Individual-Based Modelling: A study of the correlation between mopane caterpillar outbreaks and the movement of African elephant

> Michelle de Klerk 26066981

October 20, 2009

Abstract

The research study aims to determine whether elephants move in relation to mopane caterpillar outbreaks. This will be done by means of mathematical modelling and an Individual-Based Model (IBM). The IBM will be developed in relation to a Geographic Information System (GIS) and will strive to realistically represent the individuals and environment which form part of the model. The IBM will serve as a Decision Support Tool (DST) which will aid researchers at Save the Elephants-South Africa (STE-SA) in deciding whether an investment in this research field will render any meaningful returns. The study will focus on three main species, namely the African elephant (Loxodonta africana), the mopane caterpillar (Imbrasia belina) and the mopane (Colophospermum *mopane*) tree. The pivot point of the research study is the mopane tree, which serves as the main connection point between two very contrasting species, namely elephants and mopane caterpillars. Elephants are mixed feeders and incorporate both grass and browse into their diets. Mopane is classified as a staple food item for elephants and can therefore have a significant impact on the foraging of elephants. The mopane caterpillar feeds on mopane leaves until pupation, and induces a change in the composition of the leaf chemistry. This change renders the leaf more palatable, as the amount of tannin in the leaf is reduced. Elephants, in turn, feed on the mopane. As a large quantity of an elephant's day is spent eating, it can be deduced that the distribution of mopane may have a large effect on the movement of the elephant. Therefore, the possibility exists that defoliation by the mopane caterpillars can have an effect on the movement of elephant due to the decrease of tannin in the leaf once the tree flushes with new foliage after defoliation. The DST will strive to save STE-SA time and money by making quantified predictions with regard to the movements of elephants in relation to mopane caterpillar outbreaks.

Contents

Co	onter	its	1
\mathbf{Li}	st of	Figures	3
\mathbf{Li}	st of	Tables	5
\mathbf{Li}	st of	Acronyms	5
1	Intr	oduction and Background	7
	1.1	Three interlinked species	7
	1.2	Interaction Point between the mopane caterpillar and the elephant	9
	1.3	Research Hypothesis	9
	1.4	Study Site	10
		1.4.1 The Associated Private Nature Reserves (APNR)	10
		1.4.2 Elephants in the APNR	11
	1.5	Method \ldots	13
	1.6	Document Structure	13
2	The	ory and Literature Review	14
	2.1	Animal Movement	14
	2.2	Simulation Modelling Approaches	16
	2.3	IBM and Movement Ecology	18
	2.4	Conclusion	18
3	The	IBM Framework	19
	3.1	The IBM Data	19
	3.2	Preliminary Data Analysis	20
		3.2.1 Elephant Population Data	20
		3.2.2 Global Positioning System (GPS) Data	21
	3.3	Inputs	24
		3.3.1 Elephants	24
		3.3.2 Mopane Caterpillar Population	25

		3.3.3	Mopane Tree Population	26
		3.3.4	Movement	26
4	The	IBM	Model	28
Т	4.1		Jp Screen	_
	1.1	4.1.1	Interface	
		4.1.2	Design	
	4.2		Design	
	1.2	4.2.1	Simulation Window Interface	
		4.2.2	Design	
	4.3		unts	
	4.0	4.3.1	Life Cycle Stages	
		4.3.2	Modelling Elements	
	4.4	Herds		
	7.7	4.4.1	Statechart	
		4.4.2	Modelling Elements	
		4.4.3	The Mopane State	
	4.5	-	e Caterpillars	
	4.6		e Trees	
	4.0 4.7	-	Testing and Validation	
	4.1	4.7.1	Initial Agent Values	
		4.7.1		
		-	Elephant Population Growth Rates	
		4.7.3	Elephant Movements	35
5	Res	ults an	d Recommendations	56
	5.1	Simula	tion Results	56
	5.2		nsion	
	5.3	Future	Research Opportunities	58
р:	hlian	monher		50
DI	gona	raphy		59
A	ppen	dices		61
\mathbf{A}	Defi	nitions	5	63
в	Sim	ulation	Data and Results	65

List of Figures

1.1	The APNR and the Kruger National Park (KNP)	10
1.2	Vegetation Distribution in the APNR	12
3.1	Population Data	22
3.2	Male elephant movements in the APNR	23
3.3	Female elephant movements in the APNR	23
3.4	High level view of the IBM	24
3.5	Mopane Data Analysis Sequence	27
4.1		29
4.2	The Start-Up Screen	31
4.3	1	32
4.4	The Main Simulation Window	34
4.5	Male Elephant Statechart Window	35
4.6		36
4.7	Rainfall Table Function	36
4.8	Statechart of a Female Elephant	38
4.9	Statechart of a Male Elephant	39
4.10	Female Parameters and Variables	40
	0	41
4.12	Male Parameters and Variables	42
4.13	Male Locations within a Bachelor Herd	42
4.14	Statechart of a Breeding or Bachelor Herd	43
4.15	Breeding Herd Parameters and Variables	45
4.16	Bachelor Herd Parameters and Variables	46
4.17	The Mopane State	47
4.18	Caterpillar Events	48
4.19	Caterpillar Outbreak within the Mopane Veld	49
4.20	Tree Events	49
4.21	Tree Colours	50
4.22	Validation of Male Elephant Values	52

4.23	Validation of Female Elephant Values	53
4.24	Validation of Caterpillar Values	54

List of Tables

3.1	Elephant Input Parameters	25
3.2	Mopane Caterpillar Input Parameters	25
3.3	Mopane Tree Input Parameters	26
3.4	Mopane Movement Data Analysis Results	27
3.5	Averages of Mopane Movement	27
4.1	Averages of Mopane Movement	44
4.2	Validation of the Population Growth Rate	54
5.1	Average Probabilities	56
B.1	Elephant Population Statistics	65
B.2	Elephant Population Data	66
B.3	Average Rainfall (2005-2008)	67
B.4	Simulation Results	68

List of Acronyms

APNR	Associated Private Nature Reserves
DST	Decision Support Tool
GIS	Geographic Information System
GPS	Global Positioning System
GSM	Global System for Mobile Communications
IBM	Individual-Based Model
KNP	Kruger National Park
ODD	Overview, Design Concepts and Details
РОМ	Pattern-Oriented Modelling
SSM	State-Space Modelling

 $\ensuremath{\mathsf{STE-SA}}$ Save the Elephants-South Africa

Chapter 1

Introduction and Background

The research study is centered around three very different but interlinked species: the African elephant (*Loxodonta africana*), the mopane caterpillar (*Imbrasia belina*) and the mopane tree (*Colophospermum mopane*). A possible link between the movement of elephants and mopane caterpillar outbreaks will be the main focus of the study and will be modelled with an Individual-based Model (IBM). The key link between these two species is the mopane tree, as this is the only shared food resource between the mopane caterpillar and the elephant. The IBM's main purpose is to serve as a DST to aid researchers at STE-SA in deciding whether this field is worth further investigation. To fully explain the aim of this research study, a more comprehensive understanding of the existence of each of the abovementioned species is necessary.

1.1 Three interlinked species

Mopane (*Colophospermum mopane*) is a semi-deciduous tree occurring in dry, lowland woodland and is an indicator of clayey, poorly drained and often alkaline soil. It prefers altitude ranges of 300-1000m and covers a range of approximately 550 000 km². Mopane is widely distributed throughout Southern Africa, in countries such as Botswana, Angola, Namibia, Zimbabwe, Mozambique and South Africa. The factors determining the distribution of mopane appears to vary over its range and include frost, soil type, minimum rainfall, length of the growing season and the number and occurrence of competing plant species (Timberlake, 1995). The tree sheds its leaves in an irregular fashion and is generally leafless from August to October. The first leaf flush¹ usually occurs with the first summer rains, but Styles and Skinner (1997) note that leaf flush can also occur independently of rainfall. Mopane is characterised by its butterfly shaped leaves which fold closed and hang down during very hot periods, thus casting little shade. The tree is an important browsing agent for many herbivores, such as eland (*Taurotagus oryx*),

¹See Appendix A for details of scientific processes and terms

kudu (*Tragelaphus strepsiceros*), impala (*Aepyceros melampus*) and elephant. Invertebrate species, such as the puss moth larva (Family: Notodontidae, Order: Epicerura) and the mopane caterpillar (*Imbrasia belina*), also feed on the leaves of the mopane tree (Hrabar, 2005).

Two species frequently found in association with the distribution of mopane are elephants and the mopane caterpillars. The elephant is classified as a mega herbivore, due to its large size and is seen as a high impact species of the savanna. Elephants are mixed feeders, incorporating both grass and browse into their diets (Codron et al., 2006). Mopane, when distributed within an elephants range could make up a large proportion of its diet and consequently could be classified as a staple food item for elephants (Smallie and O'Connor, 2000). Elephants feed on mopane mainly via branch breakage and bark and leaf stripping, thus having a 'pruning' effect on the tree. Branch breakage occurs mainly at the end of the dry season (August) when other food resources are limited. Any type of damage caused by elephants has a significant impact on the mopane tree, resulting in a variety of changes in the growth rate and the size of the leaves. Changes include an increase in the growth rate of new and remaining shoots and an increase in leaf size with a decrease in the amount of leaves produced. No change in the chemical defences of the leaves were observed (Hrabar et al., 2009).

The mopane caterpillar, larva of the Anomalous Emperor moth (*Gonimbrasia Belina*), is a widespread invertebrate and can be found in Southern Africa, Tropical Africa and East Africa (Hrabar et al., 2009). The caterpillar feeds on a wide variety of tree species, including the marula (*Sclerocarya birrea*), the tall common corkwood (*Commiphora glandulosa*), the umbrella thorn (*Acacia tortillis*) and the well known mopane (*Colophospermum mopane*) (Hrabar, 2005). Mopane caterpillar outbreaks usually occur twice a year during the summer season, with the first, more abundant one in October/November and the second in March/April (Gaston et al., 1997). In more arid regions, usually only one outbreak per summer season occurs due to the scarcity of resources. Large outbreak populations are only found in mopane woodland, as this tree is their main host plant (Hrabar, 2005).

The larva passes through five instars (or stages) in a period of six weeks before pupation, during which time the caterpillar's body mass increases by about 4000 fold. The fifth instar climbs down the tree and burrows itself into the soil, where it pupates for approximately six to seven months. The adult moth emerges and has two to three days to lay eggs before it dies. During this brief lifetime, the only function of the female moth is to find a mate and lay eggs. No time is spent on eating, as the moth has undeveloped mouth parts and relies only on the nutrition and water accumulated during its time as a caterpillar (Holm and De Villiers, 1983). A female moth will lay a single cluster of 30-335 eggs on the leaves, stem or branches of a mopane tree. After a period of ten days, the larva emerges and the process is repeated. Defoliation by mopane caterpillars could result in the damage of large areas of mopane. This damage results in a decrease in shoot and leaf size and a change in chemical defences in the leaves (Hrabar, 2005).

1.2 Interaction Point between the mopane caterpillar and the elephant

Browsers, such as the elephant, prefer woody species with specific chemical composition, such as high concentrations of protein and minerals, and low concentrations of fibre and tannin (Holdo, 2003). A study done by Hrabar et al. (2009) found that a reduction in the tannin to protein ratio and a decrease in total polyphenolic concentration took place due to extensive defoliation by mopane caterpillars. This reduction in tannin caused by defoliation can hold advantages for large mammalian browsers, as a lower level of the bitter tasting tannin will render the leaf more palatable. Tannin can also inhibit digestion of proteins and carbohydrates, thus lower levels of this polyphenol can only hold positive implications for herbivores (Bryant et al., 1991).

Due to the abovementioned changes, with the next leaf flush after mopane caterpillar defoliation, the mopane leaves will resultantly have a lower level of tannin. This change can potentially be realised by elephants and may influence their movement patterns. Elephant movements are predominantly influenced by the availability and palatability of food and the abundance of water.

1.3 Research Hypothesis

It is the focus of this research study to investigate the possible influence which mopane caterpillar outbreaks have on elephant movement via their shared food resource, mopane. This is a research field not yet explored and Hrabar et al. (2009) mentions as a concluding statement to their article that a research field deserving further study would be to investigate whether elephants and mopane moths choose their feeding areas on the basis of prior feeding by the other species.

With careful consideration of all of the abovementioned information, the research hypothesis to be investigated is:

"Elephants move in relation to mopane caterpillar outbreaks due to their shared food resource, mopane."

1.4 Study Site

The research project will be done in collaboration with STE-SA. This organisation is based in four regions of Africa with their focus in South Africa being on the possible drivers of elephant movements within reserves to the east, west and north of core conservation areas such as the KNP. This study will take place within the APNR to the west of the KNP and can be seen in Figure 1.1.

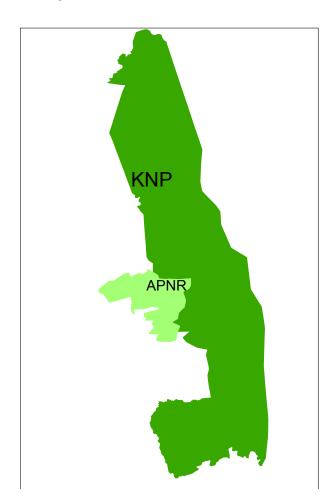


Figure 1.1: The APNR and the KNP

1.4.1 The APNR

The APNR consists of the Klaserie, Timbavati, Balule and Umbabat Private Nature Reserves which, in total, comprises approximately 180 000 ha (Greyling, 2004). The climate throughout the APNR is mostly dry and hot with an average annual temperature of 22°C. Mean annual rainfall is less than 600mm and is known to increase from north to south and east to west. Water is drained from the uneven terrain via the permanent Klaserie and Olifants rivers and via the seasonal Timbavati river. The dominant geological features found in the APNR is granite and gneiss rock which are intersected by dolerite intrusions. The dark-coloured gabbro is found in the central and southern regions, and is rich in iron and magnesium. The main vegetation types associated with the APNR are divided into nine landscape types, namely: (1) Knob-Thorn Tree (*Acacia nigrescens*) / Red Bushwillow (*Combretum apiculatum*) woodland, (2) Mopane veld, (3) Red Bush-willow open woodland, (4) Mopane woodland / *Combretum* spp., (5) Silver Cluster-Leaf (*Terminalia sericea*) woodland / *Combretum* spp., (6) Mixed *Combretum* spp. / Silver Cluster-Leaf woodland, (7) Mixed veld on Gabbro, (8) Olifants River Rugged veld, (9) Shrub Mopane veld (De Villiers, 1994).

The distribution of the vegetation types throughout the APNR is important, as the research study will only focus on landscape types which include mopane trees and shrubs. A detailed representation of the vegetation distribution in the APNR can be seen in Figure 1.2:

Mopane is represented on the vegetation map as dark or medium green, and therefore the research study will mainly focus on the North-Eastern section of the APNR. Small patches of mopane are found in the Northern and lower Eastern sections of the APNR, and will not go unnoticed during the research study. Other colours present on the vegetation map are vegetation types not applicable for this research study.

1.4.2 Elephants in the APNR

Prior to 1962, no elephants were found outside the KNP due to the fencing of the western boundary of the KNP. Elephants were irresponsibly hunted two centuries ago and caused an almost eradication of elephants throughout most of South Africa (Hall-Martin, 1992). The KNP and the adjacent privately owned land was repopulated by immigrant elephants from Mozambique. The elephant numbers in the APNR were estimated at approximately 189 in 1983 and stabilised in 1992 to just more than 500. From 1996 to 2001 another increase from 500 to just over 800 was seen, and this is assumed to be due to the removal of the boundary fence between the APNR and the KNP in 1993/1994 (Greyling, 2004).

The social arrangement of elephants within the APNR follow the same general trend as in the rest of Africa, with elephants occurring in either bachelor herds, as lone bulls or as family units consisting of females and their offspring. STE-SA has conducted extensive research and have collared a large amount of elephants in the APNR with GPS satellite or GPS/Global System for Mobile Communications (GSM) collars. The position of the elephant is daily downloaded at hourly intervals which makes allowance for tracking of elephants in the field in order to ground truth their position and collect additional data on their social status. One of the main objectives in accumulating elephant tracking data is to gain insight into the home ranges of individual elephants. An elephant's home range is defined as the area in which it moves throughout the year, including migration. The most recent home range calculations of the elephants have produced interesting results.

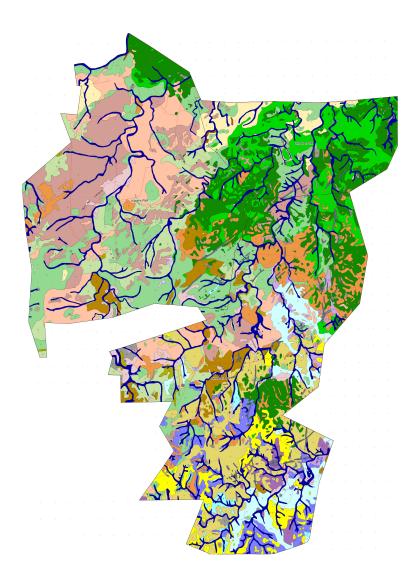


Figure 1.2: Vegetation Distribution in the APNR

Henley and Henley (2009) found the average home range of females to be 994 km², which is an increase of more than 100% from the range estimated by De Villiers and Kok (1997), which found the ranges to be between 115 and 465 km². An extensive increase was seen with the home ranges of male elephants. Henley and Henley (2009) found an increase of more than 500% in the home ranges of male elephants, with senior bulls (age >35) at 1575 km², adult bulls (25 <age >35) at 1836 km² and young adults (age <25) at 4416 km². Both De Villiers and Kok (1997) and Henley and Henley (2009) used the minimum Convex Polygon method in calculating the home ranges, which allows comparitive results.

1.5 Method

The possible correlation between elephant movements and mopane caterpillar outbreaks will be mainly investigated by means of a simulation model. The simulation model to be developed should realistically portray the reality of the ecosystem and should provide useful insight into the interaction between elephants, mopane caterpillars and their environment. A strong core in ecological theory should form the base of the model and a thorough understanding into the dynamics of the system is imperative.

Extensive data and information gathering will take place before the simulation model can be developed. Anylogic will be used to build the simulation model and will be combined with GIS software to enable the realistic spatial relationships between the individual agents and the environment.

1.6 Document Structure

The rest of the report is divided into Chapter 2, Chapter 3, Chapter 4 and Chapter 5. Chapter 2 will give a brief overview of the current literature available on the research subject and will focus on three main areas, namely Animal Movement, Simulation Modelling Approaches and IBM and Movement Ecology. Chapter 3 will in turn focus more on the data to be included in the IBM and will provide more information regarding the inputs required for the construction of the IBM. In Chapter 4, the detail design of the simulation model is discussed and all relevant information regarding the model development and structure is given. The research study results and conclusions are discussed in Chapter 5 and are based on the outcomes of the IBM.

Chapter 2

Theory and Literature Review

Hrabar (2005) directly links elephants and mopane caterpillars via their shared food resource, the mopane tree. The effect of elephant consumption of mopane trees on caterpillar abundance was studied. Throughout the study, attention was given to the differential effect that defoliation by caterpillars and pruning by elephants have on the trees. This effect was determined by means of leaf and shoot length measurements as well as measurement of the nutritional value of the leaves. It was concluded that defoliation and pruning each have a considerable but different impact on the regrowth characteristics of mopane and that both decrease the tannin to protein ratio. The results indicated that adult mopane moths choose their host plant primarily due to tree size and not with regard to mopane leaf chemistry. It was also found that pruning by elephants had a negative effect on the abundance of mopane caterpillars. This is due to the negative impact which elephant pruning had on the density of tall trees in the specific areas. No attention was given to the movement of elephants in relation to defoliation by caterpillars.

A recent publication by Hrabar et al. (2009) agree with Hrabar (2005) on the effect which defoliation and pruning has on the regrowth reponses of mopane. It was found that defoliation resulted in a decrease in the size of shoots and leaves with pruning having the opposite effect. In contrast, however, Hrabar et al. (2009) found that a decrease in the chemical defences of mopane leaves only occurred with defoliation and not with pruning. A closing statement by Hrabar et al. (2009) state that an important aspect of future studies would be to determine whether elephants and mopane moths choose feeding areas in mopane woodland due to prior feeding by the other species. This underlines the importance and relevance of the possible results to be found by the current research study.

2.1 Animal Movement

The movement of animals, scientifically known as movement ecology, has been an area of intense research for the past 25 years. In the last decade, nearly 26 000 papers referring to organismal movement were published. The movement of an organism is thought to be

due to either long-term or short-term goals. Short-term goals can include goals such as reproduction, maintenance, feeding, survival and escaping threats. On the other hand, long-term goals are more orientated towards fitness implications, avoidance of inbreeding and population extinction (Holyoak et al., 2008). Over the years, ecologists have gained invaluable knowledge on the behaviour of individuals and their interaction with the environment. This was done in an effort to understand the future impacts of climate change and habitat loss (Schick et al., 2008). Even though extensive research on the movement of organisms has been conducted, a general unifying paradigm with which movement ecology can be placed within a common context, is still lacking (Nathan et al., 2008).

The four basic components of movement, as stated by Nathan et al. (2008), are the internal state (why?), motion (how?), navigation (when and where?) and external factors. A framework is introduced with which the interaction between the four basic components of movement can be depicted. This framework is aimed at integrating movement research into a structured paradigm and hopes to stimulate the development of new methods. The paradigm is directed at providing a basis for hypothesis generation and strives to facilitate the comprehension of the causes, mechanisms and spatiotemporal patterns of movement. It is hoped that this framework will aid in the greater understanding of the role of movement in ecological processes. Movement of an organism is thus a function of each of these four components, and must therefore be modelled in this way.

Schick et al. (2008) mention that various tools have been used to examine the interaction between the organism and its environment. The tools include: random walks, fractal analysis, first passage time, Lèvy flights, multi-behavioural analysis, hidden markov models, and state-space models. The key factor which most of the mentioned tools lack, is the ability to test the extent to which landscape features influence the movement process. Together with the increase in movement modelling, an increase in the use of hierarchical Bayesian models can be seen. Bayesian models allow for the separation of the available data (e.g in the form of GPS coordinates) and the movement process itself. A new hierarchical model is introduced by Schick et al. (2008) which addresses both the state of the individual in motion as well as the state of the map over which the organism is moving. The proposed model moves away from traditional random walks and strives to direct inference on how moving organisms with intricate behaviour interact with their environment and make choices about its suitability.

State-Space Modelling (SSM) is proposed by Patterson et al. (2008), as this technique is statistically robust and allows for the infusion of insights from animal behaviour, biogeography and spatial population dynamics. SSM has its origin in engineering, but has found applications in a wide variety of different disciplines. It is mentioned that movement data is inherently stochastic and subject to observation errors. SSM combines a process model, which describes the movement of an individual, with an observation model. The process model is tightly associated with Markovian mathematics, as it predicts the future state (position) of an animal given its current state. The observation model, in turn, gives the probability of an observation conditional to the animal's current state. Partly due to its predictive ability, the authors state that SSM is the most promising avenue towards a fresh type of movement ecology.

A fresh way of modelling movement and looking at the connectivity among populations and habitats is introduced by McRae et al. (2008). They propose using simple electrical circuit theory to predict movement patterns and to identify habitat patches and movement corridors. Individual movement of an organism is linked to resistance, current and voltage and ecological interpretations corresponding to each are given. Resistance is linked to the opposition offered by a habitat type to the movement of an organism. Current can be used to predict the expected net movement of random walkers and voltage is employed to predict the probability that a random walker will reach a given destination before an event such as mortality. The relationship between random walk theories and circuit theory is discussed throughout the article. Electrical circuit theory has been used to analyse connectivity in chemical, neural, economic and social networks and holds potential for ecology and conservation as well.

2.2 Simulation Modelling Approaches

As can be seen from the above literature, much attention is given to the formulation of animal movement, but it is not visually represented in a user-friendly and easy understandable way. A means of combining modelling and visual representation is needed. Simulation can be used as a modelling tool where visual representation of the model by means of visual graphics on a computer, is allowed.

A general problem encountered by many ecologists is that several simplifying assumptions must be made when mathematical modelling and simulation is used to gain an understanding of an ecological system. This brings about an incompatibility with the reality of ecological systems (DeAngelis and Gross, 1992). Models used for more traditional modelling, known as classical models, see a population as an aggregate of average individuals and don't compensate for the fact that a population consists of unique individuals. Individuals are seen as identical and very little detail of an individual's life cycle is taken into account (Grimm and Uchmanski, 1996). This is in contrast with the fact that any part of nature is unique and has its own, specific characteristics (Breckling, 1992). If a realistic view of an ecological system is to be obtained, less assumptions and more individuality must be accounted for.

With more focus needed on the individual, the focus of modelling has changed. IBM, or Agent-based modelling, changes the focus of modelling from aggregated to individual. IBM has received much attention over the past decade and a half, with the number of articles published on the subject increasing linearly (DeAngelis and Mooij, 2005). IBM

allows for variation in the form of age, sex, size and behaviour between individuals and attempts to better represent the reality of a system. It is stated that the inclusion of such variation is imperative to the continual progress in ecological and evolutionary theory. IBM models a system as a collection of autonomous decision-making and interacting entities within a specific environment. Gregory et al. (2006) state that the major advantage of IBM is that it is evolutionarily open-ended. Thus, the birth and death of virtual species can be observed as the simulation runs and the traditional technique of assuming x amount of species at the start of simulation time, is abandoned. IBM can be seen as the most natural way to represent behavioural entities (Bonabeau, 2002).

Grimm et al. (2006) describes IBM as being important for both theory and management, as they allow researchers to consider aspects which are usually ignored in analytical models. These aspects include variability among individuals, local interactions and an individuals adaptation to the ever changing internal and external environment. Even though IBM holds great potential, it comes with a cost. It is inherently more complex and difficult to analyse and understand than analytical models.

To alleviate the complexity in the understanding of IBM, Grimm (1999) present a list of heuristic rules in order to advance the practice of IBM and to ensure that more general lessons are learned in the future from IBM than have been done in the past. A mini-review of 50 individual-based animal population models was conducted in order to gain insight into why the models were designed and to aid in the compilation of the set of heuristic rules. After the review was completed, it was concluded that the most successful and useful models were those that were based on a pattern observed in nature. These models led to new insights and their results served as building blocks for a more general ecological theory.

The basis of the natural sciences is the inherent patterns which are observed in nature (Grimm et al., 1996). With the desire of getting to the bottom of patterns in nature being the basic research program of science, a new strategy for individual-based ecological modelling is introduced. The strategy is termed Pattern-Oriented Modelling (POM) and takes its orientation from the observed patterns in nature. POM provides a unifying framework with which the internal organization of an individual-based complex system can be decoded. Model structure can be optimised, theories for individual behaviour can be tested and parameter uncertainty can be reduced. The main idea of POM is to guide the design of models by the multiple patterns observed in the real system. Variables and processes are chosen such that the observed patterns which characterise the system and its dynamics, are reproduced.

2.3 IBM and Movement Ecology

IBM has seen a number of applications in the world of movement ecology, with DeAngelis and Mooij (2005) classifying movement ecology as one of the seven major groups of studies using IBM. Fish-migration models, models of migrating birds and the simulation of wind dispersal of seeds are only a few individual-based movement models in the literature. McRae et al. (2008) also mentions the use of individual-based movement models to predict the connectivity between different habitat patches. It is also important to note that these individuals must be modelled against a realistic environment. This is mostly achieved by combining IBM with a GIS. This brings about another level of complexity, as the distinction between agent entities and spatial entities becomes a challenge (OSullivan, 2008).

2.4 Conclusion

The above literature shows that there is a well established link between the modelling of animal movement and individual-based modelling. IBM is an alternative way of representing ecological systems and might alleviate the burden of extensive data gathering. A reliable prediction, given that modelling is done accurately, can save researchers some time in deciding whether a certain field of research is worth pursuing. A combination of the abovementioned tools and processes will be used to model the movement of elephants in relation to mopane caterpillar outbreaks. Additional insights into the underlying patterns and interactions between the various individuals will also be gained by analysing the IBM.

Chapter 3

The IBM Framework

To successfully construct the IBM, data gathering of various items must take place. When constructing any type of model, there can be differentiated between ideal data and realistic data. As everything in reality is subject to certain constraints, data gathering will be no exception. Time, resources and availability of data are only some of the constraints placed on successful data gathering. The ideal and the currently available data will be explained and analysed in the following chapter.

3.1 The IBM Data

Under ideal circumstances, extensive field research should take place to gather the necessary data. The field research would include the following:

- Data gathering of individual elephants found in the APNR, in the form of GPS tracking, and information regarding their behaviour to understand their unique population dynamics and to identify key behavioural variances from other elephant populations found throughout Africa.
- Tagging and monitoring of individual mopane trees to distinguish between trees that are used by mopane caterpillars and elephants and trees which are not.
- Data gathering of mopane caterpillar outbreaks via a microlight to determine their frequency and distribution.

The gathering of the abovementioned data will stretch over a period of a few years to enable the successful and reliable capturing of mopane caterpillar outbreak data. A large amount of time and resources will have to be employed to gather the abovementioned data. In the current research study, neither the time nor the required resources are available to capture the ideal data sets. This brings the validity and usefulness of the current research study into question. The data which are currently available in the research study include:

- Elephant tracking data, in the form of GPS records.
- Aggregate mopane tree distribution throughout the APNR.
- Data regarding one outbreak of mopane caterpillars during November/December 2008.

To answer whether the research study is still viable, one must take into consideration what one wants to achieve by the research study. The IBM needs to serve as a DST to aid the researchers at STE-SA in whether the mopane caterpillar-elephant research field is worth pursuing. Therefore, the IBM will not serve as the main research study and will only be supplementary to the final study. The DST will also come in handy once further data analysis of the elephants, excluding the mopane caterpillar interaction, is needed. It is also important to note that even if extensive data gathering is done, there will always be an element of randomness in the data. The mopane caterpillar outbreaks almost never occur in the exact same place and elephant movements remain unpredictable. Steps will be taken to reduce the effect of the lacking data to such an extent that it will not influence the validity of the model, and will include:

- Intensive analysis of research done by Hrabar (2005) and Hrabar et al. (2009) In-depth data regarding mopane trees, mopane caterpillars and elephants were captured. The captured data will be converted into useful parameters which will form the backbone of the parameters to be included in the model.
- **Extrapolation of current data** This will be done with careful consideration of the patterns and parameters observed and calculated in the aforementioned step.

By closely following the steps outlined above, the IBM will result in an applicable and useful tool and will serve its main purpose.

3.2 Preliminary Data Analysis

3.2.1 Elephant Population Data

Population data regarding the elephants monitored by STE-SA was received for the years 1992-2008. As is shown in Figure 3.1a and Figure 3.1b, the data is very noisy and at some instances, inaccurate. A number of factors can contribute to the inaccuracy of the data, and include the following:

 It is very difficult to make an accurate estimation of the elephant population in the APNR, as this is a large area and the fence between the APNR and the KNP has been removed. This allows the elephants to move freely between the two protected areas.

- 2. Births and deaths are difficult to monitor, as carcasses are not always found and births are not always recorded. Calf carcasses are especially difficult to record as they are obscured by vegetation.
- 3. All counts are done by humans, and it is impossible to accurately count animals over such a large area.

Figure 3.1a clearly shows that the elephant population in the APNR increased steadily over the past 17 years. The elephant population can be divided into two types of herds, breeding herds and bachelor herds. The breeding herds consist of breeding females and male and female youngsters with the bachelor herds consisting only of male elephants over the age of 14 years. The number of breeding herds to bachelor herds is shown in Figure 3.1a, with the breeding herds dominating the overall elephant population.

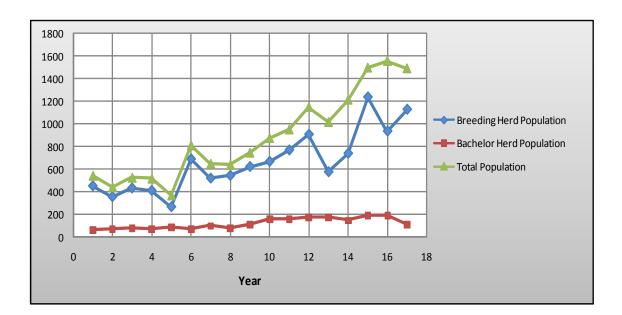
The number of births and deaths is presented as a percentage of the total elephant population size and is shown in Figure 3.1b. In Figure 3.1b, it can be seen that the number of births as a percentage of the total population is decreasing. The number of deaths as a percentage of the total population size appears to be constant. If one assumes these trends as indicative and a forecast is made based on these trends, the elephant population will eventually become extinct. This is however not the current case in the APNR as the total population is growing at a steady rate. This contradiction between the reality and the data can be attributed to inaccurate and non-representative data.

The graphs discussed in the preceding paragraphs will be used to derive the input values necessary to build the IBM and will be discussed in more detail in Section 3.3. Details regarding the elephant population data can be found in Appendix B.

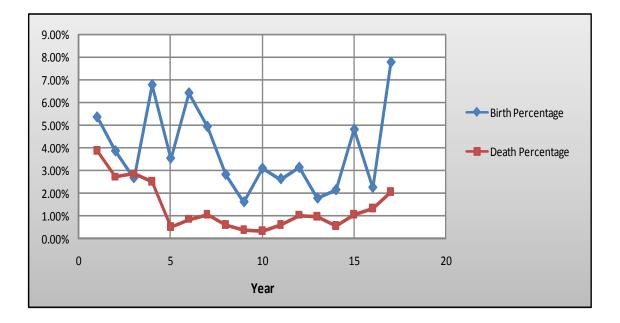
3.2.2 GPS Data

The GPS data supplied by STE-SA was analysed and some interesting observations were made. On average, mostly male elephants were found in mopane veld with the breeding herds found feeding more irregularly in this specific vegetation type. These results were in accordance with previous findings by Henley and Henley (2005). The periods that will specifically be looked at will be during the first and second leaf flush after defoliation.

Figure 3.2 and Figure 3.3 show four examples of male and female elephant movements in the APNR. The data represented was collected over a period of two years from 2006 - 2008. The difference in home ranges between the four elephants are clearly visible as well as the movement of the elephants between the APNR and the KNP.



```
(a)
```



(b)

Figure 3.1: (a) General Population Data; (b) Births and Deaths as a percentage of Total Population

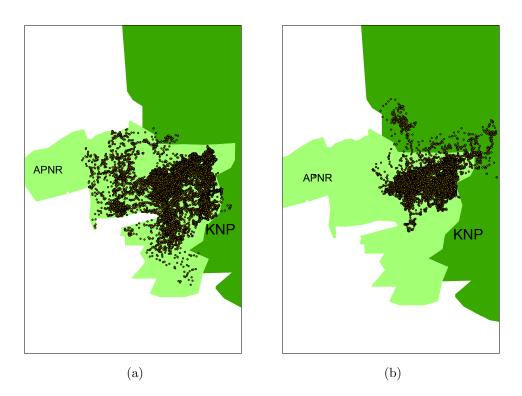


Figure 3.2: Male elephant movements in the APNR: (a) Male elephant 1; (b) Male elephant 2.

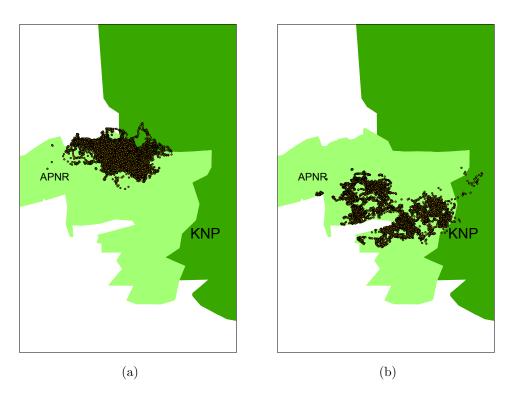


Figure 3.3: Female elephant movements in the APNR: (a) Female elephant 1; (b) Female elephant 2.

3.3 Inputs

The inputs for the IBM can be divided according to the three different species (agents) present in the model, namely the elephant, the mopane caterpillar and the mopane tree. Each of these agents are treated differently as the level of representation for each differs. As this IBM focusses on the effect these agents have on one another, different levels of processes exist. The model can be visualised on a high level scale in Figure 3.4.

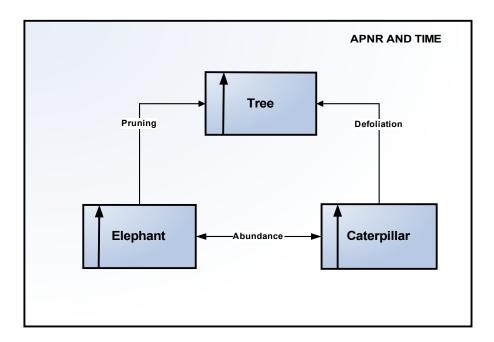


Figure 3.4: High level view of the IBM

Each of the agents represented in Figure 3.4 have internal processes occurring over time, represented by the internal arrows. The time unit used in the IBM is months, as all the important processes are triggered by the passing of this time unit. The inputs with regard to each species is discussed in the following sections.

3.3.1 Elephants

The inputs used to determine the values associated with the elephant population are derived from data supplied by STE-SA. The data was analysed to determine the growth rate of the population. Birth and death rates were also calculated according to the current data, but the rates were found to be inconsistent with the population growth rate. This can be attributed to inaccurate data collection. Therefore, the values had to be adjusted to ensure an inherent consistency. The elephant population is assumed to be in a steady state condition, ie. there is an even age distribution in the population. A constraint is placed on the extent to which the population is able to increase, due to natural factors influencing the carrying capacity of the APNR. The input parameters for the elephant population is shown in Table 3.1. The initial population size is specified by the user of the IBM and is constricted to a value between 400 and 1000 elephants. The amount of breeding herds and bachelor herds present in the population is governed by the calculated ratios represented in Table 3.1.

Description	Amount
Population Growth Rate Birth Rate Mortality Rate Initial Population Size Range of Initial population size % Breeding Herds of population	6% 8% 2% User 400 - 1000 80%
% Bachelor Herds of population	20%

 Table 3.1: Elephant Input Parameters

3.3.2 Mopane Caterpillar Population

The input parameters for the mopane caterpillar population is very simple, as can be seen in Table 3.2. The range within which the caterpillar population size can vary is expressed in mopane egg masses/ha. A mass of eggs consists approximately of 100 eggs. The range of values include zero, as mopane caterpillar outbreaks do not necessarily happen each time and is dependent on the degree of rainfall in the environment.

As mentioned previously, the caterpillar is in its larva state for approximately 6-7 weeks. It is assumed that the caterpillars completely defoliate a given mopane tree within this time. Therefore, the defoliation time is approximately 1.5 months from the point of larva outbreak.

Description	Amount
Egg masses per hectare	0 - 500
Eggs per mass	100
Available hectare	45000
Defoliation Time	1.5 Months

Table 3.2: Mopane Caterpillar Input Parameters

3.3.3 Mopane Tree Population

Table 3.3 shows the input parameters for the mopane tree population. The amount of trees within a given mopane veld is a random variable varying between 700 and 1400 trees/ha (Hrabar, 2005). The size of the APNR and the distribution of mopane veld within the APNR was used to determine the approximate amount of hectare of mopane veld within the APNR. Hrabar (2005) observed that the tree flush process is complete within three weeks after defoliation. Therefore, with respect to the IBM, the tree is flushed within a month after caterpillar defoliation. Flushing only commences once the larva state of the mopane caterpillars are over.

Table 3.3: Mopane Tree Input Parameters

Description	Amount
Size of Mopane Veld	45000 ha
Range of Population Size	700 — 1400/ha
Flush Time	1 Month

3.3.4 Movement

Extensive analysis of the GPS movement data was done to extract relevant rates and indicators to govern the movement of the elephants. Due to the purpose of the research study, analysis was only focussed on the time that the elephants are in the mopane veld (MV). The important months that were focussed on are December, January, March and April as this is the time in which the mopane tree reflushes after defoliation.

The steps that were followed in the data analysis process are outlined in Figure 3.5. This process was followed for each elephant and resulted in the numbers shown in Table 3.4. Even though some of the percentages might seem large, they must be seen in perspective. One example is Female elephant 4 with 89% of her time in the mopane veld being spent during the specified months. But the total percentage time that she spent in the mopane veld relative to her total amount of points is a mere 1%.

The most important results to notice are those presented in column 4 and 6 of Table 3.5. The conclusion that can be drawn is that male elephants spend on average 20% of their time in the mopane veld, and of that 20%, only 37% is during December, January, March or April. Similarly for the female elephants which only spend on average merely 6% of their time in the mopane veld of which 57% is during the specified months. This data will be used as input to the movement of the elephants and will govern when and why they move to the mopane veld. All relevant inputs and parameters are complete to now allow for the successful development of the IBM.

Elephant	Total GPS points	Total points in MV	% Time in MV in D/J/M/A	% Time in MV relative to	% Time in MV in D/J/M/A
	points	111 IVI V	$\lim D/J/M/A$	Total points	relative to Total points
Male 1	20419	13153	49	64	32
Male 2	18334	14356	31	78	24
Male 3	16161	7027	28	43	12
Male 4	9740	3198	23	33	8
Male 5	19066	17027	37	89	33
Male 6	19865	2019	53	10	5
Female 1	18749	3376	48	18	9
Female 2	9354	3903	38	42	16
Female 3	6273	571	42	9	4
Female 4	10888	135	89	1	1
Female 5	17956	198	67	1	1

Table 3.4: Mopane Movement Data Analysis Results

Table 3.5: Averages of Mopane Movement

Elephant	Total GPS	Total points	% Time in MV	% Time in MV	% Time in MV
	points	in MV	in $D/J/M/A$	relative to	in $D/J/M/A$
				Total points	relative to Total points
Males	17267	9463	37	53	19
Females	12644	1636	57	14	6
Temales	12044	1050	51	14	0

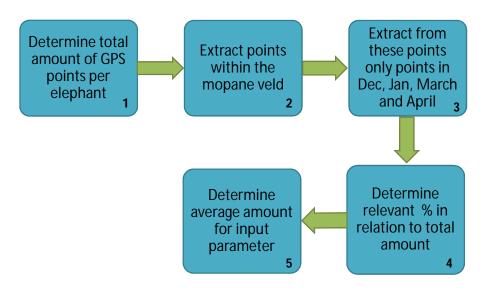


Figure 3.5: Mopane Data Analysis Sequence

Chapter 4

The IBM Model

A high-level representation of the IBM is shown in Figure 4.1. The diagram was designed to give a broad understanding of the model and to orientate the user with regard to model inputs and outputs. The software package used for the building of the IBM is Anylogic. This package is the only tool that supports the simultaneous combination of methodologies of System Dynamics, Discrete Event and IBM in one simulation model. Anylogic employs Java as its language and thus the IBM is structured according to the principles of the Java programming language. Each active object class is discussed separately as well as the manner in which they interact and depend on one another. The IBM was originally planned to only consist of three agents, the elephant, the mopane caterpillar and the mopane tree. But during model development, the need for the creation of additional agents was identified. These agents include breeding herds, bachelor herds and two separate agents for elephants, namely male and female. The breeding and bachelor herds are primarily created to serve as a vehicle for the movement of the elephants with the male and female elephants as the passengers of the vehicle. The time unit used in the simulation model is months and correspond to one second in real time. The model will be explained by following a top-down approach and will start with the start-up screen and work down to the individual building blocks of the model.

4.1 Start-Up Screen

4.1.1 Interface

The start-up screen is the first screen the user will encounter once the simulation model is run and is shown in Figure 4.2. The main reason for the start-up screen is to allow the user to change certain input parameters of the model. This is to give the IBM more flexibility and to allow users to observe the effects of changing the input values.

The initial values of the agents can be interactively set by the user by adjusting the slider bars. The parameters are arranged into three different groups, namely male

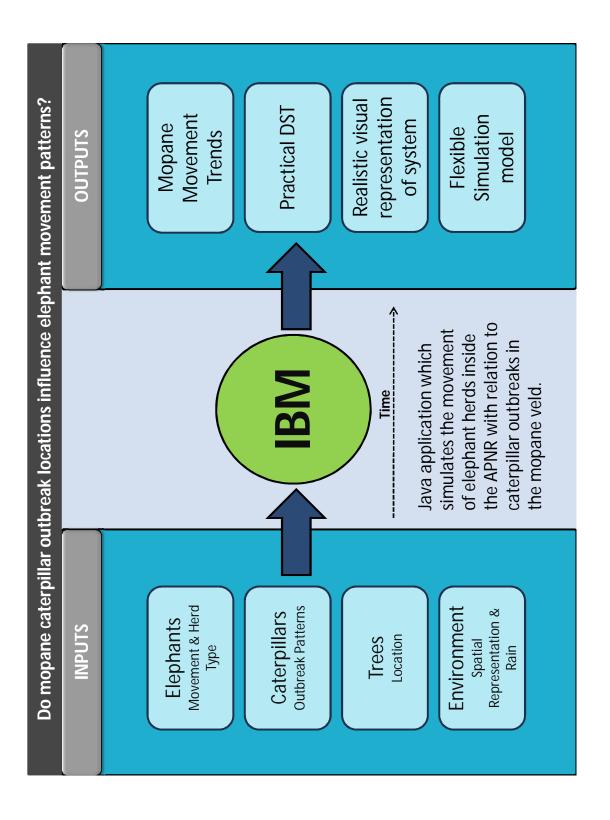


Figure 4.1: Conceptual Representation of the IBM

elephants, female elephants and mopane caterpillars. These are the only agents for which input values are allowed to vary. Default values for each parameter are initially shown on the left-hand side of each slider bar, but once the slider bar is toggled, the value changes. Limits are set on the slider bar amounts according to the allowed amount per agent to keep the simulation feasible and realistic.

A radio button on the lower right-hand side of the screen allows the user to run the simulation model. Once this button is pressed, the main simulation window appears. The main simulation window is the interface of the Main object class and will be discussed in Section 4.2. Whenever the model is stopped by the user, the model will return to the start-up screen and the user will be able to reset the initial parameters according to the user's preference.

4.1.2 Design

The start-up screen is designed in the Simulation object class of the simulation model. A set of variables corresponding to all the values available for adjustment in the startup screen is created in order for the model to communicate these input values to the corresponding agents (refer to Figure 4.3).

In the Simulation object class the model time unit is set to months. Each month in simulation time corresponds to one second in real time. The manner in which simulation runs are reproduced are set to be unique, with the choice of the random number generator's seed to be chosen randomly.

The variables shown in Figure 4.3 correspond to parameters specified in the Main object class which is the next point of discussion.

4.2 Main Object Class

The Main object class can be seen as the combination point for all the different object classes and is mandatory in the Java language. This allows for the separate building blocks of the model to be combined into a single class from which the model is run. The different object classes which make up the model are embedded in the Main class and are referred to as "embedded objects". The interface of the main simulation window is created in the Main class and will be discussed in the following section.

4.2.1 Simulation Window Interface

The main simulation window is encountered by the user as soon as the model is run and is shown in Figure 4.4. The APNR map is drawn in the window and provides the space in which all of the agent movement takes place. The breeding and bachelor herds are represented by magenta and blue respectively and can be seen moving around inside the

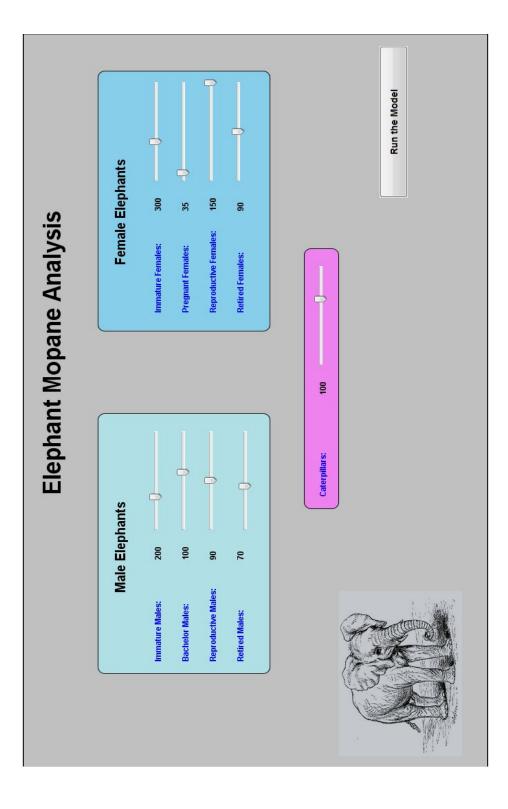


Figure 4.2: The Start-Up Screen

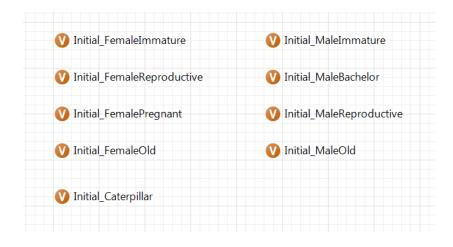


Figure 4.3: The Start-Up Variables

APNR and KNP in Figure 4.4. The mopane veld under examination is indicated in the upper right-hand corner of the APNR and is the main area to be observed. The elements and interactions which make the image in the main simulation window possible will be discussed in Section 4.2.2.

The buttons on the right hand side of the screen allows the user to open a statechart of a randomly selected male or female elephant. The statechart will show in which state the elephant is and whether it is in the mopane veld or not. The age and herd in which the given elephant is is also shown. Figure 4.5 is an example of a randomly selected male elephant with an age of 20 years and which forms part of bachelor herd number 6. The breeding herd variable is currently inactive as the male is not presently part of a breeding herd. The male is currently in the bachelor state and not presently in the mopane veld.

The two graphs visible in the simulation window have different roles. The graph at the top of the simulation window counts the number of elephants which move into the mopane veld. This graph only counts an elephant when it moves into the mopane veld as a result of a direct order and not due to random movement. The validity of the research hypothesis will be tested by the results shown in this graph. The graph at the bottom of the page is to keep track of the amount of elephants present in the elephant population. The stack chart is divided into three parts to differentiate between the different parts in which the population is split into, namely breeding herds, bachelor herds and immature males still forming part of the breeding herds. This graph is especially used in the validation of the model and will be further discussed in Section 4.7.

A legend is provided to aid the user in differentiating between the different agents

visible in the simulation. The simulation time can be seen at the bottom left-hand corner of the screen and indicates the amount of months passed. The simulation can be sped up or slowed down by toggling the buttons at the top of the simulation window. No time limit is set on the simulation and will run indefinitely until the user presses the stop button at the top left-hand corner of the simulation window.

4.2.2 Design

To make the interface of the main simulation window possible, certain elements need to be successfully characterised and described in the Main object class, shown in Figure 4.6. Each object class present in the model is embedded in the Main class. The building blocks necessary to build this IBM is represented by the embedded objects on the right-hand side of Figure 4.6. The objects associated with the grey circles are classified as "Agent" object classes. This implies that each replication of this class is unique and is associated with a unique index. The mopane tree class is the only class not specified as being an "Agent" class and explains why its icon is a red circle. The motivation for this difference will be explained in Section 4.6. The ellipsis visible at the end of each "Agent" embedded object indicates that the object is replicated. This replication is governed by the initial parameters shown on the left-hand side of Figure 4.6.

The parameters, enclosed in the top left-hand block of Figure 4.6, are primarily used for model initialisation but are occasionally used when two or more object classes share the same parameter. The parameter is then accessed from the separate object classes via the Main class. The parameters containing the word "Initial" are used to set the initial amount of each agent in the simulation model. These parameters communicate with the variables explained in Section 4.1.2 and relay the initial amounts to the corresponding agents. Two of the three remaining parameters are used to set the amount of breeding and bachelor herds to 30 and 10 respectively. These values are based on the amounts identified in the data and are used to keep the model as realistic as possible. The final parameter is a parameter shared by the male and female elephants and provides the life expectancy of an elephant. This parameter is a necessary element in the governing of the mortality rate of the elephant population and is set to 75 years.

The second group of elements in Figure 4.6 are the table functions and variables. A table function is a function defined in a table form. This function is mostly used to define complex non-linear relationships which can not easily be described by a standard function. An associated variable needs to be created for each table function to allow programmatic control throughout the model. The rainfall table includes the probabilities shown in Appendix B and an example of how a table function is constructed is shown in Figure 4.7. The rainfall table is used to govern the outbreaks of the mopane caterpillars and will be further discussed in Section 4.5. The displacement and angle tables are used

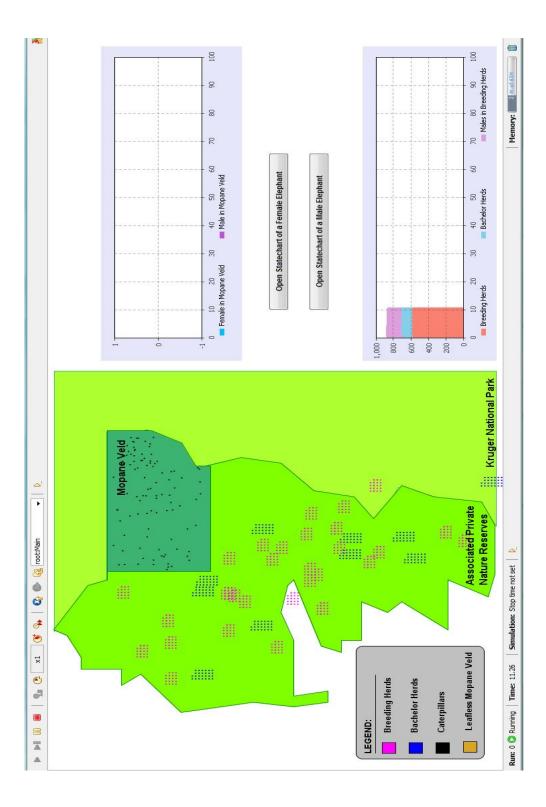


Figure 4.4: The Main Simulation Window

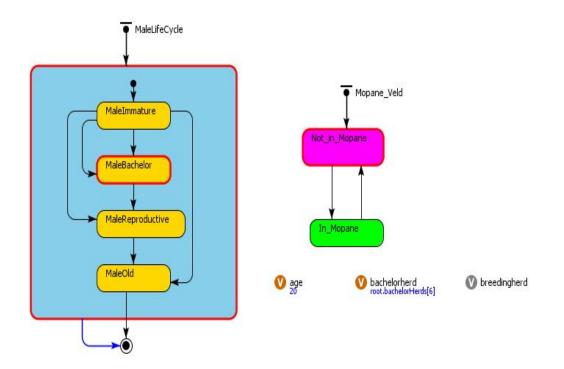


Figure 4.5: Male Elephant Statechart Window

during the movement of the elephant to set the elephant's velocity and to allocate a specific heading to its movement. These tables are specifically utilised by the breeding and bachelor herd object classes and will be explained in Section 4.4.

The data sets at the bottom of Figure 4.6 are used to store data concerning whether a specific elephant is in the mopane veld or not. A specific mopane statechart is constructed within each of the male and female elephant object classes to enable the capturing of this data. The manner in which this data is captured can only be explained in full once each of the male and female object classes are discussed. These two data sets are used to construct the graph at the top of the main simulation window and will be used to formulate the final conclusion of the research study.

The building blocks of the model will be discussed separately in the remainder of the chapter to enable the complete understanding of the workings of the IBM.

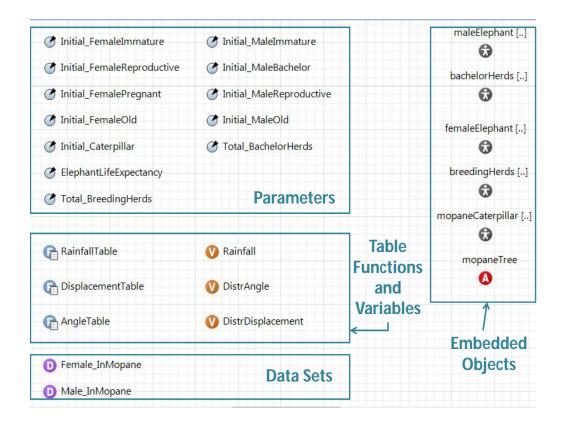


Figure 4.6: Main Class Variables and Parameters

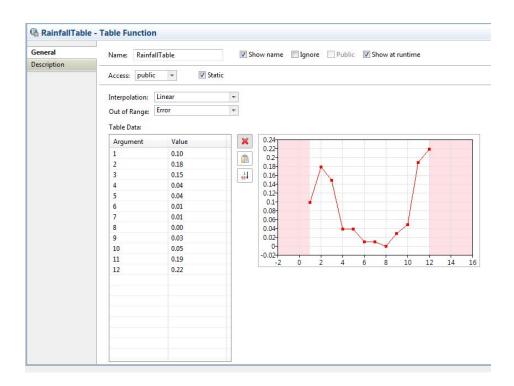


Figure 4.7: Rainfall Table Function

4.3 Elephants

The main agents present in the IBM are the male and female elephants. The elephants are divided into two separate active object classes due to the difference in certain key characteristics and to simplify model coding. Males and females differ in terms of life cycles states as well as the ages related to these states. These differences demand separate classification of each sex and the details with regard to each are discussed.

4.3.1 Life Cycle Stages

Female Elephants

The female elephant's life cycle can be divided into different states according to its specific age. A statechart was constructed within the female elephant's active object class to govern the state in which a specific female is. Immature, reproductive, pregnant and old are the four states in which a female can be and each is associated with a given age.

Females between the ages of 0 and 9 years are classified as immature. Once they reach the age of 9, they become sexually mature and a transition to the reproductive state is made. Females remain reproductive up to the age of 60 years and only then become classified as old. The transition between reproductive and pregnant is governed by the birth rate of the population. Once a female moves to the pregnant state, an elephant is added to the model to simulate the birth process. The gender of the new born elephant is guided by the trends identified in the data and was included as such. The gestation period for elephants is 22 months, after which the mother of the new born will only start considering breeding after another two years. The transition time from pregnant to reproductive is governed by this time and thus the female will only become reproductive after the passing of 4 years.

In Figure 4.8, the arrows in the statechart indicated with number 1, 2 and 3 are used with model initialisation. Once the model is initialised, the population of female elephants are divided into different states to ensure that all female agents are not in the immature state, as this is the initial state of the chart. A message is sent to the female elephant's statechart to order a specified amount, governed by the input values specified by the user, of female elephants into states other than immature. This is only done at the start of the model. As soon as the female agent is ordered to move to a state other than immature, an age is randomly selected from a uniform distribution within the associated state's age range and assigned to the agent. This is to enable the correct age distribution within the female elephant population.

The state indicated by number 4 is used to govern the mortality of the elephant population. The state encompasses all other states as elephants are randomly selected to die at any stage in their life cycle. Arrow numbered 5 indicates the transition to the final

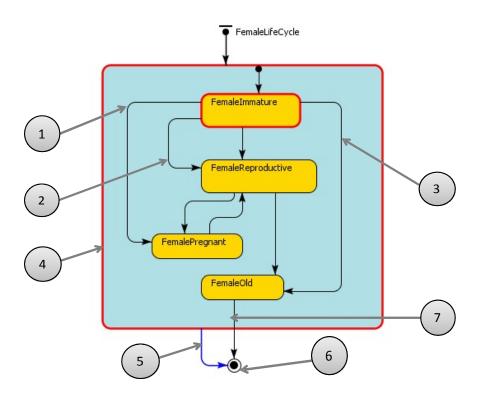


Figure 4.8: Statechart of a Female Elephant

state (death), indicated by number 6, and is based on the population's mortality rate. The transition indicated by number 7 is regulated by the life expectancy of an elephant and is set to 75 years. Once the old female reaches the age of 75, it will take the transition to the final stage. When the female elephant reaches the final state, it is removed from the population.

Figure 4.8 shows a statechart of a randomly selected female elephant presently in the immature state, indicated by the red outline.

Male Elephants

Similarly to female elephants, male elephants have a statechart within their object class. The states in which a male can be is immature, bachelor, reproductive and old, with the transitions between the states governed only by age.

A male between the age of 0 and 14 years is classified as immature and resides in the breeding herd. Once the male reaches the age of 14 years, it will leave the breeding herd and join or form a bachelor herd. The model incorporates this herd change and removes from and adds the male to the specific herd. At the age of 25 years, the male reaches sexual maturity and becomes reproductive. The male remains reproductive up to the age

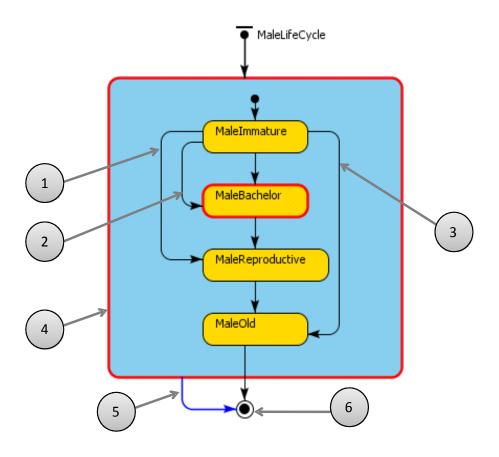


Figure 4.9: Statechart of a Male Elephant

of 60 years and is then classified as old.

The statechart presented in Figure 4.9 is of a male in the bachelor state, indicated by the red outline. The transitions labelled with 1, 2 and 3 serve the same purpose as those in the female statechart and are used at model initialisation. A message is sent to the statechart to order it to move a specified amount of the males to states other than the initial state, which is immature. An applicable age is chosen from a uniform distribution for each male to ensure the correct age distribution across the male elephant population.

Transitions indicated in Figure 4.9 by numbers 4, 5 and 6 serve the exact same purpose of that explained for female elephants.

4.3.2 Modelling Elements

Female Elephants

Within the female elephant's object class, certain elements are defined to characterise the elephant appropriately. In Figure 4.10, the associated variables, parameters, function and event is shown for each individual female elephant.

The variables needed to identify each female elephant is age, its associated breeding

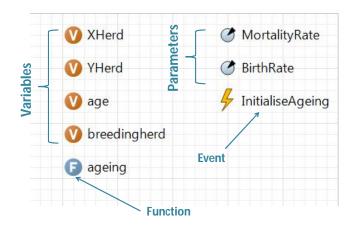


Figure 4.10: Female Parameters and Variables

herd and the x and y coordinates of its breeding herd. At model initialisation, female elephants are divided equally, according to age group, into different breeding herds. They remain in this breeding herd for the entire simulation. Each breeding herd has a specific x and y coordinate with the placement of each elephant within the herd being relative to these coordinates. The x and y coordinates of the female are used to assign a place in the herd for the female. The herd can be visualised as an n x 5 matrix where each female is assigned a designated column and row location. The way in which a breeding herd is represented in the model is shown in Figure 4.11 with the placement of each elephant clearly visible.

The ageing function ensures that the age variable of the female is updated each year with an increase of one. The event "InitialiseAgeing" invokes this function once every year.

The parameters included are the birth and death rate of the elephant population and are specified according to the input values discussed in Section 3.3.1. It is necessary to include these two parameters within each female's class as some of the statechart transitions are dependent on these rates.

Male Elephants

The elements present in the male elephant object class correspond to the elements of the female elephants and serve the exact same purpose. There is, however, some differences with regard to herd identification, as males belong to both breeding and bachelor herds during their lifetime.

Provision is made for the difference in herds by adding a variable for each herd in the

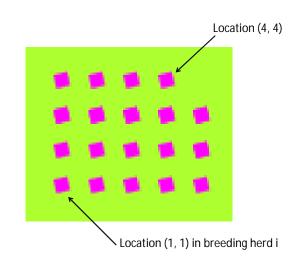


Figure 4.11: Female Locations within a Breeding Herd

male's object class. Corresponding x and y coordinates for each herd are provided for by "XBCHerd" and "YBCHerd" for the bachelor herd and "XBRHerd" and "YBRHerd" for the breeding herd (Figure 4.12). Males are placed in the herds similarly to the females with the bachelor herd placement shown in Figure 4.13. The amount of columns within the bachelor and breeding herd matrices are limited to 5 with the amount of rows being able to vary according to the amount of elephants allocated to a specific herd. This amount is directly influenced by the initial input values chosen by the user at model start-up.

4.4 Herds

The herds in which the elephants are grouped into are divided into two separate object classes. This is due to the differences in behaviour of breeding and bachelor herds as well as the difference in input values. However, some correlations do exist between these two objects and will be explained in the following sections.

4.4.1 Statechart

Breeding Herds

The most important reason for the existence of breeding herds within the model is that they provide the structure within which the female and immature male elephants move. Therefore, the modelling of these specific elephant movements are done within the breeding herd object class.

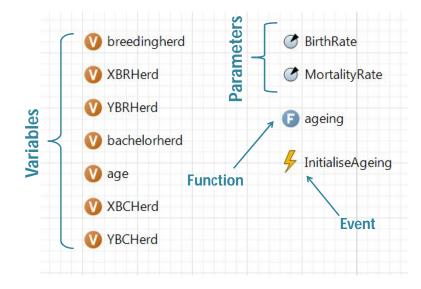


Figure 4.12: Male Parameters and Variables

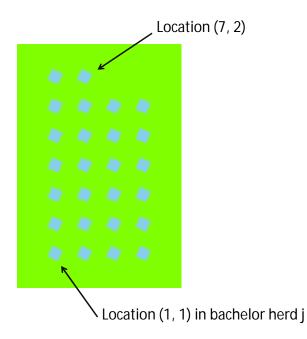


Figure 4.13: Male Locations within a Bachelor Herd

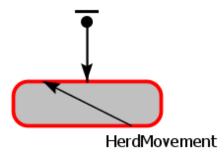


Figure 4.14: Statechart of a Breeding or Bachelor Herd

A breeding herd contains a statechart with which the movement of the herd is governed. Figure 4.14 shows the statechart consisting only of one state. The herd is always within this state and the internal transition is dependent on the probability of moving into the mopane veld. The inputs discussed in Section 3.3.4 with regard to movement are used to govern the movement of the breeding herd into the mopane veld. Table 4.1 is shown again for ease of explanation.

The breeding herd undertakes the internal transition with a probability of 0.06 which corresponds to the 6% in column 6 of Table 4.1. As this transition is made, it is again dependent on another probability of 0.57 as specified in column 4. The second probability is included to ensure that the herds (breeding or bachelor) only move to the mopane veld in the simulation during December, January, March or April. This simplifies the capturing of relevant herd movement as herds will now only move into the mopane veld during the months of December, January, March or April. This is the most important event to record during simulation as it is the only event which is linked to the research hypothesis.

Whenever the breeding herd is not moving towards the mopane veld due to the abovementioned conditions, it moves randomly through the environment. All of the breeding herd's movement is governed by specific functions which will be discussed in the Section 4.4.2.

Bachelor Herds

Similarly to breeding herds, bachelor herds have a statechart to control their movement and is a replicate of the breeding herd statechart. It functions on the same principles as the breeding herd's with the only difference being the difference in probabilities governing the

Elephant	Total GPS	Total points	% Time in MV	% Time in MV	% Time in MV
	points	in MV	in $D/J/M/A$	relative to	in $D/J/M/A$
				Total points	relative to Total points
Males	17267	9463	37	53	19
Females	12644	1636	57	14	6

Table 4.1: Averages of Mopane Movement

time of movement to the mopane veld. The internal transition is taken with a probability of 0.19, which is 0.14 higher than the probability used for the breeding herds. Once this transition is taken, it is again dependent on another probability of 0.37 to judge whether it will move to the mopane veld. During simulation, herds will occasionally be seen moving through the mopane veld, but this is not always due to the internal transition and is only a result of random movement. Only when both the conditions specified earlier are fulfilled will the model record the movement into the mopane veld.

4.4.2 Modelling Elements

Breeding Herds

The elements included in the breeding herd object class differ from the female and male elephant's and are shown in Figure 4.15. A new type of variable is introduced and is known as a collection variable. This is to store the members of the herd's details and to enable the collective control of the members via the breeding herd. As stated earlier, a breeding herd consists of female elephants as well as immature male elephants.

The x and y coordinates of the herd are used to initially place the herd in the simulation window and to enable the relative placing of female and male members relative to these coordinates. These coordinates remain constant throughout simulation as they are only used at model initialisation.

The three most important functions in the model is located within the herd's object class. These three functions govern the movement of the elephants and are dependent on certain specified conditions. The "Movement" function is only invoked once the internal transition of the herd's statechart is active. Within the movement function an "If" statement determines whether the herd is required to move to the mopane veld or not. With a probability of 0.57, the herd will move to the mopane veld, otherwise it will keep moving in a random fashion. If the "Movement" function proves to be true and orders the herd into the mopane veld, certain lines of code are executed. Firstly, a random x and y coordinate within the mopane veld is chosen from a uniform distribution to serve as the relative point to which all herd member's coordinates will be calculated. A certain velocity is chosen for all herd members and will be set for each individual member. Secondly, a "for" loop runs through all herd members to set each member's individual



Figure 4.15: Breeding Herd Parameters and Variables

velocity and location of destination relative to all other herd members, thus keeping in mind the member's individual location within the herd matrix. Within the "for" loop, a message is sent to each individual's mopane statechart, and will be discussed in further detail in Section 4.4.3.

The "HeadingRandom" function is invoked by the event "RandomMovement" and is continually run throughout the simulation. The movement of the herd is restricted to the boundaries of the APNR but are allowed to occasionally wander across to the KNP due to absence of boundary fences. The code executed within this function firstly selects an x and y coordinate within the APNR which is not within the mopane veld. The APNR's shape complicates the manner in which a coordinate can be selected as the shape is irregular. For simplification, the APNR was divided into two large rectangles to enable the selection of coordinates from uniform distributions. The function is coded such that a point will be selected from any of the two rectangles with equal probability. The selected x and y coordinates will then again serve as the relative point to which all herd member's locations will be calculated. A common velocity is again given to each member to ensure that all members move at the same pace. The event "placeBreeding" and the function "HeadingRandom2" is only used at model initialisation to place the herd within the boundaries of the APNR and is therefore only run once during simulation. "HeadingRandom2" works on the same principle as "HeadingRandom" and will thus not be explained again.

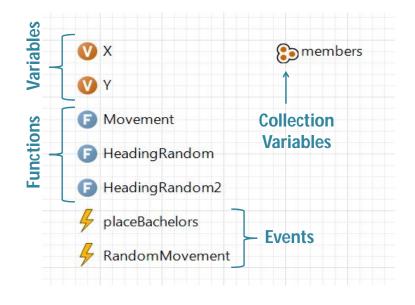


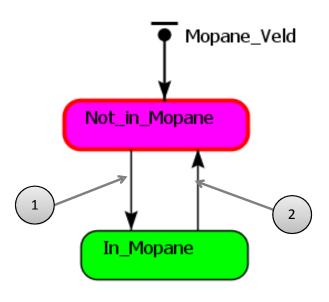
Figure 4.16: Bachelor Herd Parameters and Variables

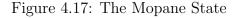
Bachelor Herds

The variables and parameters of the bachelor herd serve the same purpose as that specified for breeding herds and only differ with respect to their collective variables. Bachelor herds only consist of male elephants and therefore no distinction between the respective members is required. The probability of the movement function to guide the herd to the mopane veld is 0.37, which is 0.2 lower than that of the breeding herd.

4.4.3 The Mopane State

Within each of the object classes of male and female elephants, another statechart is included. This statechart is primarily used to record the presence or absence of any given elephant in the mopane veld. Once a herd is told to move to the mopane veld, a message is sent to each of the member's mopane statecharts to move from the state of "Not In Mopane" (transition 2 in Figure 4.17) to "In Mopane" (transition 1 in Figure 4.17). Once the herd moves out of the mopane veld, another message is sent to the member's statecharts and the transition is made back to the state of "Not In Mopane". The elephant associated with the mopane statechart presented in Figure 4.17 is currently in the "Not In Mopane" state, as shown by the red outline. Only once an elephant is in the "In Mopane" state does the model take note of it and captures it in the data sets discussed in Section 4.2.2.





4.5 Mopane Caterpillars

The mopane caterpillar active object class does not include a statechart but only two events. Therefore, the different states in which a mopane caterpillar can be will not be shown in the model. This is to keep the main simulation window as user friendly as possible, as the showing of each caterpillar state will make the simulation too busy and cluttered. The scale difference between the APNR and the caterpillar also pose a challenge as both need to be visible in the model. Realistically, the caterpillar will not be visible if one takes a bird's eye view of the APNR. But for purposes of this model, the caterpillar is shown at the same size as the elephant, as otherwise it would be too small and not visible the the user.

The two events shown in Figure 4.18 are responsible for regulating the time and place of the caterpillar outbreaks. The outbreaks are restricted to the mopane veld and occur either in October/November or March/April. The location of the outbreaks are chosen randomly from a uniform distribution of points found within the mopane veld. The occurrence of the March/April outbreak is dependent on the degree of rainfall during the summer season and will thus be regulated by a specified probability. This probability was derived from historical rainfall data collected of the APNR for the years 2005 - 2009, shown in Appendix B.

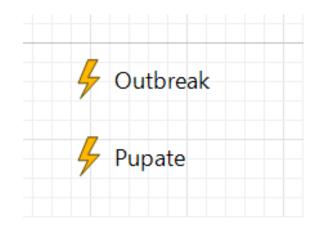


Figure 4.18: Caterpillar Events

Figure 4.19 shows how a typical outbreak will look during simulation time. One black square in Figure 4.19 represents an egg mass of approximately 100 eggs. The caterpillars are visible for approximately two months (equal to two seconds simulation time) after which they will pupate and become invisible.

4.6 Mopane Trees

Mopane trees are represented collectively in the simulation and are not individually modelled. This is purely with regard to model simplicity and to keep the simulation window as uncluttered as possible. The mopane veld is represented as a single green block within the APNR and changes colour from August to October as this is when the trees are leafless. Only two events are included in the object class of the mopane trees to regulate the flushing and leafless appearance of the trees. The events are shown in Figure 4.20 and only orders the colour of the mopane veld to change when the event occurs (Figure 4.21).

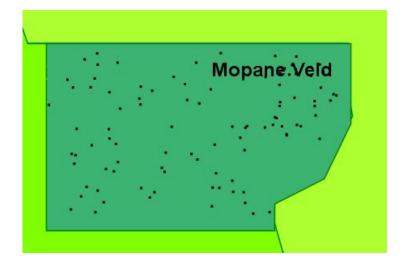


Figure 4.19: Caterpillar Outbreak within the Mopane Veld



Figure 4.20: Tree Events

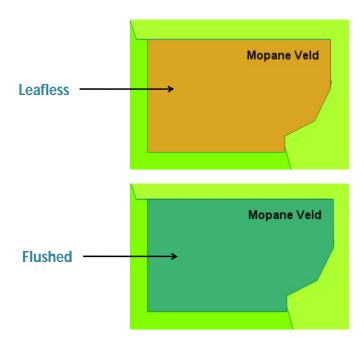


Figure 4.21: Tree Colours

4.7 Model Testing and Validation

The testing of the model is done continuously throughout the model development process and is aided by error messages provided by Anylogic. The error messages ensure that all written code are executable and in the correct form. The model is primarily based on actual data and therefore only the manner in which this data is included and represented in the model should be validated. The model is validated by examining and analysing the outputs of each of the corresponding inputs. Certain elements were created especially for the purpose of model validation and are not included in the actual model. These specific elements are discussed and will focus primarily on the growth rate of the elephant population as well as the initial amounts of each agent in the model.

4.7.1 Initial Agent Values

To validate whether the initial amount of male elephants are correctly communicated to the model, the parameters associated with each value was made visible in the main simulation window. The value of each parameter is indicated below the parameter and in Figure 4.22, the initial input values are shown with the corresponding parameter values as recorded in the main simulation window. It is clear that all the values are correctly communicated and that the amount of bachelor herds are correctly set at 10.

The same test was done with regard to the initial amount of female elephants in the simulation and is presented in Figure 4.23. All the parameters are correct and the amount of breeding herds correspond to the correct amount of 30 herds.

The value corresponding to the amount of caterpillars are tested and validated in Figure 4.24.

4.7.2 Elephant Population Growth Rates

The elephant population growth rate was validated by taking the results of 20 consecutive simulation runs of one year each and comparing the average growth rate with the actual growth rate observed in the data. Table 4.2 shows the results of the simulation runs and indicates that the average population growth equals 6.61%. This corresponds to the actual population growth rate of 6% specified as an input in Table 3.1. Therefore, the elephant population birth and death rates are correctly incorporated in the model and produce the correct overall population growth.

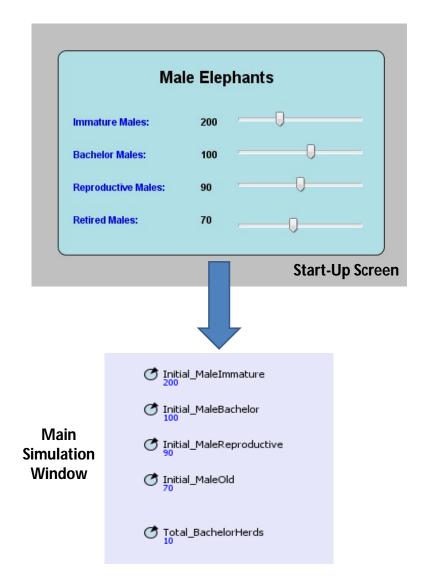


Figure 4.22: Validation of Male Elephant Values

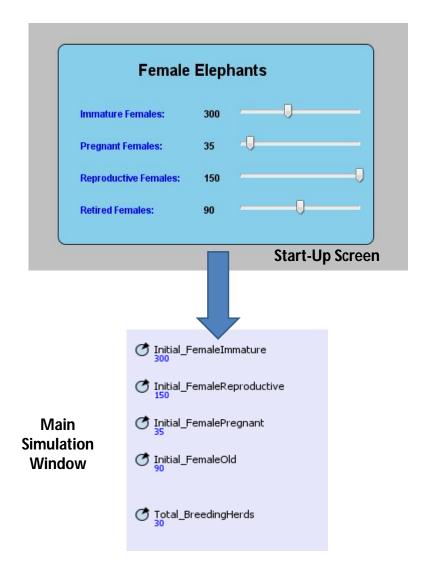


Figure 4.23: Validation of Female Elephant Values

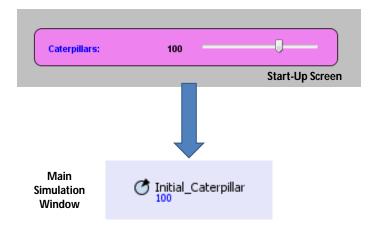


Figure 4.24: Validation of Caterpillar Values

Run	Initial Population	Final Population	Population Change	Growth $\%$
1	880	934	54	6.14%
2	880	936	56	6.36%
3	880	937	57	6.48%
4	880	938	58	6.59%
5	880	941	61	6.93%
6	880	911	31	3.52%
7	880	951	71	8.07%
8	880	939	59	6.70%
9	880	952	72	8.18%
10	880	908	28	3.18%
11	880	977	97	11.02%
12	880	947	67	7.61%
13	880	914	34	3.86%
14	880	946	66	7.50%
15	880	938	58	6.59%
16	880	935	55	6.25%
17	880	952	72	8.18%
18	880	945	65	7.39%
19	880	921	41	4.66%
20	880	942	62	7.05%
			Average	6.61%

Table 4.2: Validation of the Population Growth Rate

4.7.3 Elephant Movements

The movement of the elephants are one of the most important features in the IBM and must therefore especially be evaluated for logic errors and incorrect model interpretation. The movement outside of the mopane veld is not of importance for this IBM and will thus not be the focus of this section. The only requirement for the random movement of the elephants are that they must stay within the boundaries of the APNR.

The mopane movement is not simple to validate as no numbers can be compared for input and output and no simple mathematical formula can be analysed and validated. The most effective way to test this movement was to simply change the colour of the elephants which were heading for the mopane veld due to the specified conditions. This is one of the only visual ways in which the mopane movement can be tested and confirmed that it is functioning correctly. The associated probabilities enclosed in the function are correct and follow the trends observed in the data.

Although the movement is difficult to validate fully, the running of the model confirms that the movement works effectively and seems to portray what is expected of the model. It can therefore be concluded that the IBM functions correctly and accurately and fulfils the purpose for which it was constructed.

Chapter 5

Results and Recommendations

Nature is complex and intricate and will never be fully understood. The IBM developed in this research study attempted to portray the reality of the natural system and proved to be more challenging than expected. Reality and usefulness needed to be always kept in mind in order for the IBM to serve as a usable DST. Several assumptions and simplifications were made due to time and resource constraints, but model integrity was never jeopardised. Interesting results were produced by the simulation model and will be discussed in further detail in Section 5.1.

5.1 Simulation Results

During model development, certain key characteristics were modelled in order to collect the appropriate data needed to successfully test the research hypothesis. The simulation was run 40 consecutive times for a period of 2000 months and resulted in the outcomes presented in Table 5.1. Detailed results are presented in Appendix B.

Female and male elephants were found to be in the mopane veld after caterpillar defoliation with an average probability of 0.07 and 0.18 respectively. These probabilities were determined by analysing the outcomes of each individual simulation run and are based on the amount of times elephants move into the mopane veld after caterpillar defoliation.

Table 5.1: Average Probabilities

	Probability
Males	0.18
Females	0.07

Some challenges arise with the analysis of these results. Firstly, these probabilities only suggest that the elephants move to the mopane veld but not that they move there due to caterpillar defoliation. This movement might rather be attributed to home range preference or vegetation preference. The home ranges of the elephants especially pose a challenge as a large amount of the elephants represented by the actual data's home ranges are within the mopane veld. This brings the question to mind as to whether the mopane movement is due to caterpillar defoliation or rather just normal movement within the elephant's home range.

Secondly, the elephants might seem to move to the mopane veld due to caterpillar defoliation, but it is not clear as to whether the elephants actually eat from the trees that were defoliated. Not all trees within the mopane veld are defoliated by caterpillars and fluctuate from season to season. This can only be successfully determined by tagging and monitoring trees for caterpillar defoliation and elephant pruning.

Finally, only two year's worth of movement data was used for analysis. This excludes caterpillar outbreaks, which has not been recorded at all in the past. By conducting more thorough ground research with regard to outbreaks and by monitoring elephant movement specifically with regard to mopane movement might greatly influence the research conclusion. The probabilities presented in Table 5.1 reflect that males are more prone to spend time in the mopane veld and are in line with previous findings by Henley and Henley (2005).

5.2 Conclusion

With respect to the results shown in Table 5.1, the research hypothesis is found false and no real correlation between elephant movements and mopane caterpillar defoliation could be found. This is the conclusion suggested by the simulation model but should not be seen as a foolproof answer. The IBM was subject to many assumptions and simplifications due to limited data, time and resources. Although the IBM was built as accurately and realistically as possible, the factor of randomness and autonomy will always exist in nature. Therefore, these results can only be seen as preliminary results and leave much room for improvement, as will be discussed in Section 5.3.

The IBM served as a DST to decide whether any potential exists within the elephantcaterpillar research field. The IBM is not the final deciding factor as to whether this research field is worth investigating but only aids in predicting the research returns. Scientists interested in this field are advised to apply their expert knowledge alongside the simulation model in deciding whether to pursue the field of interest.

The relationship between the three species examined in this study still hold great potential for further investigation. The expansion opportunities for this IBM is endless and it is hoped that the researchers at STE-SA will benefit from the results provided by the IBM. This is a very challenging research field as it investigates the question of "Why?" animals move and what the drivers are behind their seasonal movements. No correct answer is possible as at best, only accurate predictions and possible motivations for animal movement can be found by conducting extensive research.

5.3 Future Research Opportunities

The DST still holds much potential for expansion and improvement and only served as an initial indicator for the given research field. Several opportunities exist for future model development and will only be constrained by the availability of resources.

To improve the realistic representation of the APNR, the vegetation found in the reserve can be included in the model. This will enable the modelling of animal vegetation consumption as well as water consumption. Expansion of current data sets and incorporation of more realistic animal behaviour will improve the usefulness of the DST to a great extent.

The amount of input values which are controlled by the user can be increased. This will allow the DST to be more flexible and adjustable with regard to the needs of the user. The more features are included in the model, the greater the possibility of including a wider variety of adjustable input values.

The interface of the IBM can also be improved and changed to suit the needs of the associated user. Many tools are available to make the interface more user friendly and attractive. The interface must be designed to compliment the purpose of the IBM and should not complicate the using of the model.

An important area for improvement is the movement of the elephants. This can be modelled more true to reality, but will be one of the greatest challenges for future model developers. This is undoubtedly one of the most complex areas regarding animal behaviour and will require extensive research and expert knowledge to enable accurate modelling.

The opportunity for model improvement is endless but will be constrained by model capability and ease of visual representation. The manner in which the model is improved and expanded will depend on the individual needs and requirements of the user.

The IBM developed in this research study served as the first step towards a better understanding of the possible interaction between elephants and mopane caterpillars and will hopefully benefit future researchers.

Bibliography

- Bonabeau, E. (2002). Agent-based modeling: Methods and Techniques for simulating human systems. Proceedings of the National Academy of Sciences of the USA, 99(3):7280– 7287.
- Breckling, B. (1992). Uniqueness of ecosystems versus generalizability and predictability in ecology. *Ecological Modelling*, 63(11):13–27.
- Bryant, J. P., Provenza, F. D., Pastor, J., Reichardt, P. B., Clausen, T. P., and du Toit, J. T. (1991). Interactions between woody plants and browsing mammals mediated by secondary metabolites. *Annual Review of Ecology and Systematics*, 22(1):431–446.
- Codron, J., Lee-Thorp, J. A., Sponheimer, M., Codron, D., Grant, R. C., and De Ruiter,
 D. J. (2006). Elephant (Loxodonta Africana) diets in Kruger National Park, South
 Africa: Spatial and Landscape Differences. *Journal of Mammalogy*, 87(1):27–34.
- De Villiers, P. A. (1994). Aspect of the behaviour and ecology of elephant (Loxodonta africana) in the Eastern Transvaal Lowveld with special reference to environmental interactions. PhD thesis, University of the Orange Free State.
- De Villiers, P. A. and Kok, O. B. (1997). Home range, association and related aspects of elephants in the eastern Transvaal Lowveld. *African Journal of Ecology*, 35(3):224–236.
- DeAngelis, D. L. and Gross, L. J. (1992). Individual-Based Models and Approaches in Ecology: Populations, Communities and Ecosystems. Chapman & Hall. Preface.
- DeAngelis, D. L. and Mooij, W. M. (2005). Individual-based modeling of ecological and evolutionary processes. Annual Review of Ecology, Evolution and Systematics, 36(1):147–68.
- Gaston, K. J., Chown, S. L., and Styles, C. V. (1997). Changing size and changing enemies: the case of the mopane worm. *Acta Oecologica*, 18(1):21–26.
- Gregory, R., Saunders, J. R., and Saunders, V. A. (2006). The Paton individual-based model legacy. *Biosystems*, 85(1):46–54.

- Greyling, M. D. (2004). Sex and age related distinctions in the feeding ecology of the African Elephant. PhD thesis, University of Pretoria.
- Grimm, V. (1999). Ten years of individual-based modelling in ecology: what have we learned and what could we learn in the future? *Ecological Modelling*, 115(2-3):129–148.
- Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., Goss-Custard, J., Grand, T., Heinz, S. K., Huse, G., Huth, A., Jepsen, J. U., Jorgensen, C., Mooij, W. M., Muller, B., Pe'er, G., Piou, C., Railsback, S. F., Robbins, A. M., Robbins, M. M., Rossmanith, E., Ruger, N., Strand, E., Souissi, S., Stillman, R. A., Vabo, R., Visser, U., and DeAngelis, D. L. (2006). A standard protocol for describing individual-based and agent-based models. *Ecological Modelling*, 198(1-2):115–126.
- Grimm, V., Frank, K., Jeltsch, F., Brandl, R., Uchmanski, J., and Wissel, C. (1996). Pattern-oriented modelling in population ecology. *The Science of the Total Environment*, 183(1-2):151–166.
- Grimm, V. and Uchmanski, J. (1996). Individual-based modelling in ecology: what makes the difference? *Trends in Ecology and Evolution*, 11(10):437–440.
- Hall-Martin, A. J. (1992). Distribution and status of the African elephant *loxodonta* africana in South Africa, 1652-1992. *Koedoe*, 35:65–88.
- Henley, S. R. and Henley, M. D. (2005). Unpublished report to the Associated Private Nature Reserves. 53 pp.
- Henley, S. R. and Henley, M. D. (2009). Final Report to the Kruger National Park. 17pp.
- Holdo, R. M. (2003). Woody plant damage by African elephants in relation to leaf nutrients in western Zimbabwe. *Journal of Tropical Ecology*, 19(2):189–196.
- Holm, E. and De Villiers, W. M. (1983). Ons eie insekte. Tafelberg, Cape Town.
- Holyoak, M., Casagrandi, R., Nathan, R., Revilla, E., and Spiegel, O. (2008). Trends and missing parts in the study of movement ecology. *Proceedings of the National Academy* of Sciences of the USA, 105(49):19060–19065.
- Hrabar, H. (2005). Indirect interactions between elephants (Loxodonta Africana) and mopane caterpillars (Imbrasia belina) through their shared food resource - mopane trees (Colophospermum mopane). PhD thesis, University of Pretoria.
- Hrabar, H., Hattas, D., and Du Toit, J. T. (2009). Differential effects of defoliation by mopane caterpillars and pruning by African elephants on the regrowth of *colophospermum mopane* foliage. *Journal of Tropical Ecology*, 25(3):301–309.

- McRae, B. H., Dickson, B. G., Keitt, T. H., and Shah, V. B. (2008). Using circuit theory to model connectivity in ecology, evolution and conservation. *Ecology*, 89(10):2712–2724.
- Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., and Smouse, P. E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences of the USA*, 105(49):19052–19059.
- OSullivan, D. (2008). Geographical Information Systems: agent-based models. *Progress* in Human Geography, 32(4):541–550.
- Patterson, T. A., Thomas, L., Wilcox, C., Ovaskainen, O., and Matthiopoulos, J. (2008). State-space models of individual animal movement. *Trends in Ecology and Evolution*, 23(2):87–94.
- Schick, R. S., Loarie, S. R., Colchero, F., Best, B. D., Boustany, A., Conde, D. A., Halpin, P. N., Joppa, N., McClellan, C. M., and Clark, J. S. (2008). Understanding movement data and movement processes: current and emerging directions. *Ecology Letters*, 11(12):1338–1350.
- Smallie, J. J. and O'Connor, T. G. (2000). Elephant utilization of Colophospermum mopane: possible benefits of hedging. African Journal of Ecology, 38(8):352–359.
- Styles, C. V. and Skinner, J. D. (1997). Seasonal variations in the quality of mopane leaves as a source of browse for mammalian herbivores. *African Journal of Ecology*, 35:254–265.
- Timberlake, J. R. (1995). Colophospermum mopane: Annotated bibliography and review. The Zimbabwe Bulletin of Forestry Research.

Appendices

Appendix A

Definitions

- **Browse** A type of predation in which herbivores feed on high growing plants, such as leaves of trees, as well as low vegetation, such as grass
- Combretum spp. Combretum is a group of plants with four-winged seed pods
- **Corridors** An area of habitat connecting wildlife populations separated by human activities
- Dolerite Medium-grained igneous rock formed below the earth's surface
- Gabbro A dark, coarse-grained mafic igneous rock
- Gneiss A common and widely distributed rock formed by regional metamorphic processes
- Granite A light-coloured, coarse-grained rock with a random arrangement of minerals
- Flush Regrowth of new leaves after the old foliage is lost
- **Instar** The developmental stages of a larva (see next description) until maturity is reached
- Larva The young form of an animal which needs to pass through certain developmental stages to reach the adult form
- Minimum Convex Polygon Method Calculates a convex polygon for a percentage of the total points in a given data set
- **Polyphenol** A group of chemical substances found in plants
- **Pupation** The stage in the development of certain insects where the larva becomes encased in a hard shell
- Savanna A dry grass-covered plain with only a few trees

Spatiotemporal Of, relating to, or existing in both space and time

Tannin Bitter plant polyphenols that either bind or precipitate or shrink proteins

Appendix B

Simulation Data and Results

 Table B.1: Elephant Population Statistics

Total Population	
Average Amount	882.28
Standard Deviation	386.43
Breeding Herd	
Average (as a % of Total Population) Standard Deviation	$76.45\%\ 8.99\%$
Bachelor Herd	
Average (as a % of Total Population)	14.37%
Standard Deviation	3.87%
Births	
Average (as a % of Total Population)	3.85%
Standard Deviation	1.85%
Deaths	
Average (as a % of Total Population)	1.39%
Standard Deviation	1.04%

Data
opulation
Д
Elephant
B.2:
Щ
Table

Year	Bulls	ear Bulls Breeding Herd	Total	Births	Deaths	Total Births Deaths Breeding Herd % Bulls %	Bulls %		Births % Deaths %	Total %
1992	63	450	542	29	21	83.03%	11.62%	5.35%	3.87%	0.00%
1993	70	354	441	17	12	80.27%	15.87%	3.85%	2.72%	-18.63%
1994	80	431	525	14	15	82.10%	15.24%	2.67%	2.86%	19.05%
1995	73	409	517	35	13	79.11%	14.12%	6.77%	2.51%	-1.52%
1996	06	265	368	13	2	72.01%	24.46%	3.53%	0.54%	-28.82%
1997	71	688	811	52	2	84.83%	8.75%	6.41%	0.86%	120.38%
1998	66	518	649	32	2	79.82%	15.25%	4.93%	1.08%	-19.98%
1999	79	542	639	18	4	84.82%	12.36%	2.82%	0.63%	-1.54%
2000	113	621	746	12	က	83.24%	15.15%	1.61%	0.40%	16.74%
2001	158	691	876	27	က	78.88%	18.04%	3.08%	0.34%	17.43%
2002	160	292	952	25	9	80.57%	16.81%	2.63%	0.63%	8.68%
2003	176	939	1151	36	12	81.58%	15.29%	3.13%	1.04%	20.90%
2004	174	825	1017	18	10	81.12%	17.11%	1.77%	0.98%	-11.64%
2005	147	1024	1215	26	2	85.76%	12.10%	2.14%	0.58%	19.47%
2006	191	1693	1499	72	16	112.94%	12.74%	4.80%	1.07%	23.37%
2007	188	1335	1558	35	21	85.69%	12.07%	2.25%	1.35%	3.94%
2008	109	1268	1493	116	31	84.93%	7.30%	7.77%	2.08%	-4.17%

Table B.3: Average Rainfall (2005-2008)

Month	Rainfall (mm)	Probability
January	52.05	0.1
February	95.75	0.18
March	81.5	0.15
April	20.75	0.04
May	18.95	0.04
June	2.95	0.01
July	4.56	0.01
August	1.76	0.001
September	15.81	0.03
October	26.38	0.05
November	100	0.19
December	119.33	0.22
Total	539.79	

Run	Total Females	Total Females	Probability of being	Total Males	Total Males	Probability of being
		in Mopane Veld	in Mopane Veld		in Mopane Veld	in Mopane Veld
, 1	2399	171	0.07	678	236	0.35
2	2399	133	0.06	748	198	0.26
က	2459	114	0.05	840	166	0.20
4	2460	228	0.09	778	202	0.26
IJ	2481	209	0.08	804	144	0.18
9	2273	152	0.07	683	126	0.18
7	2525	209	0.08	795	92	0.12
∞	2602	190	0.07	856	112	0.13
6	2489	171	0.07	801	80	0.10
10	2174	133	0.06	746	68	0.09
11	2455	228	0.09	757	176	0.23
12	2476	95	0.04	836	134	0.16
13	2370	228	0.10	751	228	0.30
14	2489	114	0.05	848	114	0.13
15	2529	133	0.05	890	120	0.13
16	2494	133	0.05	808	172	0.21
17	2483	114	0.05	797	140	0.18
18	2379	133	0.06	812	94	0.12
19	2448	133	0.05	761	172	0.23
20	2467	209	0.08	765	144	0.19
Average	2443	162	0.07	788	146	0.18

Table B.4: Simulation Results