree might die as a result of extensive canopy removal. The time each elephant spend on a particular tree ( $h$ ) is set in the range of 10 minutes to 5 hours, i.e. 1.9E-5 year to 5.7E-4 year when converted to year units for the purpose of the model.

The parameter  $g$  is the number of trees required to support each elephant if the system is to remain at equilibrium. It is important to realize that  $g$  is independent of  $d_T$  because all the trees required for an elephant to survive might not be destroyed. Elephant browse on trees continuously but will only destroy some of them. From system (4.2), we can see that  $g=T/E$  at elephant equilibrium.

As mentioned earlier, Kruger National Park has regions with average tree densities between 100 000 trees/km<sup>2</sup> and 250 000 trees/km<sup>2</sup> (VanWyk & Fairall, 1969). Elephant population densities declined after reaching 0.37 in the northern sub-population, where it is dryer (Whyte, 2001). In the southern sub-population, where it is wetter, elephant densities reached 0.51 before declining (Whyte, 2001). Thus a possible range for the parameter  $g$  ( $T/E$ ) is 270 000 trees/elephant to 500 000 trees/elephant.

The ranges of parameters for system (4.2) are given in Table 4.1



	<b>Lower limit</b>	<b>Upper limit</b>	<b>Average conditions</b>
$r_T$ (/year)	0.01	0.04	0.025
$r_E$ (/year)	0.02	0.18	0.1
$K$ (trees/km <sup>2</sup> )	50 000	500 000	275 000
$d_T$ (km <sup>2</sup> /elephant/year)	0.05	0.3	0.175
$h$ (elephant*year/tree)	$1.9 \times 10^{-5}$	$5.7 \times 10^{-4}$	$3.0 \times 10^{-4}$
$g$ (trees/elephant)	270 000	500 000	385 000

**Table 4.1 Parameters range**

#### **4.4. STABILITY ANALYSIS**

Stability analysis is an important tool since it allows for an investigation of some of the global characteristics of the model without solving it. An understanding, a feel, for the equations is possible. More importantly, some of these characteristics can be essential to understand the system itself. In this example, investigating under what conditions equilibrium will exist is a major aspect of the system ecology; in other words, under which conditions both elephant and their food source (trees) survive successfully and if equilibrium exists, what type of equilibrium it is. For the situation described here, it could be a stable equilibrium point, called a node, or the dynamic equilibrium of a stable limit cycle.

To investigate stability, the method suggested by Tanner (1975) is used. Details of this analysis were worked out by K. Duffy in Stretch and Duffy (2003) and are summarised below.

The first step is to simplify the equations (4.2) by dividing the variables and some parameters by the value of tree density at equilibrium ( $T_0$ ):

$$x = \frac{T}{T_0}, y = \frac{E}{T_0}, a = \frac{K}{T_0}, b = \frac{1}{d_T h T_0} \quad (4.4)$$

Applying this transformation, allows for a simpler solution because at equilibrium,  $x = 1$ .

The new equations are:

$$\begin{aligned} \frac{dx}{dt} &= r_T x \left(1 - \frac{x}{a}\right) - \frac{xy}{h(b+x)} = f(x, y) \\ \frac{dy}{dt} &= r_E y \left(1 - \frac{gy}{x}\right) = g(x, y) \end{aligned} \quad (4.5)$$

which has equilibrium points  $x_0 = 1, y_0 = 1/g$ .

The stability of the system close to equilibrium is of interest. It is sufficient to consider a linearised version of the system because close to equilibrium, it will closely approximate the original (4.2). A simplified version of (4.2) linearised in matrix form is given by:

$$D \begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} \frac{\partial f(x_0, y_0)}{\partial x} & \frac{\partial f(x_0, y_0)}{\partial y} \\ \frac{\partial g(x_0, y_0)}{\partial x} & \frac{\partial g(x_0, y_0)}{\partial y} \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix} \quad (4.6)$$

D is called the Jacobian or community matrix. The following theorem applies:

**Theorem:** For a continuous system  $F(x, y)$ , if the eigenvalues of the associated Jacobian matrix have negative real part then the equilibrium points  $(x_0, y_0)$  are stable (for a proof see Hale and Kocak (1991)).

Using matrix algebra, the eigenvalues of D are:

$$\lambda = 0.5[(a_{11} + a_{22}) \pm \sqrt{(a_{11} + a_{22})^2 - 4(a_{11}a_{22} - a_{21}a_{12})}]$$

Thus, the conditions on stability are that the determinant of D ( $a_{11}a_{22} - a_{21}a_{12}$ ) is positive and the trace of D ( $a_{11} + a_{22}$ ) is negative.

For (4.3) these conditions are:

$$\begin{aligned} r_E r_T \left( \frac{2b+3}{r_T g h (b+1)^2} + \frac{2}{a} - 1 \right) &> 0 \\ r_T - r_E - \frac{2r_T}{a} - \frac{b}{r_T g h (b+1)^2} &< 0 \end{aligned} \quad (4.7)$$

For stability, both equations in (4.7) must be true. It is possible to manipulate these equations further. For example, one could consider the case where  $a \gg 1$ , which is realistic for the ecosystem studied here. Some terms would then be removed from (4.7). However, the accessibility to powerful computers allows one to test (4.7) directly. Each parameter combination can be tested for stability by using a simple loop in a computer program.

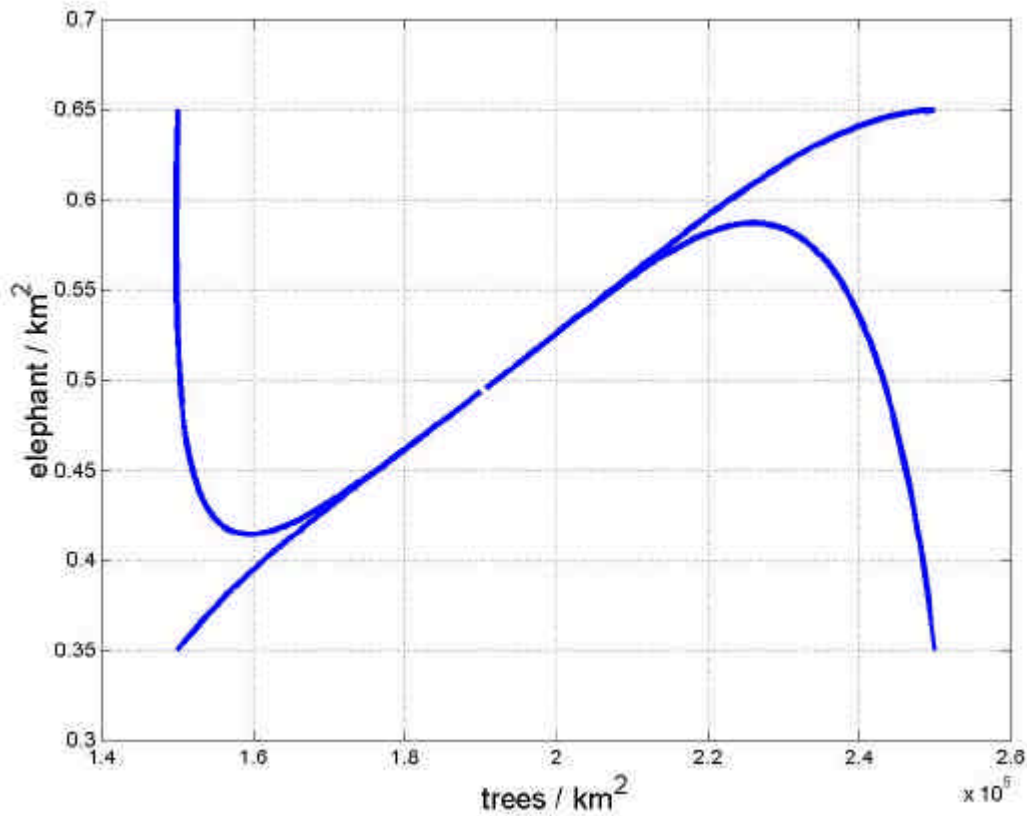
An interesting situation occurs when the dynamics tend to a stable limit cycle. In this situation, elephant and trees could co-exist but, given enough time, would continually fluctuate in a cycle. Thus, it is important to test for the possibility of limit cycles. If when substituting one or more parameters, stability changes from a node (one equilibrium point) to a limit cycle, the location at which this change takes place, is called a Hopf bifurcation. It can be shown that a Hopf bifurcation will occur when, for a change in parameters, the real part of the eigenvalues of  $D$  becomes zero and the imaginary part of the eigenvalues exists. In this case, with a further change in the same parameters, a limit cycle will occur when the real part of the eigenvalues becomes positive. The eigenvalues of  $D$  will be of the form  $I = I_1 \pm iI_2$  and then the conditions for a limit cycle :  $I_1 > 0$ ,  $I_2 > 0$ .

## 4.5. RESULTS

### 4.5.1. Parameter analysis

Using a simple program loop to test (4.7), all 64 combinations of the values in the parameter range (Table 4.1) resulted in stable equilibrium points. In other words, all of these solutions are stable but none is a stable limit cycle. The parameters for a stable limit cycle are significantly different (see section 4.5.2).

An example of model trajectories is given in Fig. 4.1 for an average set of parameters and from different initial conditions.



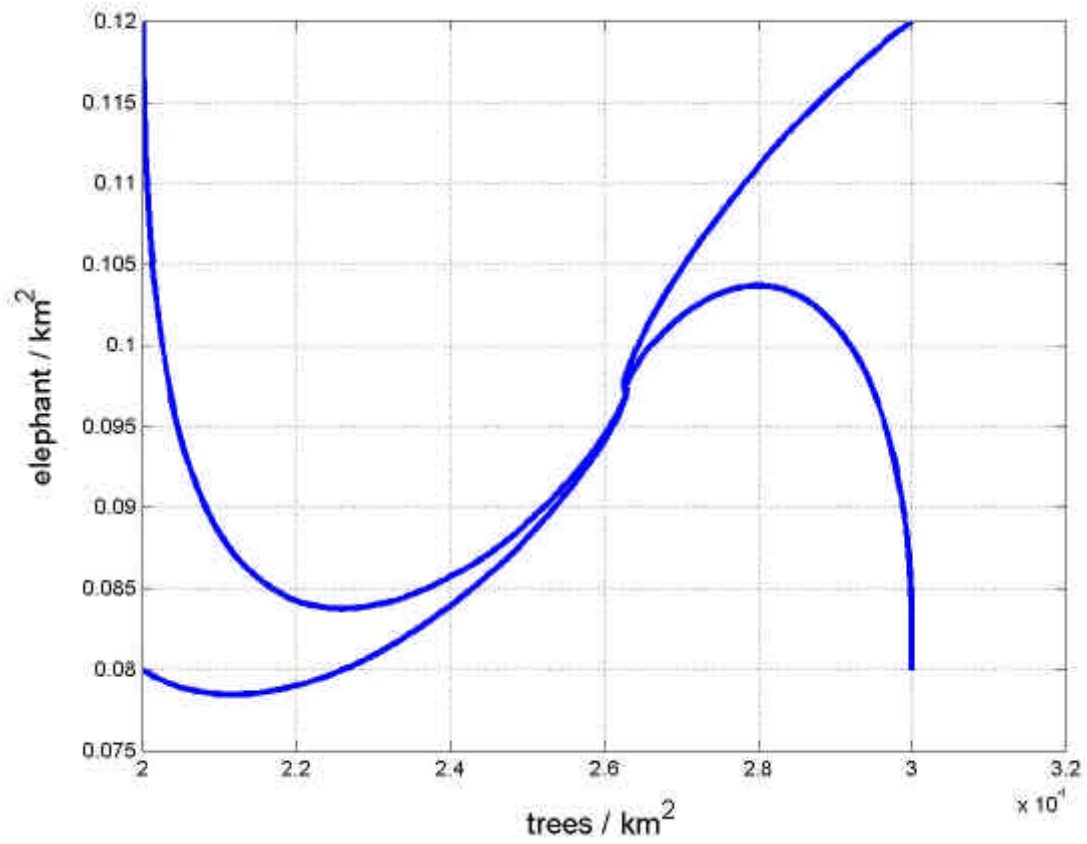
**Fig. 4.1** Model trajectories for tree density against elephant density started from different initial conditions ( $T=150000$  or  $250000$  trees/ $\text{km}^2$  and  $y=0.35$  or  $0.65$  elephant/ $\text{km}^2$ ). Parameters are taken from the average conditions in Table 4.1. The trajectories tend to an equilibrium point ( $E_0=0.5$  elephant/ $\text{km}^2$  and  $T_0=190000$  trees/ $\text{km}^2$ ).

This representation allows a comprehensive assessment of the dynamics. The resulting equilibrium is realistic and matches possible values for the Kruger National Park ( $E_0=0.5$  elephant/ $\text{km}^2$  and  $T_0=190000$  trees/ $\text{km}^2$ ). It is interesting to note that some trajectories in Fig. 4.1 are quite curved with elephant decreasing or increasing in density markedly before returning to equilibrium. One can see the significance of this result: if true, there is no need for park managers to intervene to control the elephant population since the steep increase in elephant and decrease in trees would peak and return to equilibrium. The management of

elephant populations has always been a controversial issue. Before 1994, annual culling maintained Kruger National Park population at about 7 500 (approximately 0.4 elephant/km<sup>2</sup>) and there are now about 11 000 elephant in the Kruger National Park (B. Page, *pers. comm.*). However, some believe that the optimum population is around 7 000 and culling is currently being debated. It would be interesting to know what would happen if there was no intervention. If the dynamics followed a similar trajectory to the right hand bottom one of Fig. 4.1, then elephant density might peak and return to equilibrium. However, simulations in the model were run for 250 years so the dynamics of a real system may occur over very long periods.

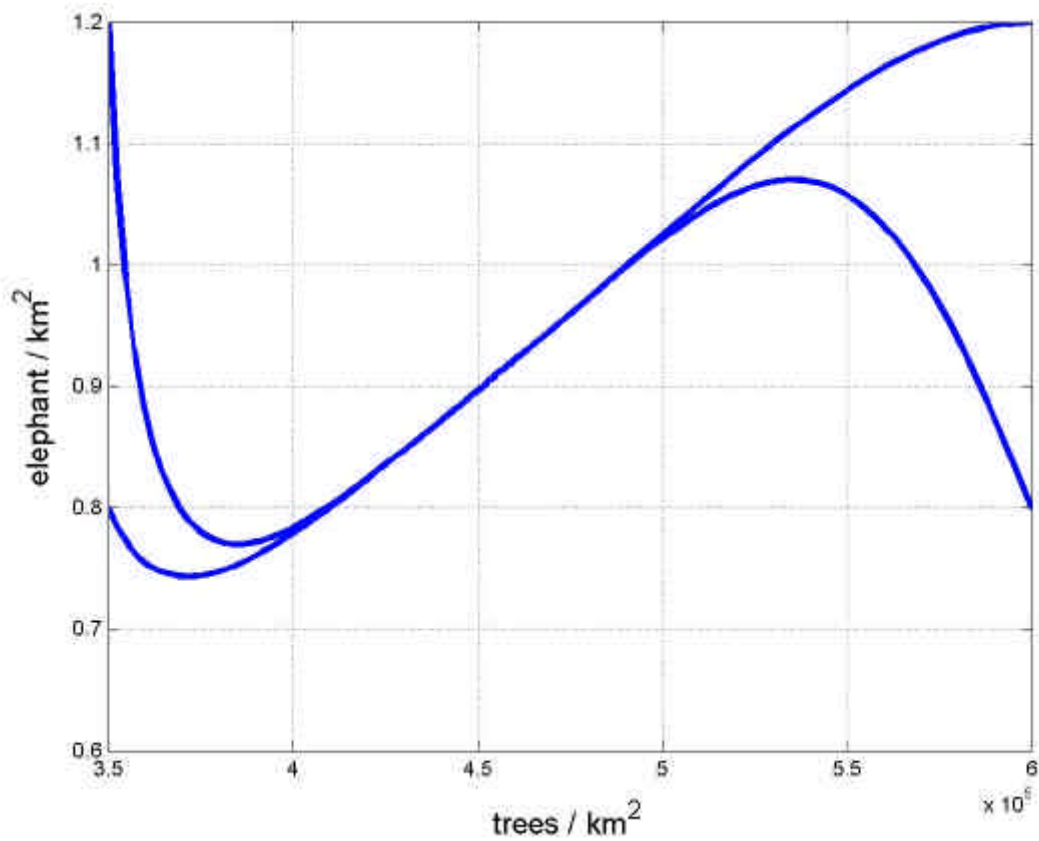
One should note that global models such as the one presented here, ignore environmental variability. They can nevertheless be used to establish bounds on elephant and tree density estimates. Table 4.1 gives upper and lower limits of parameter values obtained from the literature. The range of values is the result of different environmental conditions such as rainfall and temperature. Low rainfall areas, for example, can be expected to carry less elephant and trees than high rainfall areas.

Fig. 4.2 shows trajectories for model runs using the lower range of parameters. As expected, the densities of trees and elephant are significantly lower than in Fig. 4.1 and would represent harsher environmental conditions. The Knysna elephant population in South Africa has not recovered significantly from a density of 0.02 elephant/km<sup>2</sup> but elephant in Addo National Park in South Africa have recovered from 0.1 elephant/km<sup>2</sup> (Dudley, 1996). Thus, a density between these numbers appears to set a limit for low elephant densities and Fig. 4.2 has densities trajectories in this range.



**Fig. 4.2** Model trajectories for tree density against elephant density started from different initial conditions ( $T=20000$  or  $30000$  trees/ $\text{km}^2$  and  $y=0.08$  or  $0.12$  elephant/ $\text{km}^2$ ). Parameters are taken from the lower limits in Table 4.1. The trajectories tend to an equilibrium point ( $E_0=0.1$  elephant/ $\text{km}^2$  and  $T_0=26271$  trees/ $\text{km}^2$ ).

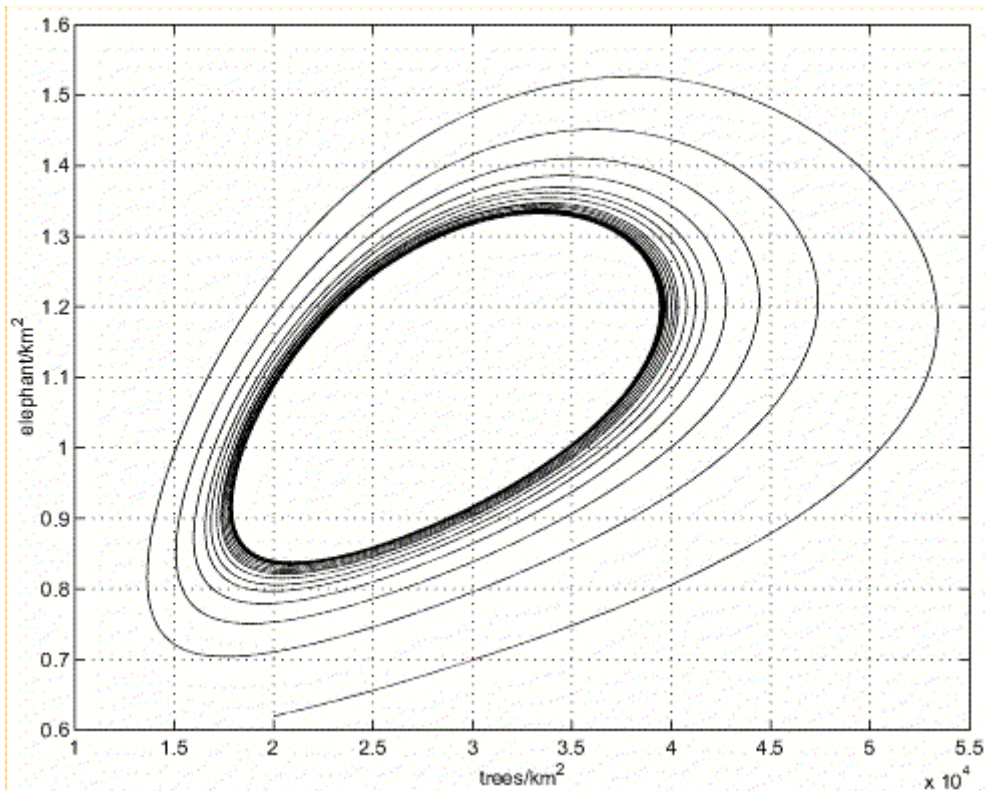
Fig. 4.3 shows trajectories for model runs using the higher range of parameters. As expected the densities of trees and elephant are significantly higher than the ones in Fig. 4.1 and Fig. 4.2 and would represent more clement environmental conditions. An elephant density as high as 2.1 elephant/km<sup>2</sup> has been recorded and the trajectories in Fig. 4.3 are below this density.



**Fig. 4.3** Model trajectories for tree density against elephant density started from different initial conditions ( $T=350000$  or  $600000$  trees/km<sup>2</sup> and  $y=0.8$  or  $1.2$  elephant/km<sup>2</sup>). Parameters are taken from the upper limits in Table 4.1. The trajectories tend to an equilibrium point ( $E_0= 0.9$  elephant/km<sup>2</sup> and  $T_0 =456700$  trees/km<sup>2</sup>).

#### 4.5.2. Limit Cycle behaviour

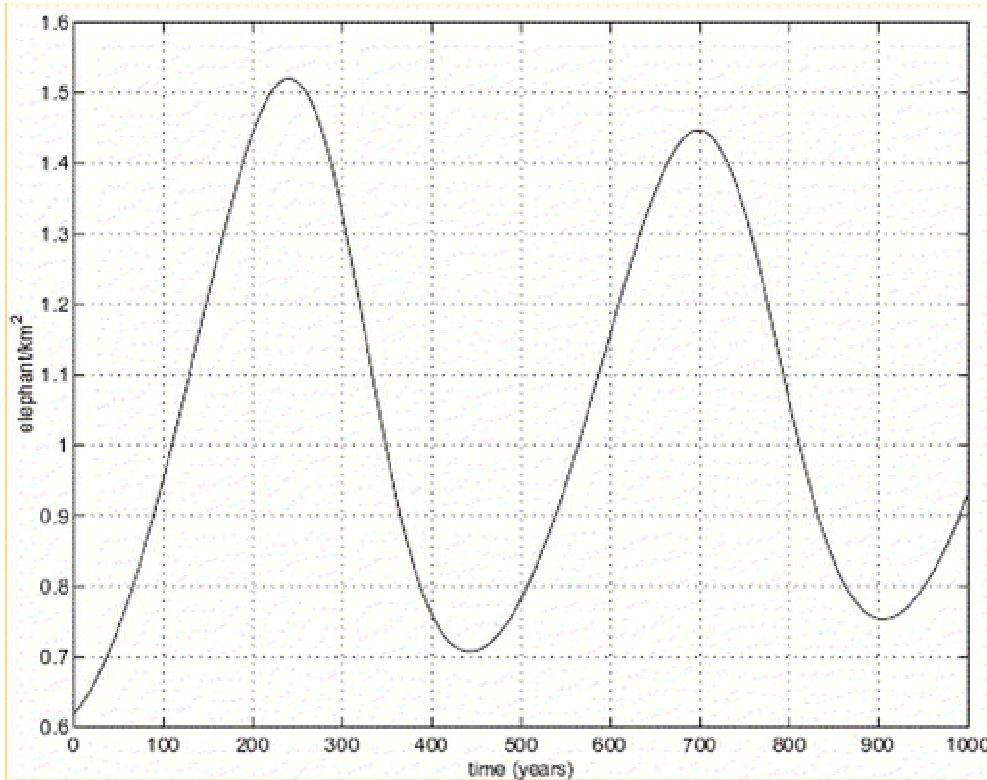
So it appears that limit cycle stability is not a very realistic possibility. There are however, parameter combinations that do result in limit cycles. Fig. 4.4 is a model solution with a limit cycle for a set of artificial parameters. The values chosen are  $r_T=0.04$ ,  $r_E=0.01$ ,  $h=0.001$ ,  $d_T=0.1$ ,  $g=25000$  and  $K=10000$ . Here  $r_T = 4r_E$ , which means that tree recruitment is very high but the elephant population is growing very slowly. Such a situation is highly unlikely but might be possible where there are plenty of trees with very poor nutritional value which cannot provide enough sustenance for the elephant population to grow at a normal rate. As shown in the previous section, all realistic parameter combinations result in equilibrium points.



**Fig. 4.4** Model trajectory for tree density against elephant density resulting in a limit cycle. Parameters are as follows:  $r_T=0.04$ ,  $r_E=0.01$ ,  $h=0.001$ ,  $d_T=0.1$ ,  $g=25000$  and  $K=10000$



Fig. 4.5 shows the change in elephant density over time (for the same parameters as Fig 4.4), where a large fluctuation in elephant density occurs. This type of fluctuation has not been observed but one needs to bear in mind the extremely long time periods involved.



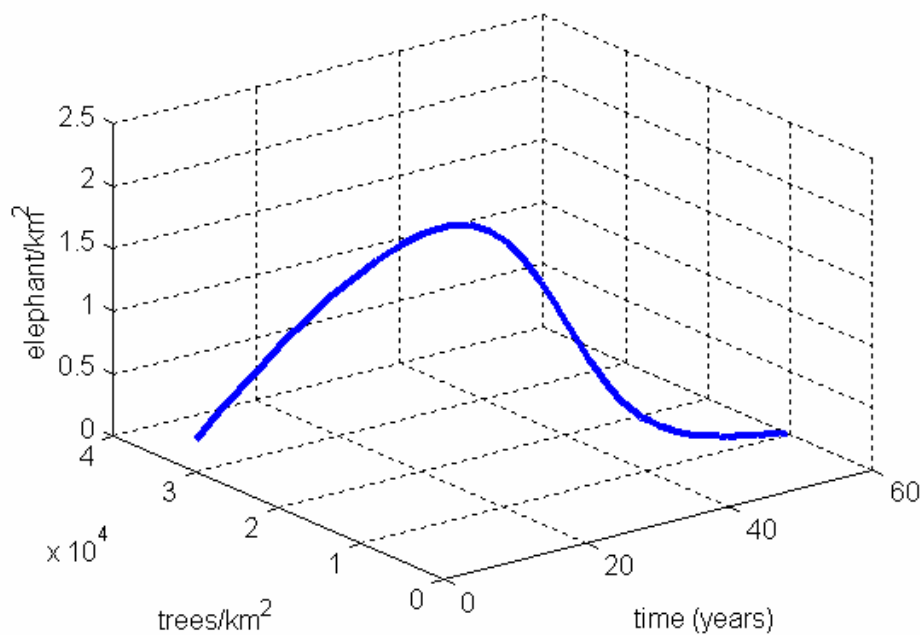
**Fig. 4.5 Model trajectory for elephant density against time which would result in a limit cycle. Parameters are the same as in Fig. 4.4.**

#### **4.6. RESULTS FOR THE PONGOLA GAME RESERVE**

In the Pongola Game Reserve, trees were initially reduced by 0.035 /year with a relatively low elephant density of 0.3 elephant/ km<sup>2</sup> (see Chapter 3). Running the model with all parameters of Table 4.1, could not mimic this trend even when using the very high elephant population growth found in the Pongola Game Reserve (0.18 /year). The conditions found in the Pongola Game Reserve can be obtained by setting the parameter  $g$  (density of trees required for elephant equilibrium) to 8000 trees/elephant. This value is almost two orders of magnitude lower than the lower value for the Kruger National Park. In other words, elephant

can survive on far fewer trees in the Pongola Game Reserve. The parameter  $g$  is a measure of the size of a home range in terms of trees needed for the elephant to survive but not necessarily destroyed by elephant. The fact that the value of  $g$  can be far lower for the Pongola Game Reserve could be explained by the limitless availability of water. As a result, the elephant use the entire range for browsing

Dynamics over the next 60 years are considered for the Pongola Game Reserve in Fig. 4.6.



**Fig. 4.6** Model trajectory for tree density against elephant density over time (initial conditions are: trees =30000 trees/km<sup>2</sup> and elephant =0.3 elephant/km<sup>2</sup>). This replicates the situation when elephant were reintroduced to the Pongola Game Reserve. Parameters are taken from the average conditions (Table 4.1) except for  $g= 8000$  trees/elephant. The trajectory tends to an equilibrium point ( $E_0=0.2$  elephant/km<sup>2</sup> and  $T_0=1000$  trees/km<sup>2</sup>).

A large increase in elephant with a decrease in trees occurs for the first thirty years, followed by a crash in the elephant population with a return to approximately the initial density of elephant. Equilibrium is found at a low density of trees and elephant. Although grass is

ignored in the model, it is evident that this scenario would represent a switch from wooded savannah to grassland.

#### **4.7. DISCUSSION**

The model presented here is rather simple but can be used to understand the dynamic trends of a system by varying the parameters. It has been shown that the model can describe fairly realistic results using parameters drawn from literature data on African savannahs.

However, setting the parameters can prove difficult for a specific situation. Some parameters depend on the exact characteristics of the environment, specially in cases where the areas considered are small like the Pongola Game Reserve. Simulations of elephant and tree dynamics in the Pongola Game Reserve, indicate that a drastic reduction in tree densities is likely. However, this result is largely dependent on the parameter  $g$  which describes the number of trees needed per elephant for equilibrium. Increasing this parameter would significantly alter the results. Data from the Kruger National Park, for example, gives  $g$  a much higher value. With that value, the model predicts that the wooded savannah would persist.

It must be accepted that at a certain density of trees, elephant will decline in numbers. If so, some simple dynamic must occur at a global scale and yet it is difficult to know precisely what form this dynamic takes. The results suggest that one important aspect is to consider the number of trees per elephant required for the elephant population to remain close to equilibrium. They also suggest that this number will be different depending on the exact characteristics of a particular reserve (including both environmental and human factors).

In conclusion, it appears that the predator-prey model (4.2) can describe some of the global characteristics of an elephant tree ecosystem. The equilibrium conditions are realistic. The possibility of limit cycles appears unlikely. This result was also shown by Duffy *et al.* (1999) using a different model. The fact that the results of the two models agree, gives

further confidence in the global characteristics of the system but whether the exact dynamics of equation (4.2) describe real systems, remains to be proven. However, the analysis gives insight into different scenarios. For example, the possibility that a sharp increase or decrease in elephant or tree densities could be followed by a peak and a return to equilibrium is an important idea that has yet to be tested in the field.

## **CHAPTER FIVE**

### **UNDERSTANDING ELEPHANT AND TREE LOCAL DYNAMICS WITH A GRID BASED MODEL**

#### **5.1. INTRODUCTION**

In this chapter, a square grid is imposed on the Pongola Game Reserve. Dynamics are modelled separately for each square and elephant move between grid cells of 0.125 km<sup>2</sup>.

The simulations focus on the aspects of elephant movement which might be important and the way the dynamics evolve with time. In this way, variation in space can be considered.

Some of the data presented in Chapter 3 is reconsidered and compared to the simulation results and a possible explanation as to what might appear as discrepancies in this data is put forward.

#### **5.2. BACKGROUND AND EXISTING RESULTS**

The model is based on the method used to estimate elephant population dynamics in the Tuli Block in Botswana (Duffy and Page, 2002). It shows how one can estimate threshold elephant densities that will allow for vulnerable tree species to survive. Those simulations using a range of realistic parameters give threshold densities of 0.1 – 6.0 elephant/km<sup>2</sup>. This range is within the recorded figure for the African elephant, 0.01 - 8.24 elephant/km<sup>2</sup> (Caughley 1976; Dudley 1996; Said *et al.* 1995; Hall-Martin 1992). Thus, their method appears to be valid.

Duffy and Page (2002) showed that tree growth rate has a great influence on elephant population thresholds. Doubling this parameter will double elephant threshold. Thus, as might be expected, the growth characteristics of various tree species are important in determining viable elephant thresholds.

Duffy and Page (2002) also showed that if there is bias toward riverine thicket, the difference between individual cells can be as much as 5 times what it would be without bias and the variation is such that tree density increases in some cells and decreases in others. This source of an increase in heterogeneity, possibly indicates the importance of the proximity of thicket to woodland in the Pongola Game Reserve. Some trees could be visited more, and therefore threatened more, because of their location. It would be interesting to test this result with field experiments in the Pongola Game Reserve.

Rare tree species often have patchy distributions, so the Monte Carlo nature of the simulations should improve the biological relevance of the predictions, although Duffy and Page (2002) point out that this is difficult to prove.

### **5.3. METHODS**

A cellular based model is used to represent the essential dynamics of the Pongola Game Reserve system. A rectangular grid with square cells, is used as a base for elephant movement. The main constituent processes are considered to have a stochastic component that is implemented using Monte Carlo methods. Monte Carlo methods utilise probability distributions to simulate random processes.

The concept of a 'tree killing unit' (TKU), initially developed by Duffy and Page (2002) is used. A TKU is defined as any adult bull or group of elephant destroying trees at a rate approximately equal to that of an adult bull (over 30 years of age). This simplification is feasible because large trees are destroyed mainly by adult elephant bulls or groups of younger bulls (Barnes *et al.*, 1994). Large trees (above 5m in height) are considered for two reasons: they are of primary concern to land owners and are an important size class influencing greatly the survival of a tree species as a whole (Duffy *et. al*, 2002).

Pongola Game Reserve has approximately 3 TKU's (1 large bull and 2 groups of females). For ease of reading in the discussions that follow, the TKU will often still be referred to as elephant.

The model separates elephant movement and the mechanisms of tree removal into different scales. Factors that influence elephant movement, operate at a global scale in which vegetation types, water, danger and social interactions dominate. However, individual tree selection operates at a local scale in which location and preference dominate.

A grid-based model is constructed where elephant move at the global scale and forage at the local scale. The model simulates elephant movement in a simplified version of the Pongola Game Reserve, i.e. we only consider the two most significant vegetation types: Thicket and Woodland. As shown in Chapter 2, Thicket (type 1) is associated with drainage lines and is important because of its high tree densities. Woodland (type 2) is important because it covers most of the Pongola Game Reserve.

The following behavioural patterns are important for the model:

At the global scale:

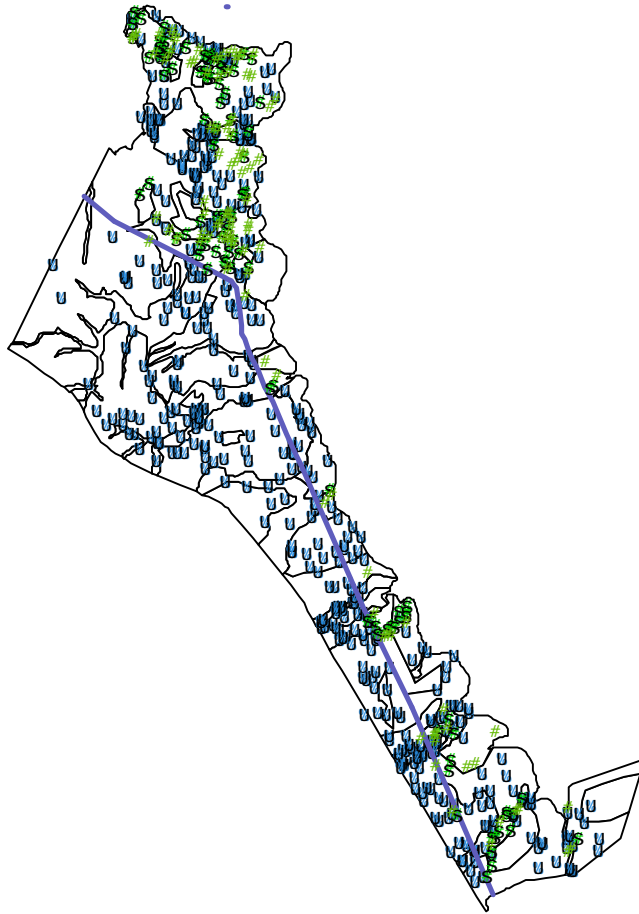
1. Most of the region has been impacted by elephant. Elephant positions (recorded GPS readings) are given in Fig. 5.1. It must be noted that the female group does not cross the railway line (which splits the reserve in two from top to bottom – blue line). It is evident from the data that both the bulls and family groups utilise their entire range.
2. Elephant enter the thicket on a regular basis for shade and water. For a large part of the year, they will be in this vegetation type for at least part of each day.
3. Elephant movement averaging between 4 km and 12 km per day are very probable (Douglas-Hamilton, 1998; Duffy *et al.*, 1999; Owen-Smith, 1988). The

distances covered per day by a group of elephant are expected to have an almost normal distribution (Duffy *et al.*, 1999).

At the local scale:

4. Elephant utilise a certain number of trees per day based on their requirements (Barnes *et al.*, 1994).
5. Foraging is assumed to occur within a 0.125 km<sup>2</sup>. This assumes that elephant forage in a radius of about 0.125 km.





**Fig. 5.1** GPS positions for the dominant bull (blue squares) recorded daily over eight months with a satellite collar. For female groups (green circles), positions were recorded intermittently by hand over a period of two years. Females do not cross the railway line (straight blue line).

In the simulations, elephant move in a biased random walk on the grid and remove trees as they proceed. Data from the Pongola Game Reserve indicates that the Pongola elephant use a random walk foraging strategy (K.J. Duffy, *pers. comm.*). The global effects are regulated in the simulations by movement biases in terms of time spent in thicket. Other factors influencing movement are taken as having random effects. These factors include proximity to water holes, other vegetation types, danger, social interactions and other behaviours

affecting movement. At the local scale, the effect of elephant on individual trees is simulated as a probability based on preference and abundance of trees. This assumes that elephant have certain preferences and will select one species over another. As more of the exact mechanisms behind tree selection are discovered, they can be included in the simulations (perhaps as sub-models).

In the simulations, rigid boundary conditions are implemented because Pongola Game Reserve has elephant proof electric fence on all its land boundaries and borders a dam on the eastern side. A time step of one quarter of a day is used. In this time frame, elephant are assumed to be in a particular part of the woodland, choosing between certain trees (local scale behaviour). As previously mentioned, the distance moved is taken from a distribution of daily displacements with an average of 4 km per day. Duffy and Page (2002) found that increasing the average displacement up to 12 km per day, affects results only slightly.

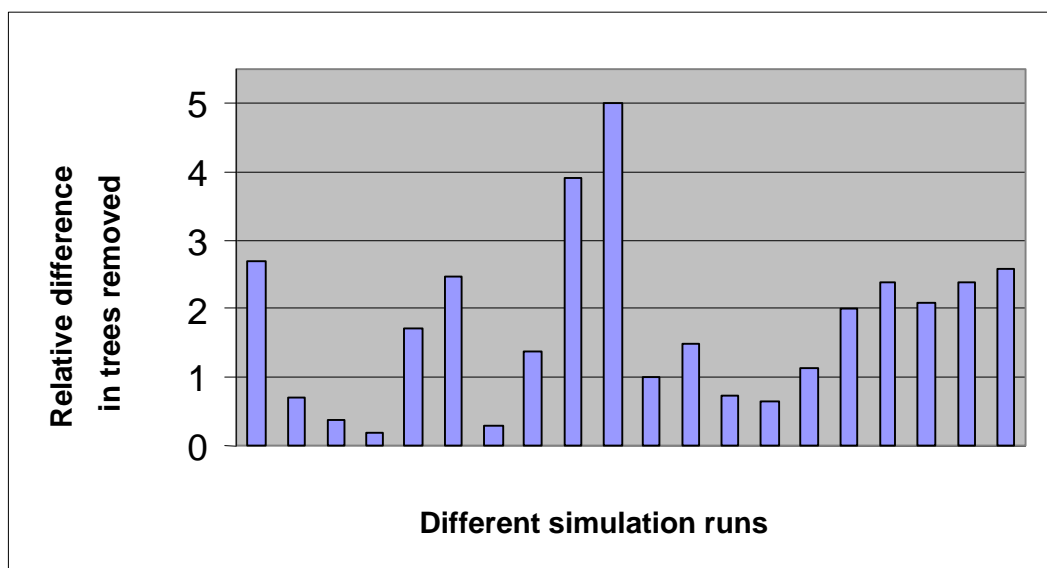
The test for the removal of a tree is a Monte Carlo calculation using a random number  $rn$  in the range of 0 to 1. If  $rn < P$  then a tree will be removed ( $P$  being the probability of a tree being removed by elephant). In this way, individual trees are removed and the system has a spatial component.

**NetLogo** software was chosen for the simulation. **NetLogo** is a programmable modelling environment for simulating natural and social phenomena (Netlogo User Manual, 2003). It is particularly well suited for modeling complex systems developing over time and can give instructions to hundreds or thousands of independent "agents" all operating in parallel. This makes it possible to explore the connection between the micro-level behavior of individuals and the macro-level patterns that emerge from the interaction of many individuals. A copy of the program used in the simulation is given in Appendix C.

#### **5.4. RESULTS**

Data from Chapter 3 shows that regions with similar elevation, species composition and distance from water were impacted differently. The difference was as much as 2 times. This

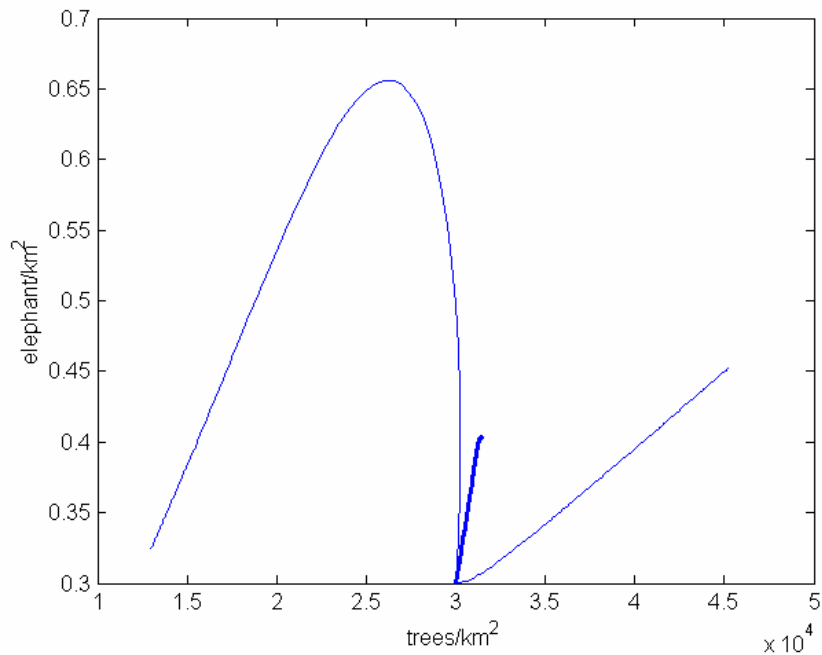
variation in impact is quite surprising because it is assumed that tree removal relates to preference based on environmental conditions and food species composition. It is possible to recreate field data from Chapter 3 with the model presented here. Using random foraging for the movement patterns of elephant, individual simulations are run for two regions with the same characteristics, over a period of 2 years. Results indicate that the number of trees destroyed in one region can be twice as high as in the other but the difference can be as high as 5 times (see Fig 5.2). Since these results depend on the stochastic nature of the movement of elephant over a short time frame, this illustrates that the field data from Chapter 3 showing very different impact for 2 similar regions, could be the consequence of random elephant foraging.



**Fig. 5.2** Simulation runs showing the relative difference in trees destroyed for two regions with similar characteristics.

These results also challenge the global model parameters used in Chapter 4. In particular, it is necessary to reconsider the density of trees required for elephant equilibrium, i.e. parameter  $g$  (this parameter was the only one based on data from Chapter 3). By varying  $g$ , it is possible to alter the degree to which trees persist. Chapter 4 indicates that the presence of

elephant can induce a change from wooded savannah to grassland. However, if parameter  $g$  is increased, the model gives different results. Fig 5.3 shows that for lower  $g$  values, trees decline and for higher  $g$  values, trees increase. For  $g=78000$  tree/elephant, there is no significant change in tree density (bold line). For  $g$  above or below this value, there is a significant decrease or increase in tree density with time (other lines).



**Fig. 5.3** Trajectories for tree density against elephant density simulated using system (4.2) in Chapter 4. The end of each line represents equilibrium. The initial conditions are trees=30000 trees/km<sup>2</sup> and elephant=0.3 elephant/km<sup>2</sup>. All parameters, except for  $g$ , are taken from the average conditions (Table 4.1).

## 5.5. DISCUSSION

The simulations presented here show that what might appear as inconsistencies in the data of Chapter 3, could be due in part to the random nature of elephant foraging. The results also indicate that a closer look at the exact meaning of parameter  $g$  is required. The unit for  $g$  is trees per elephant, independent of area. In other words,  $g$  is the fixed number of trees required per elephant for the entire region, for the elephant population density to neither

increase or decrease. Below this number of trees, elephant population density would drop. This number will depend on the exact make-up of the whole region. For example, for two similar reserves,  $g$  could be very different if, let us say, the spatial distribution of water was different. In Pongola Game Reserve, where water is found within a few kilometres of any point in the reserve, the number of trees required per elephant will include most of the trees (i.e. the entire region). However, if we consider a situation where water is only to be found in certain areas, the trees likely to be utilised by elephant will occur within at most two days walk from water. Thus, the number of trees required per elephant (for the entire region) will be higher since some of the trees in the region will never be visited. Other factors such as elevation, tree nutritional value or danger (perceived or real) will affect  $g$  in similar ways. Innovative ideas are needed to measure the range of  $g$  values for a particular region.

The results of Chapters 4 and 5 indicate that both the nonlinear dynamics of the global scale methods and the stochastic aspects influencing elephant foraging are important. Thus, a combination of these approaches should give better realism to the simulations. That will be the objective of the next chapter.

## **CHAPTER SIX**

### **UNDERSTANDING ELEPHANT AND TREE LOCAL DYNAMICS WITH A COMBINATION OF ODE'S AND GRID BASED MODELS**

#### **6.1. INTRODUCTION**

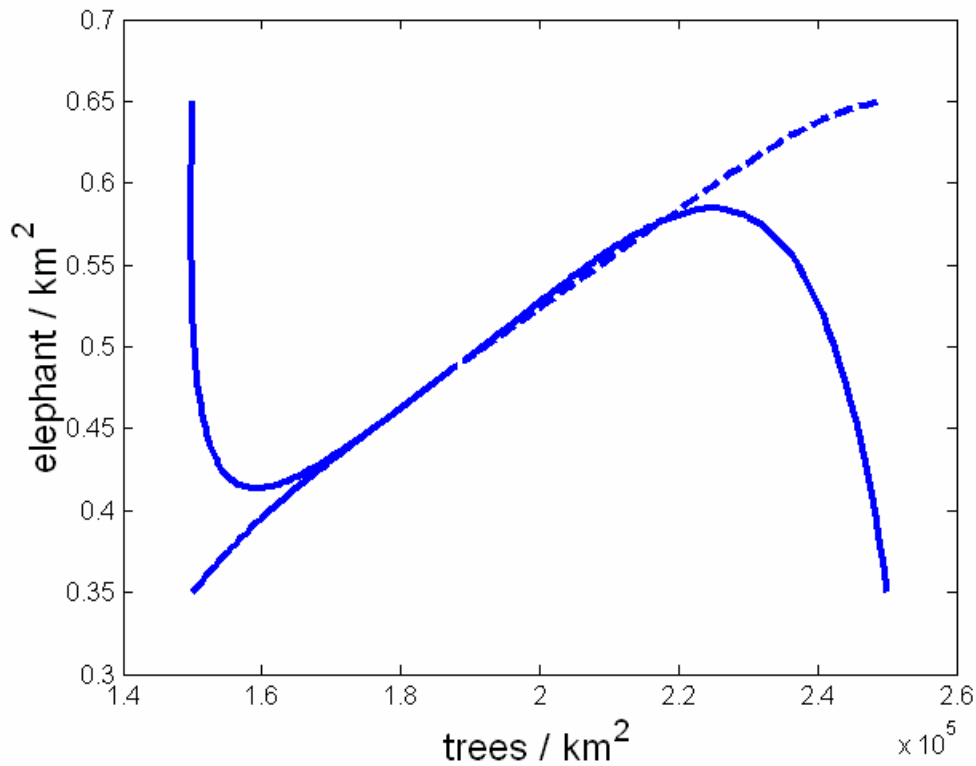
In this chapter, a square grid is also imposed on the Pongola Game Reserve and local dynamics are modelled separately for each square, i.e. elephant move between grid squares at an average rate per day. The global dynamics are modelled with the differential equations of Chapter 4. This approach combines the nonlinear dynamics of the global scale methods with the stochastic aspects influencing elephant foraging. This combination of processes should achieve better realism.

#### **6.2. METHODS**

The simulations are run and trees are removed daily by elephant moving on a grid, in the same manner as in Chapter 5. The global dynamics of trees and elephant densities are simulated using the non-linear equations (4.2). These equations are solved and updated annually using the densities of trees and elephant given by the grid simulations. The non-linear dynamics of annual growth and death rates of elephant and trees are retained since the ODE's of system (4.2) are used. This new method allows for a finer temporal scale (per day) and a finer spatial scale (per km<sup>2</sup>). It will from now on be referred to as the ODEgrid simulations (see Appendix D)

The parameters from Table 4.1 are used in the simulations. Initially, all cells in the grid have the same tree density. Simulations are run until equilibrium is achieved. A typical run is 200 years.

To illustrate that it is possible to adopt this new approach without the loss of the underlying dynamics, the new ODEgrid simulations are run with the elephant diffusing evenly throughout the reserve. This simplifying assumption should give the same results as the equations of system (4.2). The results are presented in Fig. 6.1. The unbroken lines are obtained with the equations (4.2) and the dashed line is obtained with the ODEgrid simulations. Fig. 6.1 is essentially the same as Fig. 4.1 thus establishing the cohesion of this new approach in terms of joining the ODE and grid based methods.



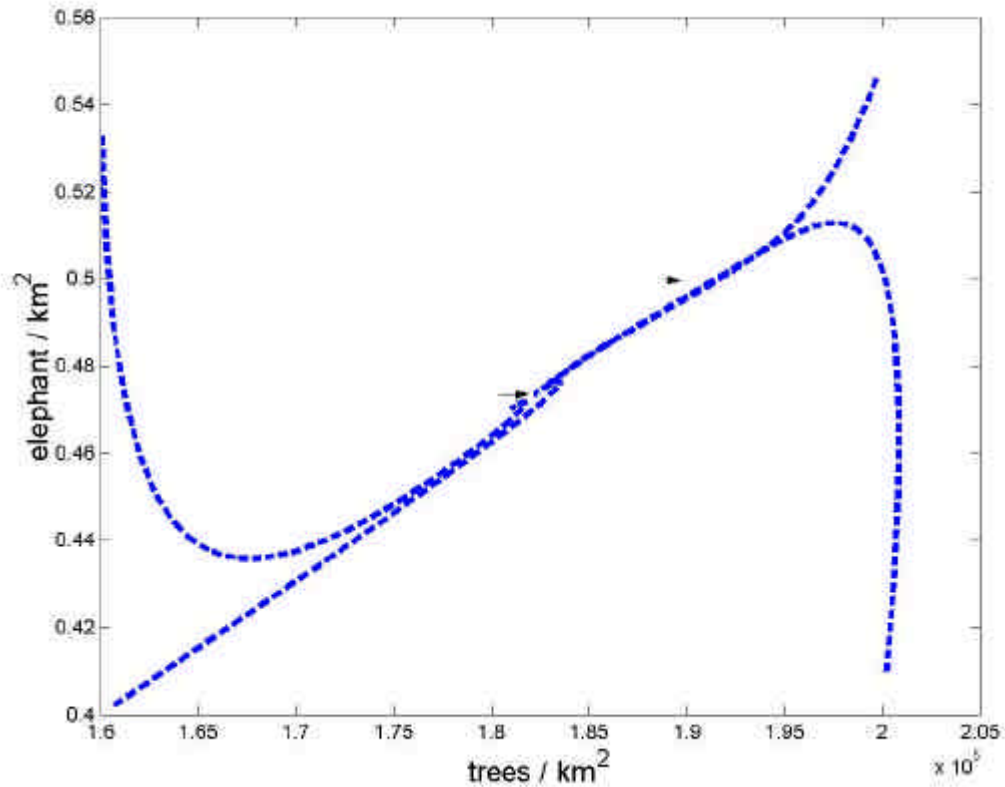
**Fig. 6.1** Model trajectories for tree density against elephant with the same conditions as Fig. 4.1. The unbroken lines are obtained using the ODE's (4.2) and the broken line is obtained from the ODEgrid simulations.

### 6.3. RESULTS

A first step toward greater realism in the simulations, is to take into account the fact that elephant generally move in groups. Although large bulls often move alone, they can be considered the optimal tree killing units (TKUs) presented in Chapter 5. At one extreme, very large groups of elephant are formed for periods of time and in fact quite often, all the elephant in the Pongola Game Reserve can be found together. It is therefore interesting to consider the impact on trees when elephant move in large groups.

Using the average parameters in Table 4.1 and having elephant move systematically from cell to cell in one large group around the grid, does not change the simulations results which are the same as the ones presented in Fig. 6.1. However, elephant are unlikely to move systematically around their range. On the contrary, new data suggests that elephant are likely to use a random walk foraging strategy (K.J. Duffy, *pers. comm.*). Thus, it is interesting to test the effects of a random walk foraging strategy on elephant and tree densities. Using the average parameters in Table 4.1, ODEgrid simulations are run with elephant moving in a random walk from cell to cell on the km<sup>2</sup> grid lattice. Results are given in Fig. 6.2.

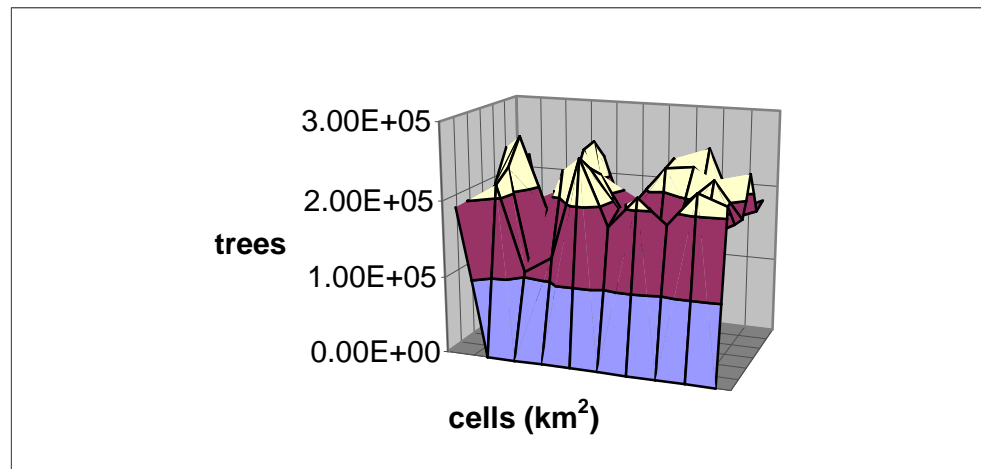




**Fig. 6.2** Model trajectories for tree density against elephant density using the ODEgrid simulations with the same conditions as in Fig. 6.1 except that elephant move as one group between grid squares using a random walk. The bottom arrow indicates equilibrium densities for this simulation and the top arrow indicates equilibrium densities for Fig 6.1.

There are two important differences between these results and those obtained with the global model of Chapter 4 or the method where elephant move systematically from cell to cell. First, the point of equilibrium has moved to lower densities of trees and elephant as indicated by the arrow of Fig 6.2. Second, the variability between cells in the grid is much higher than it was for the systematic movement (Fig. 6.3). This is an important point because the variations shown in Fig. 6.3 also explain the variability in the utilisation data given in Chapter 3 and discussed throughout this thesis. In other words, variability in elephant utilisation between transects with similar features, could be due purely to the stochastic nature of elephant movement.

The difference in equilibrium density of elephant indicated by the simulations is surprising but easy to explain. Elephant moving randomly in a group do not visit all sites equally. The sites visited less are not able to regenerate at a rate high enough to balance the ones visited more. This result is due to the non-linear nature of the equations of system (4.2). To show that this is true, the simulations are rerun with one group of elephant moving systematically from cell to cell and the original equilibrium returns.



**Fig. 6.3** Variations in tree numbers between cells after running the ODEgrid simulations of Fig. 6.2

#### 6.4. DISCUSSION

In Chapter 4, global scale dynamics between elephant and tree densities are considered but local scale dynamics are ignored. In Chapter 5, it is shown using a grid based model that foraging behaviour could have an important effect on these dynamics and explain discrepancies found in the data of Chapter 3. Here global dynamics and local dynamics are combined using the methods of Chapter 4 and 5 together. It is shown that if elephant forage using a random walk strategy, their impact on trees is significantly different and there is an increase in spatial heterogeneity of tree cover.

Other simulation approaches attempt to include a considerable amount of realism, see for example Weisberg *et al.* (2002). These approaches can be problematic because of the extensive variable and parameter count. The aim here is not to perfectly mimic the situation but to highlight the possible importance of certain variables. For example, elephant movement strategy is shown to influence the heterogeneity of the impact on trees.

The method used here is based on a new approach referred to as agent-based simulation. The agent-based modelling approach has recently become a useful simulation methodology. It has been applied in a diverse range of fields such as ecology, sociology, economics, traffic simulation, and others. Agent-based simulation allows one to gain insight into the general behaviour of the system assuming the behaviour of its elements, without having any global knowledge about the system. This chapter is a first step in using an agent based approach to investigate the environmental effects of elephant movement. The background environment in a real ecosystem is not static. In the simulations, the dynamic nature of the environment is modelled using the differential equations of Chapter 4. This representation is not completely real but provides at least a dynamic backdrop. Focus is then on the agent behaviour (elephant). This can be developed in the future by including more and more actual elephant behaviours into the simulation logic.

## CHAPTER SEVEN

### CONCLUSIONS

Many small game farmers in South Africa are reintroducing elephant on their land. To be able to predict the long term effects and ascertain whether the fenced areas in question will be able to support a growing population, it is essential to monitor the vegetation and record the impact on the various plant species. This impact is however dynamic and thus simulation models are also a useful tool in predicting damage over time. For this thesis, elephant impact on trees was assessed by completing the following goals:

- A GIS vegetation map of the Pongola Game Reserve was completed.

The overall state of Pongola Game Reserve was evaluated by constructing a vegetation map of the area with the initial densities in the various vegetation types. This vegetation map is given in Chapter 2. Five vegetation types were identified. Within these five types, Closed Woodland was found to have the highest tree density, followed by Thicket, Woodland, Open Woodland and Old Farm Land. The Old Farm Land was almost completely grassland.

- Results of field studies on vegetation and elephant damage were analysed.

Transects were used to assess the amount of tree utilisation by elephant. This method is relatively cheap to implement and the results are informative as they will highlight tree species under potential threat.

As expected, trees have been removed by elephant in the Pongola Game Reserve. Analysis of transect data shows that Marula (*Sclerocarya birrea*) is the most threatened tree species. Nonetheless there is a need for further more detailed transect studies as the distribution of Marula is likely to be patchy.

While destruction of mature trees is very obvious and tends to attract attention, the impact on seedlings and normal regeneration is more difficult to assess. In the Pongola Game Reserve, tree recruitment as a whole does not seem to be significantly affected by elephant. The present density of elephant does not appear to have reached a critical point since the rate of tree regeneration is higher than the destruction rate. However, that might not always be the case when the population of elephant increases as demonstrated by the model described in Chapter 4.

- Global dynamics of the elephant / tree system were assessed using a set of ordinary differential equations.

Using a simple differential equation model, it is shown how elephant and tree dynamics could fluctuate in density. It appears that the possibility of a limit cycle between elephant and tree densities is not a likely scenario. However, for particular simulations, there are large increases in elephant density with a decrease in tree density over about thirty years. This is followed by a crash in the elephant population with a return to the approximate initial density of elephant (low numbers). Equilibrium is found at a low density of trees which would represent a switch from wooded savannah to grassland. It should be emphasised that even if this scenario was correct, it would be very unlikely to occur as management would not allow it to play itself out. While the result is an equilibrium, it is not feasible for biological or business objectives, since such low densities would bring the risk of extinction. However, it is interesting to note that some type of balance could be possible and that this balance was shown to depend on density of trees required per elephant for the entire region. In the Pongola Game Reserve, where water is found within a few kilometres of any point, the number of trees required per elephant will include most trees (i.e. the entire region). In other words, all trees are vulnerable all year round. Thus, because the region is small, the possibility of a reasonable balance between elephant and trees is unlikely. This result

strengthens the existing drive to create corridors between the Pongola Game Reserve and neighbouring game farms. These corridors would allow elephant to migrate naturally between patches. However, the abundance of water might still inhibit these migratory movements.

- Local dynamics of the elephant / tree system were assessed using a grid based model.

It is interesting to note that according to field data, the impact of elephant appears to be non-homogeneous, i.e. different impacts were recorded in regions with very similar elevation, species composition and distance from water. One particular region was found to have as much as three times more trees pushed over than another similar region. Thus, while elephant population growth is a crucial part of the equation, population composition is also an essential component affecting the survival of trees since bulls and family group will impact the vegetation in very different ways. The computer models supporting the analysis of the interaction between elephant and their food source, highlight another possible explanation, forage behaviour, to the fact that impact appears non-homogeneous.

- Local and global dynamics of the elephant / tree system were assessed together using a combination of ode's and grid based models.

Using a combination of models, it is shown that elephant impact on trees could be non-homogenous and could increase the spatial heterogeneity of tree cover. This might be significant considering the fact that certain species of trees are a preferred part of the elephant diet and/or are simply less abundant than other species and therefore more vulnerable. Marula (*Sclerocarya Birrea*) is a prime example in the Pongola Game Reserve as it is a relatively rare tree with a patchy distribution. It is also important to the landowners because of its aesthetically pleasing tourist value.

For the scenarios presented here, random foraging behaviour could affect the survival rate of Marula, purely because elephants come across Marula trees less or more often when foraging randomly. For reserves larger than Pongola, this difference might be considerable. Thus, depending on the objectives of park management, higher elephant stocking densities might or might not be possible. However, the actual details of this type of analysis need more work and it would be beneficial to conduct a specific study for preferable species with a patchy distribution.

The models presented here are rather simple but describe some of the global and local characteristics of a tree-elephant ecosystem. Setting the parameters to run these models for specific regions, can however prove difficult and will depend on the exact make-up of the region under consideration. Innovative ideas are needed to measure the range of values of certain parameters, i.e. parameter  $g$  (fixed number of trees required per elephant) discussed in Chapter 5. Nevertheless, the analysis will give insight into different scenarios and might therefore prove a useful tool for managers.

## REFERENCES

- Barnes, R.F.W., Barnes, K.L. and Kapela, E.B., 1994. The long term impact of elephant browsing on baobab trees at Msembe Ruaha National Park, Tanzania. *Afr. J. Ecol.* 32, 177-184.
- Ben-Shahar, R., 1996. Do elephant over-utilise mopane woodlands in northern Botswana. *J. Trop. Ecol.* 12, 505-515.
- Bowland, J.M. and Yeaton, R.I., 1997. Impact of domesticated African elephant *Loxodonta africana* on Natal bushveld. *S. Afr. J. Wildl. Res.* 27(2). 31-36.
- Briske, D.D., Fuhlendorf, S.D. and Smeins, F.E., 2003. Vegetation dynamics on rangelands: a critique of the current paradigms *Journal of Applied Ecology*, 40, 601–614.
- Brown, D and Rothery, P., 1993. *Models in Biology*. John Wiley and Sons. New York.
- Caughley, G., 1976. The elephant problem - an alternative hypothesis. *East African Wildlife Journal*, 14, 265-383.
- Cumming, D.H.M., Fenton, M.B., Rautenbach, I.L., Taylor, R.D., Cumming, G.S., Cumming, M.S., Dunlop, J.M., Ford, A.G., Hovorka, M.D., Johnston, D.S., Kalcounis, M., Mahlangu, Z. and Portfors, C.V.R., 1997. Elephant, woodlands and biodiversity in Southern Africa. *S. Afr. J. of Sci.* 93, 231-236.
- Duffy, K., Swart, J.H., Page, B.R. and Bajic V., 1999. Realistic parameter assessment for a well known elephant-tree ecosystem model reveals that limit cycles are unlikely. *Ecological Modelling*, 121, 115-125.
- Duffy, K., Page, B.R. and Bajic V., 2000. Analysis and dynamics of an elephant-tree ecosystem having abundant and rare tree species. *Systems, Simulation and Modelling* 38: 663-676.



- Duffy, K., Van Os, R., Vos, S., Van Aarde, J., Elish, G. and Stretch, A-M., 2002. Estimating the impact of reintroduced elephant on the trees of a small reserve. *South African Journal of Wildlife Research. In press.*
- Dudley, J.P., 1996. African elephant in coastal refuges. *Pachyderm*, 21, 78-83.
- Du Toit, J.G., 1991. The African elephant (*Loxodonta Africana*) as a game ranch animal. The african elephant as a game ranch animal. Wildlife Group of the South African Veterinary Association, Onderstepoort.
- Ellis, J.E. & Swift, D.M., 1988. Stability of African pastoral ecosystems: alternate paradigms and implications for development. *Journal of Range Management*, 41, 450-459.
- Goodman, P.S., 1997. Ecological suitability and carrying capacity assessment for the re-establishment of elephant in the Pongolapoort Biosphere Reserve. Unpublished.
- Hale, J. and Kocak, 1991. *Dynamics and bifurcations*. Springer Verlag, New York.
- Hall-Martin, A.J., 1992. Distribution and status of the African elephant *Loxodonta africana* in South Africa, 1652-1992. *Koedoe*, 35, 65-88.
- Henning, A.C., 1976. A study of edaphic factors influencing the growth of *Colophospermum mopane*. Ph.D. thesis, University of the Witwatersrand, Johannesburg, South Africa.
- Hill, M.O., 1979. TWINSpan – a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Ecology and Systematics, Cornell University, Ithaca, New York.
- Hiscocks, K., 1999. The impact of an increasing elephant population on the woody vegetation in southern Sabi Sand Wildtuin, South Africa. *Koedoe*, 42:47-56.
- Holling, C.S., 1959. Some characteristics of simple types of predation and parasitism. *Canadian entomologist*, 19, 385-383.

- Mackey, R.L., Page, B.R., Duffy, K.J. and Slotow, R. Elephant population growth in South African reserves. Submitted to South African Journal of Wildlife Research.
- Owen-Smith, R.N., 1988. Megaherbivores: The Influence of Very Large Body Size on Ecology. Cambridge University Press, Cambridge, UK.
- Tanner, J.T., 1975. The stability and the intrinsic growth rates of prey and predator populations. *Ecology*, 56, 855-867.
- Van de Koppel, J. and Prins, H.H.T., 1998. The importance of herbivore interactions for the dynamics of African savanna woodlands: an hypothesis. *J. Trop.Ecol.* 14 : 565 - 576.
- Van Wijngaarden, W., 1985. Elephant-trees-grass-grazers. Relationships between climate, soils, vegetation and large herbivores in a semi-arid savanna ecosystem (Tsavo, Kenya). ITC Publication Number 4.
- VanWyk, P. & Fairall, N., 1969. The influence of the African elephant on the vegetation of the Kruger National Park. *Koedoe*, 12, 57-89.
- Viljoen, P. J., 1991. Elephant and habitats. The african elephant as a game ranch animal. Wildlife Group of the South African Veterinary Association, Onderstepoort.
- Whyte, I.J., 2001. Conservation management of the Kruger National Park elephant population. Ph.D. thesis, University of Pretoria, Pretoria, South Africa.
- Wiens, J.A., 1984. On understanding a nonequilibrium world: myth and reality in community patterns and processes. *Ecological Communities: Conceptual Issues and the Evidence* (eds D.R. Strong, D. Simberloff, L. Abele & A.B. Thistle), pp. 439–458. Princeton University Press, NJ.
-

Weisberg, P.J., Hobbs, N.T., Ellis, J.E. and Coughenour, M.B., 2002. An ecosystem approach to population management of ungulates. *Journal of Environmental Management*, 65, 181-197.

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# APPENDIXES

**APPENDIX A**  
**SAMPLE OF VEGETATION DATA COLLECTED**

<b>Location</b>	<b>SPECIES</b>	<b>Height</b>	<b>Height to Canopy</b>	<b>Cover</b>
Site 1	<i>Acacia Tortilis</i>	5	1.8	6.7
50m	<i>Acacia Tortilis</i>	5	1	3.2
	<i>Acacia Tortilis</i>	5	1.5	4.4
	<i>Acacia Tortilis</i>	4	1	3.9
	<i>Dichrostachys Cinerea</i>	1.6	1	1
	<i>Dichrostachys Cinerea</i>	3.5	.8	2.1
	<i>Acacia Tortilis</i>	6	3	7.4
Site 2	<i>Dichrostachys Cinerea</i>	4	.8	3.7
50m	<i>Dichrostachys Cinerea</i>	3	.5	1.2
	<i>Acacia Tortilis</i>	6	.8	4.5
	<i>Acacia Tortilis</i>	4	2	3
	<i>Dichrostachys Cinerea</i>	3	.8	.5
	<i>Acacia Tortilis</i>	4.5	1.5	7.1
	<i>Dichrostachys Cinerea</i>	5	1.2	5.5
	<i>Dichrostachys Cinerea</i>	5	1	3.5
	<i>Dichrostachys Cinerea</i>	4	1.2	6.7
	<i>Dichrostachys Cinerea</i>	3	.8	6
	<i>Acacia Tortilis</i>	3	2	3.8
	<i>Dichrostachys Cinerea</i>	3.5	1.5	3.6
Site 3	<i>Acacia Nilotica</i>	3	1	5.5
50m	<i>Acacia Tortilis</i>	4	1.5	7.7
	<i>Dichrostachys Cinerea</i>	1.5	.4	2.5
	<i>Dichrostachys Cinerea</i>	3.5	.8	5.2
	<i>Dichrostachys Cinerea</i>	3.5	1.2	4.8
	<i>Acacia Nilotica</i>	4	1.5	6
	<i>Acacia Nilotica</i>	4	1.5	3.5



## APPENDIX C

### GRID-BASED SIMULATION MODEL FOR ELEPHANT TREE DYNAMICS

Note: Programming platform is Netlogo which is a programmable modelling environment linked to an interface. The subroutines below are activated by the user on this interface. In the case of this program, the interface is the grid version of the vegetation map and the moving elephant groups.

Elephant are set up as a breed called ele and trees are set up as a patch:

```
breeds [ele]
patches-own [trees]
```

Variables global to the program:

```
globals [runs drink days year mv xpos ypos temp-per-day steps-per-day steps top up1 dn1
bot top-sq up1-sq dn1-sq bot-sq icount_1 tot tot-trees tree-remove-per-step temp start-tree-
no max-tree-no cell-12 cell-16 tot-removed cellfact]
```

Variables global to the program:

```
to move
  rt random 360
  fd 1
  if pcolor = blue [set drink drink + 1]
```

```

ifelse( pcolor = red or pcolor = blue ) [bk 1]
[set xpos xcor set ypos ycor
set steps steps + 1
set mv 1
]
end

```

```

to movegreen
fd 1
set steps steps + 1
set temp 88
set mv 1
end

```

Main program routine:
-----------------------

```

to go
set max-tree-no 60000

ask ele
[
set steps-per-day abs(8 + random 4)
set temp-per-day steps-per-day
; set tree-remove-per-step (3 / steps-per-day)

repeat (steps-per-day + 4) [ if (temp-per-day != 0) [

```



Monte Carlo steps for distance moved per day:

move

if mv = 1

[ set temp-per-day temp-per-day - 1

ifelse ((random 1) < (3 / steps-per-day)) [set tree-remove-per-step (3 / steps-per-day)] [set tree-remove-per-step 0]

if (trees > 0) [set trees trees - tree-remove-per-step set temp tree-remove-per-step]

ifelse (xcor >= -3 and xcor <= -2 and ycor >= 8 and ycor <= 9) [set cell-12 cell-12 + tree-remove-per-step]

[if (xcor >= 5 and xcor <= 6 and ycor >= -10 and ycor <= -9) [set cell-16 cell-16 + tree-remove-per-step]]

if trees < 10 [set trees 0]

if (ycor < 15 and ycor > 10 and xcor > -8 and xcor < -3)[set top-sq top-sq + 1]

if (ycor < 7 and ycor > 2 and xcor > -8 and xcor < -3)[set up1-sq up1-sq + 1]

if (ycor < -5 and ycor > -10 and xcor > 1 and xcor < 6)[set dn1-sq dn1-sq + 1]

if (ycor < -12 and ycor > -17 and xcor > 6 and xcor < 11)[set bot-sq bot-sq + 1]

; set mv 0

]

]]

]

set days days + 1

```

if (days mod 365 = 0) [set year year + 1 set days 1]
if (year mod 2 = 0 and days = 1)
  [set runs runs + 1
  do-plot
  set cellfact (cell-12 / cell-16)
  set cell-12 0 set cell-16 0]

if (year = 200) [stop]
set count_1 0
set tot 0
ask patches [if (trees > 0) [set pcolor ((trees / start-tree-no) * 45) set tot tot + trees set
count_1 count_1 + 1]]
if ((days mod 365) = 0) [ask patches [if (trees < max-tree-no) [set trees (trees * 1.02)]]]
set tot-trees (4 * (tot / count_1))

end

```

End of main program routine:

Variable settings:

```

to setup
  setup-plotting

```

```
set year 0
set-default-shape turtles "ele"
create-custom-ele 2
[set color pink setxy 1 0]
set tot-trees 0
set cell-12 0
set cell-16 0
set tot-removed 0
set days 0
set steps 0
set drink 0
set top 0
set up1 0
set dn1 0
set bot 0
set top-sq 0
set up1-sq 0
set dn1-sq 0
set bot-sq 0
end

to setup-plotting ;; set up plotting
set-current-plot "average trees per sq km"
auto-plot-on
set-plot-y-range 0 20
set-plot-x-range 0 50
```

**APPENDIX D**  
**GRID-BASED SIMULATION MODEL FOR ELEPHANT TREE**  
**DYNAMICS INCORPORATING ODE FOR POPULATION**  
**DYNAMICS**

Note: Programming platform is Matlab.

Initialise variables:

```
clear all
```

```
y=.4;
```

```
xsize=16;
```

```
ysize=22;
```

```
for xpos=1:17
```

```
for ypos=1:23
```

```
x(xpos,ypos)=0;
```

```
end
```

```
end
```

```
xpos=round(rand*4)+2;
```

```
ypos=round(rand*4)+12;
```

```
xstep=1; %randsrc;
```

```
ystep=1; %randsrc;
```

```
year=200;
```

```
xtreeinit=200000;
```

Parameter initialisation:

a=0.04; % growth rate of trees

hrs=1.5; % time at tree in hours

h=hrs/(24\*73\*5); % time at each tree per day

hrs=.07; % time at tree in hours

h=hrs/(24); % time at each tree per day

a=.025;

K=280000;

h=365\*2.95e-4;

d=.175/365;

Set up vegetation map, cells with trees (this is one example):

x(4,21)=xtreeinit;

x(1,14)=0000;

x(7,13)=xtreeinit;

x(3,12)=xtreeinit;

x(8,11)=xtreeinit;

x(6,10)=xtreeinit;

x(9,6)=xtreeinit;

x(10,7)=xtreeinit;

x(12,4)=xtreeinit;

x(12,1)=0000;

x(15,3)=xtreeinit;

for xpos=4:6

for ypos=19:20

x(xpos,ypos)=xtreeinit;

end

end

for xpos=3:6

for ypos=17:18

x(xpos,ypos)=xtreeinit;

end

end

for xpos=2:6

for ypos=13:16

x(xpos,ypos)=xtreeinit;

end

end

for xpos=4:7

for ypos=11:12

x(xpos,ypos)=xtreeinit;

end

end

for xpos=7:8

for ypos=9:10

```
x(xpos,ypos)=xtreeinit;  
end  
end
```

```
for xpos=8:9  
for ypos=7:8  
x(xpos,ypos)=xtreeinit;  
end  
end
```

```
for xpos=10:11  
for ypos=4:6  
x(xpos,ypos)=xtreeinit;  
end  
end
```

```
for xpos=11:14  
for ypos=2:3  
x(xpos,ypos)=xtreeinit;  
end  
end
```

Main program routine:
-----------------------

```
for ty=1:year % start YEAR  
ty
```

```
for day=1:365
```

```
nptest=0;
```

Different elephant movement routines:

1) Back and forth:

```
%iadd= round(round(rand*8.1)-4);  
%ipos=ipos+iadd;  
%if (ipos > 70 | ipos < 1) ipos=round(rand*70)+1;  
%end;
```

2) Move systematically:

```
%xpos=xpos+1;  
%while (x(xpos,ypos)<=0)  
%xpos = xpos+xstep;  
%if (xpos==xsize+1) ypos = ypos+ystep; xpos=1; end  
%if ypos==ysize+1 ypos=1; end  
%end  
  
%if (xpos==xsize+1) ypos = ypos+ystep; xpos=1; end  
%if ypos==ysize+1 ypos=1; end
```



3) Move using a random walk strategy in one group:

```
xstep=randsrc; ystep=randsrc;
```

```
while (x(xpos+xstep,ypos+ystep)<=0)|(xstep == 0 & ystep == 0)
```

```
    xstep=round(rand*2)-1; ystep=round(rand*2)-1;
```

```
end
```

```
xpos = xpos+xstep;
```

```
ypos = ypos+ystep;
```

```
% removing trees constantly x(ipos) = x(ipos) - 10*y*73;
```

```
x(xpos,ypos) = x(xpos,ypos) - (73*d*x(xpos,ypos)*y/(d*h*x(xpos,ypos)+1));
```

```
    if x(xpos,ypos)<=0
```

```
        x(xpos,ypos)=0;
```

```
    end
```

4) Move individually:

```
%for ipos=1:73
```

```
%x(ipos) = x(ipos) - (d*x(i)*y/(d*h*x(i)+1));
```

```
% if x(ipos)<=0
```

```
% x(ipos)=0;
```

```
% end
%end
```

```
end
```

End of DAY routine:
---------------------

```
for i=1:15
```

```
for j=1:21
```

```
if (x(i,j)>0)
```

```
    x0=x(i,j)/(1-x(i,j)/K);
```

```
    x(i,j)=x0*exp(a)/(1+x0*exp(a)/K);
```

```
    xall(ty,i,j)=x(i,j);
```

```
end
```

```
end % end i (x pos)
```

```
end %j
```

```
tspan=0:.1:1;
```

```
xx0=[y];
```

```
x1=0;
```

```
for i=1:15
```

```
for j=1:21
```

```
    x1=x1+x(i,j);
```

```
end
```

```
end
```

```
x1=x1/73;
```

```
[t,xx]=ode45('year_func_for_dayloop',tspan,xx0,[],x1);
```

```
y = xx(11);
```

```
yall(ty)=y;
```

```
end
```

```
End of YEAR routine:
```

```
for t=1:year
```

```
treeav(t)=0;
```

```
end
```

```
for t=1:year
```

```
tot=0;
```

```
for i=1:15
```

```
for j=1:21
```

```
tot=tot+xall(t,i,j);
```

```
end
```

```
end
```

```
treeav(t)=tot/73;
```

```
end
```

```
%figure
```

```
%i=1:73;tt=80:100;
```

```
%surf(i,tt,xall(tt,i))
```

```
%title('trees per km^2','FontSize',15)
```

```
%xlabel('distance in km^2','FontSize',15);
```

```
%ylabel('time in years','FontSize',15);
```

```
%i=1:73;tt=1:year;
```

```

% surf(i,tt,xall(tt,i))
% title('trees per square km')
% title('elephant per square km')
% xlabel('Distance x')
% ylabel('Time t')
% -----
% ttt=46:year;
% plot(treeav(ttt),yall(ttt),'-r','LineWidth',4);grid
% legend('A=0.05, x0=20000 /km^2','A=0.15, x0=1450000 /km^2','A=0.15, x0=20000
/km^2','A=0.15, x0=1370000 /km^2','simulation','simulation with one group')
% xlabel('trees / km^2','FontSize',15);
% ylabel('elephant / km^2','FontSize',15);
% xlabel('trees / km^2','FontSize',15,'FontName','Times Roman'); ylabel('elephant /
km^2','FontSize',15,'FontName','Times Roman');
% title('Simulation with elephant in one group (dashed line). Parameters the same.')

```