GENERALISED MATRIX AND COMPARTMENTAL POPULATION MODELS

BY

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DECLARATION

This thesis is my original work and has not been presented for a degree in any other university.

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SUMMARY OF CONTENTS

The present thesis is concerned with the development of mathematical models for structured population species. The structuring or classification may be due to age, stage of development or a combination of both in a more general perspective. The class of matrix population models are examples of such models and have been the subject of theoretical and practical study for many years. In this work attention is focussed on vector population species which are carriers of disease agents for animals. This has therefore necessitated the investigation of a class of models which deal with the interaction of vector population species and the host population. In particular the study combines both discrete and continuous population models in order to achieve its goal. Multi-dimensional coupled differential equations have proved handy in this respect.

Chapter I gives a general introduction to the work. In section 1.1 an introductory description of mathematical population models is given. In section 1.2 an overview of preliminary concepts and notations are introduced. In this section a brief description of matrix population models and continuous time models is also given. A brief review of relevant literature is presented in section 1.3. In this section, literature review specific to a stage structured population species, the brown ear tick is also given. Sections 1.4 and 1.5 deal with the statement of the problem together with the specific objectives of the study. In section 1.6 the importance of this study is briefly mentioned. In the last section of the chapter the methodology of how data was acquired and analysed is given. This section is important because the study involved a practical application to validate the models. The data was for the three host brown ear tick the causal vector for East Coast fever.

Chapter II reviews basic models for age structured populations. After a brief introduction we present the Lotka's Integral equation in section 2.2 where age and time are treated as continuous variables. The solution to this equation is reviewed in section 2.3 first by elementary mathematical methods in sub-section 2.3.1 and by Laplace transforms in sub-section 2.3.2. In particular it is shown that the solution has a real root which determines the direction of increase of a population. The asymptotic behaviour of the solution is given in sub-section 2.3.3.

In section 2.4 we review the partial differential equation describing the evolution of the population density $n(x,t)$ which is known as the McKendrick-von Foester equation. This model is a hyperbolic initial boundary value problem. Section 2.5 deals with the discretized age and time matrix model which requires a thorough understanding of the life table survivorship function, presented in sub- section 2.5.1. The actual formulation of the matrix model is given in sub- section 2.5.2. It is in this section where we demonstrate the connection of the matrix model and the McKendrick von Foerster model. One of the core problem in application of matrix population models is in the estimation of the matrix inputs. The derivation of the inputs is discussed in section 2.6 for two types of populations namely the birth flow populations and birth pulse populations. These are presented in sub-section 2.6.1 and 2.6.2 respectively.

Chapter III deals with the time homogeneous matrix model and its properties. After an introduction in section 3.1 the model is presented in section 3.2 for an age structured population. The chapter brings in the idea of the complete population projection matrix which includes both pre- and post- reproductive individuals. It is shown that after a long enough time it is the pre-reproductive part of the population which determines the projection matrix of interest. Section 3.3 outlines a list of properties of the population projection matrix. The theory of directed graphs was used quite extensively to achieve this. The Perron-Frobenius theorem for both primitive and irreducible matrices is generally stated since it is important in the study of the limiting properties of the population projections. Sub- section 3.3.1 thus talks about the stable population theory showing the asymptotic behaviour of the population structures. It is shown that the limiting population structure is independent of the initial population structure. This property is egordic in nature. Upto section 3.3 the population is structured according to age but the aim of the study is to generalise the classification. Thus in section 3.4 we present a generalized matrix model where classification is according to both stage of development and according to age within the stage. This model is more general and can be used to study the dynamics of many population species such as insects, arthropods, plants and many more. Estimation of the matrix inputs for such a model is discussed in section 3.5. In sub-section 3.5.1 we consider estimation from transition frequency data while in sub-section 3.5.2 we consider estimation from stage duration data. Finally in sub-section 3.5.3 we consider estimation from experimental cumulative distributions. The connection between the transition probabilities in the classical Leslie model and those from experimental cumulative distributions is given in section 3.6.

In chapter IV we present a mathematical model for the brown ear tick which is a three host tick and is a vector for the East Coast fever(ECF). It is a stage structured population. In section 4.1 we present several modeling approaches including terminology and definitions. In section 4.2 we present a continuous time compartmental model, cyclic in nature. The model is related to that by Metz and Diekmann(1986) for physiologically structured populations since individuals have to age within a stage with reference to chronological time before transitting to the next stage. The characteristic polynomial for the system is derived in this section and the dependence of the spectral bound on various population parameters is discussed through the implicit function theorem. We also derive the general persistent stage structure in this section. Section 4.3 gives a discussion on vector-host interaction where an additional equation describing the dynamics of the host population is added into the system of the n coupled differential equations mentioned above. Conditions for population increase or decline and co-existence of the population species are discussed. The reproduction number for the tick population as a function of host density is also discussed. Section 4.4 gives a discussion on the stability analysis of the model. Section 4.5 is on the phenomenon of competition of ticks on host which acts as a regulatory mechanism for the population species not to increase without bound. In sub-section 4.5.1 we give a discussion of general cyclic triangular systems with respect to density dependence on mortality and transition rates. An alternative method of deriving the reproduction number is also presented. In sub-section 4.5.2 we present a discussion on positive invariance paying attention to the qualitative behaviour of the system, distinguishing where the system is dissipative. In order to establish dissipativeness we find a bounded set that attracts all orbits and which is positive invariant. Sub-section 4.5.3 is on the connection between spectral radius and spectral bound; while we finish this chapter with a simulation experiment of the model based on the brown ear tick data.

In chapter V we consider the spatial distribution of the tick vector population. Section 5.1 is an introduction to this topic. Section 5.2 discusses on host distribution of vector parasites then we derive the model in sub-section 5.2.1. The null hypothesis that the on host distribution of parasites is in general asymmetric and follows the negative binomial distribution is discussed in detail. Sub-section 5.2.2 discusses the parameter estimation in the model by the MLE method, assuming the parameters are functions of several host-specific attributes. In section 5.3 density dependence and host heterogeneity on susceptibility to parasites is discussed. The effect of this on the stability of the parasite-host model is discussed in sub- section 5.3.1. Section 5.4 is about the effect of on host parasite load on the reproduction ratio of the parasite population. The general model is discussed in sub-sections 5.4.1 and 5.4.2. Section 5.5 suggests a possible area of future study aiming towards a general stochastic dynamical model particularly with respect to vector parasite populations such as ticks.

In chapter VI we demonstrate an application of the already developed theories to the brown ear tick(*R. appendiculatus*) based on Zimbabwe data. The application is based on a time dependent multiple matrix model incorporating seasonality and heterogeneity in the vegetation. Section 6.1 gives a general introduction while the model is given in section 6.2. In section 6.3 we deal with the problem of matrix parametrization estimating all the required matrices in the system stating all the assumptions made. Section 6.4 is on sensitivity analysis of the model parameters and conclusions. In chapter VII some comments regarding the significance of the results arrived at in this thesis are made. Some areas which we think need further investigation are also pointed out.

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GLOSSARY OF SYMBOLS AND NOTATIONS

a_{i_k}: reproduction rate for hosts carrying i_k type-k parasites

A^*: general transition matrix for a k stage structured population

b_{i_k}: death rate for hosts carrying i_k type-k parasites

E_k: total free living off host type-k parasites

$E(X)$: expectation operator on a random variable X

$f_j(t)$: fecundity rate for an individual in age class j

$F(x)$: $\Pr[X \leq x]$ if X is a random variable

h_{i_k}: number of hosts individuals carrying i_k type-k parasites

H_{a_k}: total number of hosts born per unit time in the presence of type-k parasites

H_{b_k}: total number of hosts dying due to type-k parasites per unit time interval

H_k: total host density carrying type-k parasites

H_{s_k}: total host density susceptible to type-k parasites

m_k: mean on host type-k parasite load

$n_i(t)$: number of individuals alive in age class i at time t

$n^i_j(t)$: number of individuals in age class j in stage i at time t

$n(x,t)$: individuals aged x at time t in the continuous population model

$p_i(t)$: probability of transition from age class i to age class $i+1$ within the time interval $(t, t+1)$

p^i_{1j}: probability of surviving and transitting into the first age class of stage $i+1$ within the time interval $(t, t+1)$ for an individual in age class j in stage i at time t

$q_n(t,x)$: probability that a host of age x at time t carries n parasites in a continuous time stochastic model

R_0: average number of individuals produced by one adult reproductive individual in its life time

R^n_+: positive orthant for an n dimensional real space

$r_{\sigma^2:\mu}$: variance to mean ratio of a distribution

s_{ij}: probability of surviving from time t to $t+1$ for an individual in age class j in stage i

s_{i_k}: susceptibility rate for hosts carrying i_k type-k parasites

$s(A)$: spectral bound of a matrix A

SC: strong connectedness property of a directed graph

u_i^k: number of individuals in stage class i after k time periods

$u(t, \mathbf{z})$: notation for a probability generating function where $\mathbf{z}$ is a vector valued dummy variable

$u_{\mathbf{z}}(t, \mathbf{z})$: partial derivative of u with respect to $\mathbf{z}$

$V(X)$: variance operator on a random variable X

$\vec{x}$: vector notation

$\dot{x}$: derivative of x with respect to time

Y_k: total type-k parasites harboured by the total host community

Y_{μ_k}: total number of type-k parasites dying per unit time due to natural mortality

α: minimum possible age to reproduce for an individual in an age structured population

β: maximum possible age to reproduce for an individual in an age structured population

$\rho(A)$: spectral radius of a matrix A

$\pi^i_{j+1,j}$: probability of transition from age class j to age class $j+1$ in the time interval (t,t+1) for an individual initially in age class j in stage i

μ_{i_k}: death rate for parasites on hosts carrying i_k type-k parasites

$\mu(x, t)$: instantaneous death rate for an individual aged x at time t

λ_{i_k}: reproduction rate for parasites on hosts carrying i_k type-k parasites

$\lambda(t, x)\Delta x$: probability that a host aged x at time t acquires an additional parasite

ϕ_{i_k}: rate at which host carrying i_k type-k parasites acquire new parasites

γ_{ij}: probability of transition from stage i to stage $i+1$ within the time interval $(t, t+1)$ for an individual in age class j in stage i at time t

$\mathrm{L}\{h(t)\}$: Laplace transform of a function $h(t)$

$\mathrm{L}^{-1}\{h(t)\}$: inverse Laplace transform of a function $h(t)$

λ_1: maximum eigenvalue of a nonnegative matrix

ω: maximum possible attainable age by an individual for an age structured population

CHAPTER I
INTRODUCTION

1.1 Matrix Population Models

The use of matrices in population mathematics has been extensively studied in relation to various population species. These include animal, human, insect, plant or tree popultions. The elements of the projection matrix are functions of survival and fertility rates, of the population in question. The basic classification of individuals in the population is by age. In this case the entire population is classified into s age classes say $1, 2, \ldots, s$. The maximum age class is thus $[s-1, s)$. Such a model is called an age structured population model. Similar models based on other modes of classification can be defined. The assumption in age structured models is that age carries most of the information about the fertility rates, $f_x(t)$, and survival rates $p_x(t)$ for each age group $[x-1, x)$ or age class at time t.

In a time homogeneous or time independent model, we assume that fertility and mortality rates are time independent. If we let $\vec{n}(t)$ denote the age structure at time t then the structure $\vec{n}(t+1)$ at time $t+1$, depends on $\vec{n}(t)$ through a constant population projection matrix M. This dependence can be used recursively to generate future population structures for example T time periods later via the matrix M^T the T^{th} power of M. However this is true only if M is strictly time independent which in practice is not the case. The assumption of time independence is possibly true only for very short time scales and conditions affecting the system remaining constant over time.

Different modes of classification apart from age may be more appropriate because that classification attribute may give more information regarding the relevant population parameters than age. For example in the case of renewable resources, such as forests, classification according to size may be more precise. The aim of modelling such a population this way could be for the purpose of formulating sound management and harvesting strategies. For insect/arthropod population species, classification according to stages of development such as egg, larvae, pupa, adult etcetera could be more ideal. Thus the classical Leslie model structured by age needs a more general treatment to cater for the different modes of classifications.

This is one of the aims in the current study. We address this generalisation for both discrete and continuous class of population models.

The time independent or homogeneous class of population models are useful when we consider a population species living in an environment where there is no food shortage and other physical conditions affecting the system are constant over time. Under such conditions the matrix M or the population evolution operator in the case of continuous compartmental models, possesses standard properties which may be exploited to infer about the stable population structure and its rate of growth. The implications of the Perron-Frobenius theorems are among some of these properties. These properties and their generalisation are also a subject of this study for both discrete and continuous class of models.

In an open environment however, the population parameters for any biological population are bound to be affected by external factors such as climatic conditions, migration, epidemics, environmental and many more. Such factors ought to be incorporated into the model, to make it more practical and realistic. This implies that, the projection matrix $M(t)$, at time t, may not necessarily be the same as $M(t+1)$, that at time $t+1$. This means that the recursive relation between the population structures $\vec{n}(t)$ and $\vec{n}(t+1)$ is no longer the same as that for the time independent case. In the current study a time dependent model is developed in relation to the life cycle of the brown ear tick (*R. appendiculatus*) which is the causal vector for East Coast fever in cattle and other ungulates. In this particular application, time dependence is brought about by several factors among them seasonal effects and differences in vegetation types in the location of interest.

In dealing with vector parasite populations one ought to study the aspect of vector-host interaction systems. This aspect is studied in detail in the current study and is given prominence for both discrete and continuous models. Density dependence is one aspect which we study in detail particularly for the continuous time models. We also use the notion of hybrid or semi-stochastic models to achieve the goal. This necessitated the need to investigate the null hypothesis that on host vector parasite distribution is asymmetric and is negative binomial. Stability of the vector-host model has also been studied in detail in the current study.

We start by studying the time independent age structured Leslie model and its relation with the continuous time deterministic models. We develop a more general stage structured model applicable to almost any biological population species. We then study the model in relation to a stage structured population , the brown ear tick a vector population for the East Coast fever disease in cattle. Related to this we develop a continuous compartmental model for a general n stage structured population. The brown ear tick life cycle is treated as a special case. A time dependent matrix model is then developed for the species incorporating seasonaliy and heterogeneity in vegetation types in the location of interest. Then we study the vector-host interaction models in detail bringing in the idea of semi-stochasticity by incorporating the on host distribution of the vector parasite by means of a system of coupled differatial equations. We then study the stability of the vector-host model in detail. Finally the aim of all the above is to be able to comment or contribute in the control strategies and how to improve on them.

1.2 Preliminary Concepts and Notations

Consider a population structured into s age classes which we. denote by $1, \ldots, n$. The age distribution at time $t+1$ given that at time t can be expressed as a system of s linear equations as will be seen shortly. Precisely the age groups are, $[0, h)$, $[h, 2h)$, and so on upto the last age group given by $[(s-1)h, sh)$ where h is the size of one model time step.

Let

$n_i(t)$ denote the number of individuals alive in the age group i to $i+1$ at time t.

$p_{ij}(t)$ denote the probability, that, an individual in the j to $j+1$ age group, at time t, will be in the age group i to $i+1$, at time $t+1$.

and

$f_{1i}(t)$ denote the reproduction rate, in the time interval t to $t+1$ per individual, aged $(i-1)h$ to ih at time t whose offsprings will be in age group 1 at time $t+1$.

For simplicity we denote $p_{ij}(t)$ by $p_j(t)$ and the $f_{1j}(t)$ by $f_j(t)$, $j = 1, \ldots, s$. Where $p_j(t)$ denotes the transition probability from age class j to age class $j+1$ and $f_j(t)$

denotes the fecundity rate for individuals in age class j. Working from an arbitrary origin of time t, the age distribution at time $t+1$, will be given by

$$n_i(t+1) = p_{i-1}(t)n_{i-1}(t) \quad i = 2,\dots,s \tag{1.1a}$$

and

$$n_1(t+1) = \sum_{i=1}^{s} f_i(t)n_i(t). \tag{1.1b}$$

The assumption here is that the size of one age interval is equal to the size of one model time step. The s equations in Eq.(1.1a) and Eq.(1.1b) can be written more compactly in matrix notation as

$$\vec{n}(t+1) = M(t)\vec{n}(t) \tag{1.1c}$$

where $\vec{n}(t)$ and $\vec{n}(t+1)$ are the vector population structures at time t and $t+1$ respectively. The matrix $M(t)$ is square of order s with elements $f_i(t)$, $i = 1,\dots,s$ in the first row and $p_i(t)$, $i = 1,\dots,s-1$ in the main subdiagonal. The quantities $f_{1j}(t) \geq 0$ may be zero for some age classes depending on the reproductive biology of the population in question and on the relative span of the pre-reproductive and post-reproductive ages. Note that if $f_{1l} = 0$ for all $l > k$ and $f_{1k} > 0$ that is a population with $s-k$ post-reproductive age classes, then $|M(t)| = 0$ that is the complete population projection matrix is non-singular.

Equation (1.1c) can be used to recursively generate the population structure, T time periods later as

$$\vec{n}(t+T) = [\prod_{j=0}^{T-1} M(t+j)]\vec{n}(t) \tag{1.2}$$

Equation (1.2) is important if for example we say there are k seasons each of duration τ_i and the season specific matrices are M_{τ_i} and $\sum \tau_i = T$. Then the population structure at the end of the complete season cycle is

$$\vec{n}(t+T) = [\prod_{i=1}^{k} M_{\tau_i}]\vec{n}(t)$$

If τ_i is equivalent to r_i model time steps of size h each and the season specific matrix per unit model time step is M_i, $i = 1, 2, \ldots, k$ then

$$\vec{n}(t+T) = \left[\prod_{i=1}^{k} M_i^{r_i}\right] \vec{n}(t) \tag{1.3}$$

where $\tau_i = hr_i$ and $\sum \tau_i = T$. A typical case is where T represents a one year period and k the number of seasons per year.

If we let $n_{ij}(t)$ denote the number of individuals moving from age class j into age class i, in a unit model time step, then the maximum likelihood estimate of $p_{ij}(t)$ is given by

$$\hat{p}_{ij}(t) = \frac{n_{ij}(t)}{n_j(t)}. \tag{1.4}$$

The basic data for the estimation of Eq.(1.1a) and Eq.(1.1b) is derived from a form of life table relevant to the kind of biological population under study. The fertility or fecundities per age class, $f_{1j}(t)$ for $j = 1, \ldots, s$ are usually derived from a table of age specific fertility or reproductive rates appropriate to the population.

It was stated that for the deterministic time independent model, the projection matrix is assumed to be constant over time, so that

$$M(t) = M \quad \forall t.$$

Equation (1.1c) therefore becomes

$$\vec{n}(t+1) = M\vec{n}(t) \tag{1.5}$$

This equation can now be used to calculate the population structure T time periods later as

$$\vec{n}(t+T) = M^T \vec{n}(t) \quad T = 1, 2, \ldots \tag{1.6}$$

Under such optimal conditions and if data is available over T time periods later, the MLE of p_{ij} is then given by

$$\hat{p}_{ij} = \frac{\sum_{t=1}^{T} n_{ij}(t)}{\sum_{t=1}^{T} n_j(t)} \tag{1.7}$$

and the fertility rates are taken as the average fertility rates, over the T time periods as

$$\hat{f}_{1j} = \frac{\sum_{t=1}^{T} f_{1j}(t)}{T} \qquad j = 1, \ldots, s \tag{1.8}$$

After a population has been in existence for a long enough time such that the post-reproductive population does not contribute in the reproduction process the matrix can be partitioned symmetrically as

$$M = \begin{pmatrix} A & O \\ B & C \end{pmatrix} \tag{1.9}$$

where

A is a square matrix of order k

B is of order $(s-k)$xk

C is also square of order $s-k$

O is a zero matrix of order kx$(s-k)$

It can be shown that

$$M^t = \begin{pmatrix} A^t & O \\ f_t(A,B,C) & C^t \end{pmatrix} \tag{1.10}$$

where the function $f_t(A,B,C)$ is given by

$$f_t(A,B,C) = \sum_{j=1}^{t-1} C^j\, B\, A^{t-i-1}$$

For large t, the submatrix A remains the only one which is principally of interest for growing population because it involves age classes in the pre- reproductive and reproductive age groups. It can be shown that

$$|A| = (-1)^{k+1}(p_{21}p_{32}\cdots p_{k,k-1}f_{1k}) \tag{1.11}$$

Therefore the matrix is non-singular and hence there exists an inverse to the matrix. The matrix can then be used to generate the forward process $\{A^t\vec{n}(t)\}$ of the population structures with time. We shall then go ahead to derive a general matrix model for a stage structured population where individuals in a stage undergo the aging process before transitting into the next stage.

In general let a population's life cycle consist of k developmental stages of variable residence times $T_i, i = 1, \ldots, k$. By residence times we mean the length of time an individual stays in a stage before transitting to the next stage. We calculate the quantities $t_i = T_i/h$ which gives the number of age classes in stage i for $i, \ldots, k$. Now let us consider an individual of age class j in stage i. We assume that this individual can survive the interval $[t, t+1)$ and transit to the next stage with probability

$$p^i_{1j} = s_{ij}\gamma^i_{1j} \tag{1.12}$$

or transit to the next age class in the same stage with probability

$$\pi^i_{j+1,j} = s_{ij}(1 - \gamma^i_{1j}) \tag{1.13}$$

We remark here that γ^i_{1j} is the conditional probability of transitting to stage $i+1$, given it survives and s_{ij} is the probability that an individual will survive over a time interval. This individual reproduces f^i_{1j} offsprings who survive and enter age group 1 of stage one just before or at time $t+1$. The population structure specific to stage i is given by

$$\vec{n}_i(t) = (n^i_1(t), \ldots, n^i_{t_i}(t))' \quad i = 1, \ldots, k \tag{1.14}$$

and the entire population structure is given by

$$\vec{n}(t) = (\vec{n}_1(t), \ldots, \vec{n}_i(t), \ldots, \vec{n}_k(t))' \tag{1.15}$$

A generalization to the matrix A is then given by

$$A^* = \begin{pmatrix} (F_1 + A_1) & F_2 & F_3 & \ldots & F_{k-1} & F_k \\ P_1 & A_2 & O & \ldots & O & O \\ O & P_2 & A_3 & \ldots & O & O \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ O & O & O & \ldots & A_{k-1} & 0 \\ O & O & O & \ldots & P_{k-1} & A_k \end{pmatrix} \tag{1.16}$$

where the matrices

$F_i, \quad i = 1, \ldots, k$ represents the reproduction process for the different age classes in the population

A_i, $i = 1, \ldots, k$ represents the intra stage dynamics

P_i, $i = 1, \ldots, k-1$ represents the interstage dynamics.

Matrix A^* is the generalised projection matrix for a general n stage population species. The matrix takes a specific form depending on the population species in question and the prevailing assumptions.

<u>The Compartmental Model</u>

Let the variable $x_1, \ldots, x_n$ denote the number of individuals in stage 1 to n respectively. Let p_i for $i = 1, \ldots, n-1$, denote the rate of transition from stage i to $i+1$. Let us assume the $p_i's$ are constant. Further let the stage specific mortality rates be μ_i for $i = 1, \ldots, n$. The model is a cyclic chain model given by the system of linear differential equations with constant coefficients as

$$\begin{aligned} \dot{x}_1 &= f x_n - p_1 x_1 - \mu_1 x_1 \\ \dot{x}_i &= p_{i-1} x_{i-1} - p_i x_i - \mu_i x_i \quad i = 2, \ldots, n-1 \\ \dot{x}_n &= p_{n-1} x_{n-1} - \mu_n x_n \end{aligned}$$

where $\dot{x}_i$ for $i = 1, \ldots, n$ denote the derivative of x_i with respect to time. The model can be written in matrix notation in a similar manner as in the discrete case as

$$\dot{\vec{x}} = A\vec{x} \tag{1.17}$$

where the matrix A is derived from the model parameters and coefficients and $\dot{\vec{x}}$ denotes the derivative with respect to time for an n dimensional vector with its i-th element equal to x_i. Vector-host interaction is introduced via an extra equation denoting the rate of change with time for the host population. This equation can be written as

$$\dot{y} = r - dy - \vec{c}^T \vec{x} y \tag{1.18}$$

where y denotes the total host population density, r is the rate of flow of hosts in a given area and $\vec{c}$ is given by

$$\vec{c} = (c_1, c_2, \ldots, c_n)^T$$

denoting the effects of the different stages of the vector population to the establishment of the host population. Equation (1.17) is then modified to include an extra component to take care of the host population in the system. The combined system of equations contained in Equations (1.17) and (1.18) are then utilized fully to investigate the stability of the vector free and infected equilibriums respectively.

On Host Distribution

Here we differentiate the host population by the number of parasites they carry. We denote by i_k the number of on host type k parasites. These are found on h_{i_k} host individuals and the total host population is denoted by variable H. The variable Y will now denote the total number of parasite individuals. We let m_k denote the mean on host type k parasite load, π will denote the dispersion or the variance to mean ratio of the on host parasite distribution. This quantity tells us about the dispersion of the on host parasite individuals in a community of a host population. We assume that all these are dynamic variables and we can talk of their derivatives with time.

The model parameters include b_{i_k} which gives the rate at which hosts carrying i_k parasites die. This class of hosts reproduce at rate a_{i_k} and their relative susceptibility is s_{i_k}. Parasites on a host carrying i_k parasites die at a per capita death rate μ_{i_k}. The per capita reproduction rate of type k parasites is λ_{i_k}. We modify this definition to mean also the moulting rate for type k parasites where in general k will now denote the off host developing stage. Hosts with i_k parasites acquire new parasites at the rate given by ϕ_{i_k}. New born hosts are assumed to be parasite free. The system of equations describing how hosts change state is thus given

$$\dot{h}_0 = -(b_0 + \phi_0)h_0 + \mu_1 h_1 + \sum_{i=0}^{\infty} a_{i_k} h_{i_k} \tag{1.20}$$

and

$$\begin{aligned}\dot{h}_{i_k} &= -(b_{i_k} + \phi_{i_k} + i_k\mu_{i_k})h_{i_k} \\ &\quad + (i_k + 1)\mu_{i_k+1}h_{i+1} + \phi_{i_k-1}h_{i_k-1} \quad i_k = 1, 2, \ldots\end{aligned} \tag{1.21}$$

where $\dot{h}_{i_k}$ denotes the derivative of h_{i_k} with respect to time. We next define the aggregated variables

$$H_k = \sum_{i_k=0}^{\infty} h_{i_k}, \quad Y_k = \sum_{i_k=0}^{\infty} i_k h_{i_k}, \quad E_k = \sum_{i_k=0}^{\infty} i_k \lambda_{i_k} h_{i_k} \tag{1.21}$$

where

H_k: denotes the total host density carrying parasites type k.

Y_k: denotes the total number of type k parasites harboured by the total host community.

E_k: denotes the total number of moulted type k parasites who await to attach on to passing hosts.

We define $g(H)$ as the probability that an off host individual will attach onto a host as a function of host density H. This function will necessarily be an increasing function of H. The product $H_k g(H_k)$ will then give the intensity of hosts that are susceptible to type k parasites in a given area and it is also an increasing function of H_k. We further define more aggregated variables as follows

$$H_{b_k} = \sum_{i_k=0}^{\infty} b_{i_k} h_{i_k}, \quad H_{a_k} = \sum_{i_k=0}^{\infty} a_{i_k} h_{i_k}, \quad H_{s_k} = \sum_{i_k=0}^{\infty} s_{i_k} h_{i_k} \tag{1.22}$$

and

$$Y_{b_k} = \sum_{i_k=0}^{\infty} i_k b_{i_k} h_{i_k}, \quad Y_{\mu_k} = \sum_{i_k=0}^{\infty} i_k \mu_{i_k} h_{i_k} \tag{1.23}$$

where

H_{b_k}: is the total number of hosts dying per unit time due to type k parasites

H_{a_k}: gives the total number of hosts born per unit time in the presence of type k parasites

H_{s_k}: gives the total host density per unit time susceptible to type k parasites

Y_{b_k}: gives the total number of type k parasites dying per unit time due to host death

Y_{μ_k}: denotes the total number of type k parasites dying per unit time due to natural mortality.

From above definitions it follows that

$$\dot{H}_k = -H_{b_k} + H_{a_k} \tag{1.24}$$

and

$$\dot{Y_k} = -Y_{b_k} - Y_{\mu_k} + H_{s_k} g(H_k) E_k \tag{1.25}$$

We exploit the two dimensional system to study the stability of the vector- host interaction system. Density dependence in the model is introduced via two alternative considerations. First we consider the case where host mortality increases linearly with on host parasite burden such that

$$b_{i_k} = b + \alpha i_k$$

We next introduced density dependence through the parasite death rate by making it a linearly increasing function of the on host parasite burden. That is

$$\mu_{i_k} = \mu + \gamma i_k.$$

We then go ahead to investigate the implication of these modifications to the stability of the system.

Next define the reproduction number R_0 as the average number of female parasites attaining maturity produced by a female parasite during her life time. For a constant population this number will take the value one. Due to possible density dependence we define the effective reproduction number as

$$R_e = R_0 f(y)$$

where $f(y)$ is the density dependence function on R_0 expressed as a function of the mean on host parasite burden in a host community. Note that in the absence of density dependence

$$f(y) = y.$$

The function $f(y)$ is investigated for different assumptions on the on host parasite distributions.

1.3 Brief Literature Review

1.3.1 General Literature Review

The use of matrix population models was pioneered by Lewis(1942) and Leslie (1945). They independently developed a matrix model, that allowed prediction of future population age structures, given an initial distribution, and corresponding age specific mortality and fertility rates. Leslie(1948) extended these ideas and showed how to determine the stable age structure. He discussed a number of properties of the projection matrix, such as the role of the dominant root in population growth. In these formulations the matrix inputs are assumed constant over time. However this is most of the time not true in practice. The population mortality and fertility rates, are bound to vary due to several factors. These could be climatic in nature or other factors such as predation for some population species, epidemics, control interventions and so on. Another shortcoming is that of classifying the population according to age alone. Other classification criteria should be possible.

Leslie(1959) suggested a density dependent matrix model by making the fertility and mortality rates functions of the previous and present number of individuals in the population. He also suggested a simple hypothetical seasonally driven model.

Lefkovitch(1965) proposed a modified Leslie model applicable to organisms grouped according to stages of development. For a population species whose stages occupy exactly equal periods of time, Lefkovitch's matrix model can as well be treated in a similar manner as the classical Leslie model. However a more general model for stage structured populations combining both stage and age modes of classifications is important. The elements m_{ij} in Lefkovitch's model denote the dependence of the i-th stage at time $t+1$ upon the j-th stage, at time t. Such a kind of model suffers from the unavoidable difficulty of a posteriori estimation of the matrix elements. The projection matrix M is estimated from census observations, taken for a suitable number of time intervals. In this situation errors in estimation can only be reduced by increasing the frequency of census observations and/or the sizes of the census samples. Unfortunately, although the model is a useful technique, the matrix elements derived from partial regression may lack biological significance. The assumption of time independence on the matrix elements is obviously not a sound one since the elements are bound to vary at different times due to several factors such as seasonal fluctuations, type of vegetation, and so on.

Usher(1966,1969), developed a more useful model in the management of renewable resources, on forest data. He argued that, for sufficiently short periods, an organism initially in class i, at time t, may at time $t+1$, either be dead, remain in class i, or progress into class $i+1$. An implicit assumption in the model is that, the survival rates apply equally to each individual in each class at any time which might not be the case in reality. Individuals might have different rates of moving into class $i+1$. In effect his assumption is that each class is characterized by a fixed residence time which we know is bound to fluctuate due to several factors.

Sykes(1966), in his Ph.D dissertation suggested three models namely the additive error model, the independent binomial trials model and the matrix random variables model. Sykes(1969) reviewed the properties of the population matrix. The work by Sykes(1966,1969), will therefore be a valuable source of background knowledge concerning the analysis of population projection matrices.

Applications of matrix population models have been undertaken extensively. Bosch(1971) examined the question of coast redwood extinction in california, in terms of expected population growth rates. However the model was deterministic in nature. It included several algebraic and model errors. Ways to improve the model include the use of more and smaller age classes, possibility of using variable elements in the matrix and the use of computer, in finding the characteristic roots of the resulting matrix which will be of high dimension. In the current study we intend to concentrate on the variability of the matrix elements and come up with a more general matrix model.

Namkoong *et al*(1974) modelled as a stochastic process survival probabilities of coast redwood populations. The ultimate probabilities of extinction of the population species was investigated in relation to the degree of mortality and the dominant positive root of the projection matrix.

There are certain restrictions associated with using a projection matrix, in which the entire population is structured by stages, instead of by age. Most importantly the probabilities in the matrix will not remain constant unless the system has attained stability. Vandermeer(1975) uses a special form of a projection matrix, structured by stages, to clarify its relationship to the standard population projection matrix. His work was a modification to the work by Lefkovitch(1965). The author attempts to calculate the underlying age distribution, from a population structured according to stages of development. We have studied this aspect in detail with more clarity and in a more general perspective.

The discrete time process described has been used to model the dynamics of a wide variety of ecological populations; for example plant population dynamics, by Sarukhan and Gadgil(1974). They considered the matrix as a function of seasons, comprising a year. We have attempted to generalise this aspect and an application developed for the brown ear tick(*R. appendiculatus*) with data collected from the highveld of Zimbabwe.

The problem of harvesting was introduced to matrix population theory by Lefkovitch(1967) and Usher(1969). That is if the population is age structured and the ultimate stable structure is $\vec{v}$, the eigenvector corresponding to the dominant root λ_1, then if $\lambda_1 > 1$ we may harvest $(\lambda_1 - 1)\vec{v}$ from the population, to maintain the constant equilibrium. The same idea can be used in the control problem where the harvesting now corresponds to a control intervention to reduce the population. Extentions to the harvesting problem are aimed at optimum harvesting policies, different from removing equal proportions from each population class or group as in Beddington(1973). The rationale being that these other harvesting policies could produce a higher yield at a sustainable level. Thus Doubleday(1975), displayed the existence of a simple mathematical solution, to the harvesting problem, using a fisheries example. Enright and Ogden(1979) applied the Leslie matrix model, to single species populations and similar transition models, to more than one tree population. They suggested that an important aspect of matrix population models is that, they provide a time scale for the trends exhibited by species that live long, in addition to predicting the magnitude and direction of future changes.

Woodward(1982), suggested a simple method for decomposing a population that is stage grouped into the underlying age structure. The population dynamics can then be predicted, using the standard age structured Leslie matrix model. He assumed that the residence in each of the stages follow a normal distribution. A weakness in this model is the assumption of normality on the residence times. We address the problem of stage distribution in relation to the residence times in the present work.

Desharnais and Laifu(1987) presented a general matrix population model, where the age-specific vital rates depend upon the age structure of the population. In more precise terms the authors were actually addressing the problem of density dependence. Fecundity and survival rates are assumed to decrease exponentially, at rates dependent on the densities of each age class. They exhibit, the existence of a non-trivial equilibrium age structure, given the population can grow without density dependence. Necessary and sufficient conditions, for the existence of a local asymptotic stability were stated. Computer simulations were used to compare the model performance and that from census data.

Yanan *et al*(1990), discusses the suitability of estimating the Leslie matrix elements from experimental cumulative distributions. The model is quite ideal for the study of an arthropod/insect or a general stage structured population, in a homogeneous system. We study this approach by developing a time dependent model for the brown ear tick(*R. appendiculatus*).

1.3.2 Literature Specific to the Brown Ear Tick

The tick *Rhipicephalus appendiculatus* is the most abundant and widely distributed tick species throughout eastern, central and southern Africa. Other tick species in that area include *Boophilus decoloratus* and *B. microplus.* Together with *R.appendiculatus*, these are vectors for animal diseases and hence cause considerable economic losses in terms of live weight loss, milk yield and hide quality reduction. Many infected animals die if no remedial measures are taken.

The life cycle of *R. appendiculatus* consists of four successive developmental stages, namely the egg, larva, nymph, and adult. The time an individual stays in any of these stages differs. Furthermore, an individual in the larval, nymphal and adult stages can be classified as being in the state of questing (host finding) , feeding (on host) or developing (off host, after feeding). This means that the larva, nymph and adult attach to the host at one time towards the end of that stage. In view of the fact that the tick species feeds on three different hosts, it is called a three host tick. It is an interesting biological question why this species has larvae, nymphs and adults that feed on hosts while other species in the same habitat and roughly the same host range feed only on one host. The phenomenon that tick species vary with respect to the number of hosts (one, two, or three) is known for ticks all over the world, for example the common European tick, *Ixodes ricinus*, is also a three host tick. It can be speculated that the three host ticks are, with respect to the life cycle, more ancient than other tick species on an evolutionary scale. Norval *et al* (1992) state that one of the reasons why *R. appendiculatus* can become very abundant in the presence of cattle or wild ungulates is that these serve as primary hosts for all stages of its life cycle. Infact it is noted that tick species in which the immature stages are able to exploit the same ungulate hosts as adults tend to become common (pests) in agricultural systems, while tick species in which the immature stages tend to feed on specific non-ungulate hosts tend to be rare.

After oviposition by an adult female, egg development usually takes place at the base of the vegetation. A typical adult female deposits about 4,000 eggs, hence the fecundity is 2,000 taking account of an estimated sex ratio of 1:1. The newly hatched larva undergoes a period of adaptation, the length of which is temperature dependent. This period is followed by questing, that is host searching, where the tick is waiting for passing grazing host (domestic or wildlife). After successful attachment, the larva enters a feeding phase (on host) during which it extracts a blood meal. Once the larva has consumed the blood meal, it drops to the pasture where it undergoes development which is also highly temperature dependent. Completion of this process leads to a newly moulted nymph which repeats the same sequence of events as the larva. The nymph moults to an adult tick which undergoes similar transformations; it also mates during the on-host period. When it completes feeding or successfully feeds (i.e engorged) , the adult female tick drops to the ground (pasture) and enters a period of oviposition which can be lengthy depending on the prevailing environmental conditions. In southern Africa the adults can undergo a diapause period of rather extended length if external conditions are unfavourable. The life cycle and questing process are illustrated in Figures 1 and 2 in page 28.

Parameters of interest in the entire life cycle are the developmental, fecundity and survival rates. Development, as mentioned earlier, is normally temperature dependent, faster at high temperatures, with a minimum and maximum temperature below which or above which development is seriously curtailed. Higher temperatures appear to prolong the ovipositioning period for adult females. Adult male survival is usually high but can be reduced by predation if number of predators in the habitat is high. Rainy seasons are more favourable for hatching than dry seasons. Therefore this suggests seasonality in fecundity rates. Survival for engorged larvae and nymphs is high in most seasons with nymphs being the hardier stage and eggs the most susceptible to adverse micro-climatic conditions.

The brown ear tick is the main vector of the *Theileria parva* group of organisms which is the causal parasite of East Coast fever and related diseases. Integrated control methods based on tick-resistant cattle, pasture spelling, strategic dipping and tick killing plants, have been suggested for control of African ticks by Sutherst(1981). One of the requirements of such methods is an understanding of the population dynamics of the tick, hence the need for mathematical models to support the approach. Data sets with information on survival, fecundity, and development have been collected (both in the laboratory and the field) by several biologists, among them Short et al. (1989a & 1989b). The models in chapters IV and VI will make use of published data on the population dynamics of *R. appendiculatus* for validation and simulation. One of the advantages of *R. appendiculatus* data is that there exists comparative data on the development and survival rates for most of its life stages in comparison with those of other tick species.

In the current study the aim is to design and investigate a series of models that will allow a better understanding of the life cycle processes of *R. appendiculatus*, the interaction with its hosts and possibly to identify biological input values that the model measure of population growth is sensitive to. This information can then be used in the design of control strategies.

The starting model is a very simple Leslie type compartment model. In all the models in the current study, the life cycle of the tick is divided into $n = 10$ stages as illustrated in the figure 1 in page 28. The initial model in chapter IV is formulated excluding tick-host interaction. It is then further extended to take into account the interaction with hosts, both wild and domestic animals and the effects of interspecific competition and density dependence.

Vector-host interaction is analysed in a qualitative context in chapter IV of the current work and the findings are important in the understanding of the system. The effect of seasonality and vegetative ecotype to tick population growth is addressed in chapter VI of the work .

An important aspect in the tick life cycle is the influence of environmental factors on the survival, development and behaviour of the different life cycle stages. Field observational and experimental studies show that there are distinct seasonal effects in the life cycle of *R. appendiculatus* especially in southern Africa (as compared to tropical regions). The field studies and laboratory experiments carried out in Zimbabwe and reported in Short *et al.* (1989a,b) distinguish three seasonal regimes to which the ticks may be exposed, namely rainy, cool and hot. A high degree of variability over these seasons was observed. The field study was conducted in the high veld of Zimbabwe under two vegetative ecotypes, defined as long grass and short grass. Type of vegetation is a factor that influences host seeking and survival. The study also indicated some aspects of predation on ticks and describes alternative hosts, in addition to cattle, such as rodents. It was also reported that *R.appendiculatus* can coexist with other tick species such as the *Boophilus* species. Zivkovic *et al.* (1986) reported that *R.appendiculatus* and *R.zambeziensis* are taxonomically not clearly separated and tend to overlap at certain altitude ranges. Cleary more information on the ecology, in particular interaction with hosts, of both species is needed.

Similar information on seasonality can be found in Short and Norval (1981) where data from eight localities in east, central and southern Africa were compared and analysed. The results show that the seasonal pattern of *R.appendiculatus* is largely dependent on the ability of the adult ticks to adapt their activity, in particular oviposition, to take into account differences in humidity, temperature and daylength. However, based on a statistical analysis of data from five sites from southern Africa, Randolph (1993a,b) questions this assumption and puts forward the hypothesis that it is the timing of the questing activity of the larvae, vulnerable to desiccation, that determines the pattern of the seasonal dynamics of the tick. In Branagan (1973a,b) it is reported that *R. appendiculatus* in cool, more humid climates (e.g. Muguga, Kenya) suffer less climatic stress than those in a warm,more arid climate (e.g. Kedong, Kenya). Eggs in this latter site were exposed to a higher degree of desiccation than those in more humid areas. During periods of maximum saturation deficiency, complete egg failure (i.e egg dessication) occurred. Survival periods for questing ticks were shorter in Kedong than in Muguga, suggesting that host availability is more crucial in warmer arid areas than in cool, moist climates. Pegram and Banda (1990) studied development and survival of free-living stages of three tick species in central Zambia among them *R.appendiculatus*. The findings were that tick activity reflects seasonality. The univoltine that is single generation ticks exhibit diapause mechanisms that effectively synchronize the life cycle of these species to climatic conditions. No diapause was observed in the multivoltine that is several generations species which are able to complete three to five generations per year with no seasonal synchronization.

All these papers indicate that temperature seems to be the critical variable as far as development times are concerned whereas humidity affects the probability of survival.

Branagan(1973a,b) also noted that development rates, including the *rate* of egg production, declines with falling temperatures, while fecundity (*total* egg production), although reduced by extreme temperature, does not vary much within the temperature regimes experienced by *R.appendiculatus* and other tick species.

The question of density dependence seems not to be well documented in most articles but Branagan (1969), observed that as the on host density of nymphs increased their feeding periods became shorter. It has been suggested that this phenomenon may be associated either to the observed clustering behavior of nymphs on the host or to some resistance mechanism of the host. In fact, in certain tick species it has been experimentally observed, with rabbits as hosts, that repeated exposure of a rabbit to ticks results in shorter attachment periods and reduced repletion (Branagan 1974).

Of the two explanations the the second seems more realistic due to the well known phenomena of acquired resistance by host species. However we cannot completely overule the first case because this tick species is known to prefer the ear for attachment than other parts of the host body hence the name "brown ear tick".

The relationship between the abundance of *R. appendiculatus* and the degree of host resistance to it has also been disscussed in the book by Norval, Perry and Young (1992). In particular they point out that this tick species becomes very abundant because several host species do not acquire a high degree of resistance to it as opposed to other tick species.

Randolph (1993a,b) indicates that density-dependent mortality factors operate between nymphs and females after the nymphs have moulted, thus working in the same competitive way as the assumed resistance mechanism.

All these studies are aimed at finding methods of controlling tick transmitted diseases and the vector tick itself. Pegram *et al.* (1991) report on experiments where herds of sanga cattle were kept under controlled conditions. Two herds were kept in traditional grazing regime for three years. One herd was kept tick free by regular acaricidal treatment while the other had no tick control. The tick free herd, as expected, performed much better in terms of milk production, growth rate, fertility and mortality but the value of additional production was much less than the treatment costs. Similar studies are reported in Pegram *et al.* (1989a,b) where in fact heavy acaricidal applications were found to lead to effects such as poor liveweight gain, especially in young cattle. They also report that combined effect of climate and ecotype also affect tick dynamics in the region of central Zambia where the studies were conducted. On the other hand it is reported that during tick seasons infestations also caused significant reductions in liveweight gain. In the same papers it is reported that below average rainfall suppressed the abundance of ticks such as *R appendiculatus*. Cattle in woodland areas carried more tick infestations than those in open pasture. The studies indicate that integrated tick control strategies which rely less on heavy acaricidal applications are more appropriate in all ways.

Pegram *et al.* (1989a,b) also report that there is a correlation between the numbers of different tick species on individual hosts over one year old. It is also clear that variations in climate, and consequent changes in grazing patterns may influence population dynamics of different tick species with varying degrees. Such issues raised above ought to be addressed when modelling such kind of population dynamics.

The dynamics of tick borne-diseases in Africa are complex because there is a variety of infectious agents transmitted variously among the hosts (cattle and other ungulates) and the vectors (ticks). The principal host of interest is cattle, due to its economic importance. Among the tick -borne infections, East Coast fever (ECF) is a disease mainly found in cattle in most parts of eastern, central and southern Africa. In endemically stable areas (mainly eastern Africa) many indigenous zebu cattle are continuously exposed to ticks, thus there is a class of hosts (cattle) referred to as immune carriers who are not susceptible to disease but may transmit the parasite to ticks thus making the transmission problem even more complex. Epidemiological models being developed (Medley *et al.* 1993) can aid in the design of optimal control policies. However these models cannot work in isolation without proper tick population models.

The economic importance of the disease is three fold. First there is damage to cattle by direct effect of ticks, for example increased irritation, blood loss, skin lesions etcetera. Secondly upgrading of cattle is impossible without extensive/intensive use of acaricides which are costly and further produce side effects and thirdly even if (disease parasite) does not cause appreciable mortality and mobidity, growth rates and productivity of the sick animals may be greatly reduced. The economic impact of the infection depends mainly on ECF-specific mortality.

Though *Theileriosis* is a vector-borne disease, its mode of transmission is slightly different from those transmitted by other vectors such as tse-tse flies which move from host to host within developmental stages. For the tick to be infected it has to feed on an infected and infectious host and since transovarian transmission is not feasible only the nymph and adult can transmit the disease to the host while feeding.

Apart from the common control method of intensive use of acaricides, immunisation provides a possible control option. This can be achieved by infection and treatment, and work is under way to develop an antigen vaccine. These methods have their own characteristic effects on the transmission dynamics which could be of importance to model building. More realistic and complex disease models derived from basic information about the disease and its vector are therefore needed. Thus there is need for careful estimation both experimentally and statistically of various disease/vector parameters.

An important aspect of the disease is the question of seasonal occurrence of the disease especially in the southern parts of Africa. This implies changes in host age at infection thus advocating for host age structured disease models. However it should be noted that seasonal occurrence may provide a larger "window" in which to immunize most animals before exposure to natural infection. The effect of seasonality to the carrier/infected status of the host is also important in this respect especially for survival if the individual has to pass the parasite through the non transmission periods.

In summary the ultimate goal in these mathematical models is to improve understanding by means of appropriate quantitative tools and to forward suggestions on future data collection aimed at aiding the design of better and efficient control programmes in order to reduce the economic impact of the disease and its vector. The book by Norval *et al.* (1992) gives a thorough account of the epidemiology of the disease and the distribution of its vector in Africa. It will serve as an important source of information for the current and future modelling work.

The modelling of tick population dynamics has been uncommonly attempted probably due to the complex life cycle patterns and poor data availability. Gardiner and Gettinby (1981) modelled the dynamics of the European tick *Ixodes ricinus*, also a three host tick. They presented a method of calculating development times based on the idea of development fractions. This method has also been used in Gettinby *et al.* (1974,1979) to determine development periods for parasitic helminths of cattle in Ireland. The method is based on the fact that one can aportion some fraction of development for each day based on functional relationships between temperature and development periods. Development is complete on that day when the sum of these fractions add up to at least 1. However comparing the predictions and observed periods the model requires further improvements.

Simulation models have also been developed to study tick dynamics. Haile and Mount (1987) and Mount *et al* (1993) developed simulation models for the American dog tick and the "lone star" tick. In the model tick individuals were classified into weekly age classes, the effects of temperature and humidity on the tick's developmental periods and vital rates are incorporated. The predictions of the model were quite close to reality but as mentioned by the authors one needs to improve on the functions relating the vital rates and environmental factors. As the modelling of tick dynamics gets more attention models on diseases transmission should also begin receiving serious attention. Byrom and Gettinby (1992) used published data, especially those of Short and Norval (1981), to develop a microcomputer software ECFXPERT to study the dynamics of *R.appendiculatus* and East Coast fever. However as mentioned by Randolph (1993a,b) there is a significant lack of fit between model predictions and observations. This calls for a better understanding of the systems and development of better mathematical models. As Nokoe (1992) puts it we need a "mixed" model approach, that is, models both deterministic and stochastic in nature to model the complex tick life systems, especially the three-host brown ear tick. One of the aims of the current study is to address the problem of the tick population model results and what is observed in the field. Quite recently Medley *et al.* (1993) formulate a mathematical model to study the transmission dynamics of *T. parva* by *R.appendiculatus* to cattle in endemically stable areas.

Mathematical population dynamics models are still in high demand in order to link them with disease models such as these in order to come up with proper control strategies for both the disease and its vector.

Matrix population models similar to Leslie (1945) models can be used. These models have undergone many modifications to include populations structured by stages rather than age classes as initially formulated. Caswell (1989) in his book on Matrix Population Models addressed the various modifications to the Leslie

(1945) matrix model to suit the different populations structured according to the stage variable other than age. Recently Sandberg *et al.* (1992) used Leslie's idea to formulate a multiple matrix model for a three host tick that is a causal vector of Lyme disease in human populations. Their tick individuals were categorized as either in year 1 or 2 and further whether they were fall-fed or spring-fed. This model is different from the common Leslie model insofar as the successive entries in the population vector do not correspond to successive states in the life of one individual but rather there are different possible life histories. These authors work out a transition matrix for each month of the year thus in fact forming a periodic discrete time dynamical system that is time dependent. The product of all twelve matrices gives the transition matrix for one year which then of course defines an autonomous system on an annual time scale. Weaknesses in the model are almost obvious even though the authors mention some of them. All of the matrices describe zero mortality in any stage except in adults after oviposition or non-fed individuals which have infinite mortality. This aspect is expressed in the matrices by either a 1 in the diagonal that is individual always remains in the same stage or, more generally, by a column sum equal to 1 describing transition without death to other stages. Infinite mortality is expressed by a row of zero entries. Looking at the schematic representation of the species life cycle it is not clear whether some of the states are clearly defined or can be distinguished in the field for example fed nymph 1 and fed nymph 2, observed in June, are distinguished by the fact that the first has fed in May-July the year before and the second May-June of the present year. However, as the authors say, the model was supposed to illustrate the technique which can be further improved to account for seasonality and environmental variability in tick dynamics. It is finally important to once again mention the general comment by Randolph (1993a,b) that past studies on seasonal dynamics of tick species have beed based on relating climatic variables to numbers of ticks rather than its underlying demographic rates, a rather unfortunate situation since, for example an adverse season always causing high mortalities may follow a period of population growth hence associating it with high tick numbers which was not the case. Thus caution should be taken when designing and formulating tick population models.

In summary mathematical models in the field of vector population dynamics and epidemiology are and will remain an important tool for analysis. There is need to improve on existing models and to develop more robust ones for this work. This kind of task no dought requires a multidisciplinary approach to research work.

1.4 Statement of the Problem

Most litrature so far indicate that matrix population models have been time homogeneous and mostly for populations structured according to age. Such models are along the lines of the classical Leslie(1945) model. In the current study we develop a more general model for a stage structured population aplicable to any general n stage structured population species. We further develop a continuous time compartmental model for this type of population. Thus the problem is addressed for both discrete and continuous class of population models.

In a time dependent model the projection matrix, $M(t)$, at time t, may not necessarily be the same as $M(t+1)$ at time $t+1$. Time dependence on the population projection matrix is studied in relation to the brown ear tick (***R. appendiculatus***). In this study time dependence is brought about by seasonal variation in the population parameters and the difference in vegetation types in the location of study, in our case the highveld of Zimbabwe.

We then develop a vector-host interaction model for a general n stage population species. The brown ear tick is chosen as an example for the continuous and discrete cases. We in addition study the problem of density dependence for a general parasite-host interaction system. The null hypothesis that the on host vector distribution is asymmetric and is negative binomial is investigated at length. We in addition study the stability of the vector-host interaction model along the lines of Adler and Kretzschmar(1992).

1.5 Specific Objectives of the Study

The specific objectives of the present study may be summarized as follows:

(i) To examine critically the time homogeneous model for age structured populations.

ii) To develop a more general matrix model applicable to a general n stage structured population species for both continuous and discrete cases.

(iii) To give ways of deriving the matrix inputs from experimental and field data.

(iv) To develop a general vector-host interaction model for a general n stage structured population with the brown ear tick as a specific case.

(v) Study the stability of the vector-host interaction model in (iv).

1.6 Significance of the Study

The results of this study will be useful in the understanding of population dynamics particularly the brown ear tick. In recent years the rapidly rising costs of acaricides and their application, as well as the growing problem of tick resistance to acaricides, have stimulated research into new innovative methods of tick control. Thus tick population models are also being developed and used to simulate and analyse the effects of control strategies, enabling veterinary authorities to select the most approriate and cost-effective strategies for given circumstances in the field. It will also bring out more clearly the relation between the discrete and continuous population models. The generalized matrix model for stage structured populations is more flexible and can be adopted for any population species.

Time dependent matrix models are expected to be more realistic. This means that monitoring and control of biological populations can in general be carried out with more reliability, especially with the advent of powerful computers and softwares.

The results will be useful in the clear understanding of complex vector-host interaction models with the aim of qualitatively and quantitatively evaluating control strategies of vector populations which are carriers of disease agents to its host(s).

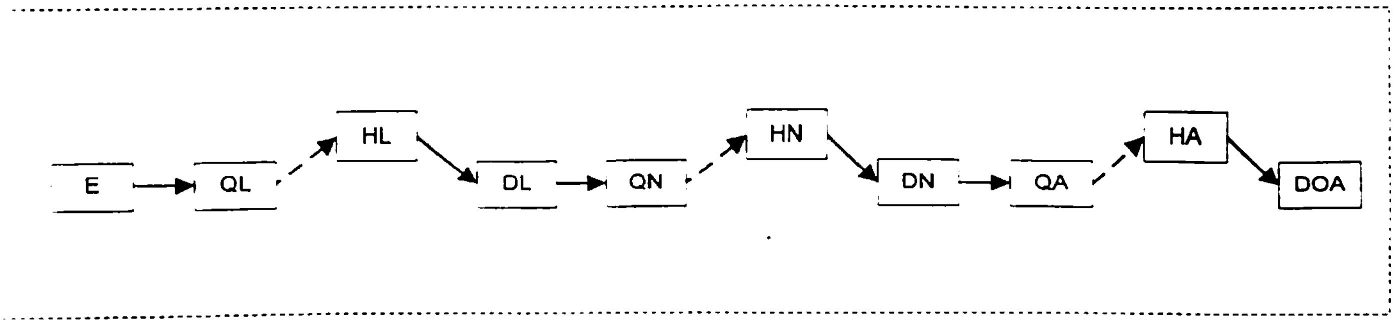
It is hoped that, the interpretation of some of the findings will contribute significantly in the study of tick population dynamics particularly the brown ear tick. Lastly the work will also serve as reference material to researchers and students in the field of mathematical population models.

1.7 Methodology

Data for the study was obtained from international research institutes. These are organisations that carry out research on specific populations for various reasons. This particular study was in close collaboration with scientists at ILRI; the International Livestock Research Institute. The population of interest namely the brown ear tick(*R. appendiculatus*) was generally categorized into a finite number of classes in this case according to stages of development. These are indexed by $1, \ldots, n$. The classification is general according to some specific attribute say age, size, developmental stages and so on depending on the population in question. Information concerning the fertility and mortality rates for each class is then obtained over a period of time. From such an information we are able to derive the required population projection matrix. This was done for the brown ear tick for different seasons and vegetation types in a location in Zimbabwe.

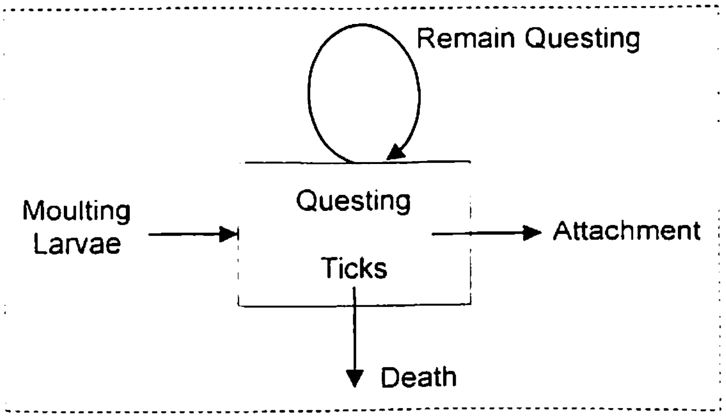
To validate the model we develop a simulation model using a statistical package, SPLUS, as described by Venables and Ripley(1994). Computer programs in C language were developed to facilitate simulations for the continuous compartmental model. Thus computer methods (simulations, graphics etcetera) enabled us to analyse and summarize the results for final thesis preparation.

Figure 1: Stages in the Life Cycle of R. appendiculatus



E: Egg QL: Questing Larvae HL: Host Larvae DL: Developing Larvae
QN: Questing Nymph HN: Host Nymph DN: Developing Nymph QA: Questing Adult
HA: Host Adult DOA: Dev/Ovipositioning Adult

Figure 2: The Questing Process



CHAPTER II

BASIC AGE STRUCURED MODELS

2.1 Introduction

In this chapter we describe mathematical models for the growth of age classified populations. First we consider models where mortality and fertility rates are functions of the age of individuals in the population. Also we treat age and time as continuous variables leading to the well known Lotka's integral equation. Then we consider the case when the two vital rates (mortality and fertility) are functions of both age and time as continuous variables leading to the McKendrick-von Foerster equation. Then finally we consider the case where the vital rates are functions of age but with discrete intervals of both age and time. This will lead us to the Leslie matrix model which is the principal model discussed in the present study

2.2 Lotka's Integral Equation

In this section we investigate the consequences of assuming that age-specific fertility and age-specific mortality are both time independent when both time, t and age, x are treated as continuous variables. Let,

$m(x)$ =number of births or expected number of offsprings per individual aged x

$m(x)\Delta x$ =expected number of offsprings per individual aged between x and $x + \Delta x$ where Δx is small

This definition makes no sense for an individual female but it is perfectly reasonable if considered as an average over a large population. In effect, it simply replaces probabilities for individuals with fractions for whole populations. The following assumptions are made about the maternity function $m(x)$

(a) $m(x)$ is continuous and differentiable

(b) $m(x) > 0$ for $\alpha < x < \beta$ and

$$m(x) = 0\, for \begin{cases} 0 \leq x \leq \alpha, & \text{pre-reproductive ages} \\ \beta \leq x \leq \infty, & \text{post-reproductive ages} \end{cases}$$

$0 \leq \alpha < \beta \leq \infty$ where α is the upper limit for the pre-reproductive ages and β the lower limit for the post- reproductive ages.

(c) depending on the population $m(x)$ could have a single or more maxima. We assume a single maxima the simplest, such as for a human population.

Let,

$n(x,t)$ =the number of individuals aged x at time t (this gives the population age distribution)

$B(t)$ = number of offsprings occuring at time t

Then it follows that

$$B(t) = \int_0^\infty n(x,t)m(x)dx \tag{2.1}$$

Since it is important to uniquely represent the quantity $n(x,t)$ in Eq.(2.1) we derive the survivorship function or (life table function) in probabilistic terms. Once these are understood it will be sufficient to replace probabilities by their estimates.

Let,

$$f(x)dx = Prob\{\text{dying between age } x \text{ and } x + dx\} \tag{2.2a}$$

then

$$\int_0^\infty f(x)dx = 1 \tag{2.2b}$$

since every individual eventually dies, so that $f(x)$ is a proper density function. If ω is the maximum attainable age then the upper limit in Eq.(2.2b) is replaced by ω. We now define the distribution function for the random variable X_d, denoting age at death, by

$$F(x) = Prob\{X_d \leq x\} \tag{2.2c}$$

and

$$F'(x) = f(x) \tag{2.2d}$$

where $f(x)$ is defined in Eq.(2.2a). It is also convenient for us to define a death rate called the force of mortality from $f(x)$ and $F(x)$ by

$$\mu(x) = \frac{f(x)}{1 - F(x)} \tag{2.3a}$$

such that for $\Delta x \to 0$,

$$\mu(x)\Delta x = Prob\{\text{dying between age } x \text{ and } x + \Delta x \mid \text{survival to age } x\} \qquad (2.3b)$$

Now let us assume we start off with a cohort of initial size $l(0)$. Let,

$l(x)$ =number of individuals in a cohort of initial size $l(0)$ who survive to at least age x;

$$p(x) = Prob\{\text{an individual survives to at least age } x\} \qquad (2.4a)$$

then assuming the fractions and probablities are interchangeable it follows that

$$F(x) = 1 - p(x) \qquad (2.4b)$$

and

$$p(x) = l(x)/l(0) \qquad (2.4c)$$

which can also be looked at as the fraction of individuals who survive from birth to age x. Hence if the survivorship function, $l(x)$, is known then $p(x)$ and $F(x)$ can easily be estimated. We state here three important properties of the $p(x)$ similar to those possessed by $l(x)$ namely,

i) $p(x)$ is continuous and differentiable
ii) it is monotonically non-increasing
iii) $0 < p(x) \leq 1$ for $0 \leq x \leq \omega$ and $p(\omega) = 0$ where ω is the terminal age for any individual.

Now at any point in time t we have two groups of individuals namely those present at time $t = 0$ and those born after time $t = 0$. Thus at time t, all individuals older than age t are in the first group, while all those individuals younger than age t fall in the second group. It is therefore true that individuals aged $x > t$ existed at time $t = 0$ and were aged $x - t$. For such idividuals,

$$Prob\{\text{individuals survives upto time } t\} = p(x)/p(x - t) \qquad (2.5a)$$

which is a conditional probability. In terms of the survivorship function $l(x)$ this probability is given by

$$P(l(x)) = l(x)/l(x-t) \tag{2.5b}$$

assuming the population was observed for a long period of time. On the other hand individuals aged $x < t$ were born at time $t - x > 0$, hence,

$$Prob\{\text{individuals survives upto time t}\} = p(x) \tag{2.5c}$$

This probability is equal to the probability an individual survives to age x.

Now in practice it is census data and not life table data that is frequently available. Therefore let

$$n(x-t,0) = n_0(x-t)$$

be the number of individuals present at the start of the census(t=0) who will be aged x at time t. Then

$$E[n(x,t)] = \begin{cases} n_0(x-t)p(x)/p(x-t), & t < x \\ B(t-x)p(x), & t > x \end{cases} \tag{2.6}$$

Substituting into the integral equation (2.1) which defines $B(t)$ yields

$$B(t) = \int_0^t m(x)p(x)B(t-x)dx + \int_t^\infty m(x)\frac{p(x)}{p(x-t)}n_0(x-t)dx \tag{2.7}$$

The product $p(x)m(x)$ in the integrand (2.7) appears repeatedly in the work and is therefore given a special notation

$$\psi(x) = p(x)m(x)$$

and referred to as the *net maternity function.* Also from the definition of $m(x)$ it is clear that the average number of offsprings born in the past to an individual who survives to the maximum reproductive age β is given by

$$\int_\alpha^\beta m(x)\,dx.$$

This is the gross reproductive rate(grr). On the other hand the average number of offsprings to be born in future to an individual itself just born is given by

$$\int_\alpha^\beta p(x)m(x)dx = R_0.$$

This is the net reproductive rate. Now the first term to the right of Eq.(2.7) represents births to individuals born after $t = 0$, while the second represents only the births to individuals already present at time $t = 0$.

Let,

$$g(t) = \int_t^\infty m(x)\frac{p(x)}{p(x-t)}n_0(x-t)dx$$

Then, (2.7) can be rewritten as,

$$B(t) = \int_0^t \psi(x)B(t-x)dx + g(t) \quad t > 0 \tag{2.8}$$

Now assuming that the population has been in existence long enough such that the initial cohort of individuals present at $t = 0$ have died out, (that is no individual out of the $n_0(x-t)$ present at time $t = 0$ is still surviving) then the governing renewal equation reduces to

$$\begin{aligned} B(t) &= \int_0^\infty m(x)p(x)B(t-x)\,dx \\ &= \int_0^\infty \psi(x)B(t-x)\,dx \end{aligned} \tag{2.9}$$

and

$$E[n(x,t)] = B(t-x)p(x)$$

Equation (2.8) is a non-homogeneous integral equation of the second order with band limited kernel since $\psi(x) \neq 0$ for $\alpha < x < \beta$ while Eq.(2.9) is homogeneous. We now describe the solutions to these equations.

2.3 Solutions to the Integral Equations

We consider the solution first to equation (2.9) assuming exponential growth then secondly the solution to equation (2.8) by method of Laplace Transforms.

2.3.1 Solution by Elementary Methods

Let us assume the homogeneous form of the integral equation (2.9) admits solutions of the form

$$B(t) = Q\exp(rt) \tag{2.10}$$

Substituting in Eq.(2.9) we get the expresion

$$Q\exp(rt) = Q\exp(rt)\int_\alpha^\beta \exp(-rx)\psi(x)dx$$

which on simplification reduces to

$$1 = \int_{\alpha}^{\beta} e^{-rx}\psi(x)dx \tag{2.11}$$

where the limits on the integral have been changed because $\psi(x)$ is nonzero only in the interval $\alpha < x < \beta$ on R_+. Equation (2.11) will in the sequel be referred as the characteristic equation. Now define $\varphi(r)$ such that,

$$\varphi(r) = \int_{\alpha}^{\beta} e^{-rx}\psi(x)dx$$

so that the characteristic equation now becomes

$$\varphi(r) = 1 \tag{2.12}$$

Now let us investigate the limiting properties of the function $r \longrightarrow \varphi(r)$. It follows that the function possesses the following properties

i) $\varphi(r) \longrightarrow 0$ as $r \longrightarrow +\infty$
ii) $\varphi(r) \longrightarrow \infty$ as $r \longrightarrow -\infty$
iii) $\varphi(r)$ is monotonically non-increasing because,

$$\frac{d\varphi(r)}{dr} = -\int_{\alpha}^{\beta} x\exp(-rx)\psi(x)dx < 0 \tag{2.13a}$$

Thus we have shown that the integral equation has exactly one real root say $r = r_1$, such that $\varphi(r_1) = 1$. We also observe from the definition of $\varphi(r)$ that $\varphi(0) = R_0$, the net reproductive number. So it follows that, $r_1 < 0, = 0, > 0$ according to whether $R_0 < 1, = 1, > 1$.

Next we show that all other roots r_j, $j = 2\ldots$ of the integral equation which appear in complex conjugates are such that $Re(r_j) < r_1$ where $Re(r_j)$ denotes the real part of r_j.

Let $r_j = u + iv$, u,v real, $v > 0$ for some $j \neq 1$. Substituting into the characteristic equation (2.11) and equating real and imaginary parts leads to

$$\int_{\alpha}^{\beta} e^{-ux}cos(vx)\psi(x)dx = 1 \tag{2.13b}$$

and

$$\int_{\alpha}^{\beta} sin(vx)\psi(x)dx = 0 \tag{2.14}$$

If Eq.(2.14) holds for v, it also holds for $-v$, so $\bar{r}_j = u - iv$ is also a root of the characteristic equation. Since $cos(vx) < 1$ then from Eq.(2.13b) we see that $u < r_1$. Hence r_1 is greater than the real parts of any of the complex roots. This is from the comparison of Eq.(2.13b) with Eq.(2.12) or more explicitly with Eq.(2.11). The conclusion here is that if $\alpha < \beta < \infty$ that is a finite fertile interval then there are infinite number of roots to the characteristic equation with only one real root while the rest appear in conjugate pairs of complex roots.

Since the renewal equation (2.8) is linear, it follows that the solutions are linear combinations of the form

$$B(t) = \sum_{j=1}^{\infty} Q_j e^{r_j t}. \tag{2.15}$$

But the real root is dominant so that for large t, $B(t)$ will tend asymptotically towards

$$B(t) = Q_1 e^{r_1 t} \tag{2.16}$$

Before we give detailed interpretation to Eq.(2.16) we consider the solution to Eq.(2.9) by method of Laplace transforms.

2.3.2 Solution by Laplace Transforms

We begin by first defining the Laplace transform of a function $h(t)$ in general

$$L\{h(t)\} = h^*(r) = \int_0^{\infty} e^{-rt}h(t)dt \tag{2.17}$$

while the Laplace transform of the convolution of two functions is given by

$$\begin{aligned} L\{h(t) * f(t)\} &= L\left\{\int_0^t h(t-x)f(x)\,dx\right\} \\ &= h^*(r)f^*(x). \end{aligned} \tag{2.18}$$

Now multiply the renewal equation (2.8) through by e^{-rt} and integrate with respect to t from zero to infinity. This gives

$$B^*(r) = g^*(r) + B^*(r)\psi^*(r) \tag{2.19}$$

where $B^*(r)$, $g^*(r)$ and $\psi^*(r)$ are Laplace transforms of $B(t)$, $g(t)$ and $\psi(x)$ respectively. Thus solving for $B^*(r)$ in Eq.(2.19) gives

$$B^*(r) = \frac{g^*(r)}{1 - \psi^*(r)} \tag{2.20}$$

Now note that,

$$\psi^*(r) = \int_0^\infty e^{-rx}\psi(x)\,dx = \varphi(r) = 1$$

which is precisely the characteristic equation (2.12) whose roots are defined as $r = r_1, r_2, \ldots$. Hence it is possible to write

$$1 - \psi(x) = (r - r_1)(r - r_2)(r - r_3)\ldots \tag{2.21}$$

and if all the roots are assumed to be distinct, a partial fraction expansion of Eq.(2.20) yields

$$B^*(r) = \frac{g^*(r)}{1 - \psi^*(r)} = \frac{Q_1}{r - r_1} + \frac{Q_2}{r - r_2} + \frac{Q_3}{r - r_3} + \ldots \tag{2.22}$$

where Q_j, $j = 1, 2, \ldots$ are real constants. In order to evaluate the numerators in Eq.(2.22) we express Q_j as

$$Q_j = \lim_{r \to r_j} \left\{ \frac{(r - r_j)g^*(r)}{1 - \psi^*(r)} - (r - r_j)\sum_{i \neq j} \frac{Q_i}{r - r_i} \right\} \tag{2.23}$$

The second term above goes to zero, but the first term has to be evaluated by l'Hospital's rule as

$$\begin{aligned} Q_j &= \frac{g^*(r_j)}{-\left.\frac{d\psi^*(r)}{dr}\right|_{r=r_j}} \\ &= \frac{\int_0^\infty e^{-r_j t} g(t)\,dt}{\int_0^\infty x e^{-r_j x}\psi(x)\,dx} \\ &= \frac{\int_0^\beta \exp(-r_j t) g(t)\,dt}{\int_\alpha^\beta x \exp(-r_j x)\psi(x)\,dx}. \end{aligned} \tag{2.24}$$

We change the limits in the last expression in Eq.(2.24) because it is assumed that individuals will start reproducing when they attain age α and stop reproducing at age β; that is the maternity function $m(x) \geq 0$ and it is positive only in the interval $\alpha \leq x \leq \beta$. Finally we make the following observation before inverting $B^*(r)$ to get $B(t)$ namely;

$$L\{Q_j \exp(r_j t)\} = Q_j \int_0^\infty \exp(-rt)\exp(r_j t)dt = \frac{Q_j}{r - r_j}$$

hence,

$$L^{-1}\left\{\frac{Q_j}{r - r_j}\right\} = Q_j \exp(r_j t)$$

It therefore follows from Eq.(2.22) that

$$B(t) = L^{-1}\{B^*(r)\} = L^{-1}\left\{\sum_{j=1}^{\infty} \frac{Q_j}{r - r_j}\right\} = \sum_{j=1}^{\infty} Q_j \exp(r_j t) \qquad (2.25)$$

which is same as what was obtained in Eq.(2.15) but the current derivation is more explicit.

2.3.3 Asymptotic behaviour of the dynamics

Notice that Eq.(2.25) and thus Eq.(2.15) may be written as

$$B(t) = Q_1 \exp(r_1 t)\left\{1 + \sum_{j \neq 1} \frac{Q_j}{Q_1} \exp(r_j - r_1)t\right\}$$

But we recall that $Re(r_j) < r_1, \quad j = 2, 3, \ldots$. Thus

$$\lim_{t \to \infty} \exp\{(r_j - r_1)t\} = 0, \quad j = 2, 3, \ldots$$

which means that

$$B(t) \to Q_1 \exp(r_1 t) \quad \text{as} \quad t \to \infty \qquad (2.26)$$

where Q_1 is obtained from the general formula for Q_j as

$$Q_1 = \frac{\int_0^\beta \exp(-r_1 t) g(t) dt}{\int_\alpha^\beta x \exp(-r_1 t) \psi(x) dx}$$

Now since from Eq.(2.6)

$$E[n(x,t)] = B(t - x)p(x), \quad t > x$$

then the asymptotic behaviour of the expected population density is thus given by

$$E[n(x,t)] \rightarrow Q_1 \exp(r_1 t)[\exp(-r_1 x)p(x)] \quad as\,, t \rightarrow \infty \qquad (2.27)$$

Equation (2.27) above tells us that in the persistent solution the time and the age behaviour separate in the long run. We notice that the persistent age distribution is a product of an exponential component and the survivorship function. Note that r_1 is the leading root of the characteristic equation (2.11) or (2.12). Thus as time elapses the age stucture or distribution grows exponentially at all ages. Recall that if the net reproductive rate $R_0 = 1$ then the dominant root r_1 takes the value zero. We say that the population reaches a state of equilibrium as $t \rightarrow \infty$. In this case therefore the age-structure is proportional to the survivorship function and the total population size remains constant.

If the net reproductive rate $R_0 > 1$ ($R_0 < 1$) then the dominant root is correspondingly $r_1 > 0$ ($r_1 < 0$). This is the case of stable population in the limit as $t \rightarrow \infty$. Relative to the stationary case, here the population age structure has an excess of young(old) individuals, hence the population as a whole increases(decreases) as time passes.

2.4 Continuous Age Structured Models

In this section we seek to derive a partial differential equation describing the evolution of population density $n(x,t)$ with respect to age and time where both age and time are taken as continuous variables. This is supposed to be an extention of the model derived in sections 2.2 and 2.3 where both natural mortatility $\mu(x)$ and fertility $m(x)$ were assumed functions of age but not time.

Again let $n(x,t)$ be the dependent variable denoting the age density at time t. Then $n(x,t)dx$ is the number of individuals aged between x and $x+dx$ at time t or simply individuals in the age interval $[x, x+dx)$. In this section we assume that the mortatility is $\mu(x,t)$ and maternity function $m(x,t)$ are continuous functions of both age and time. Clearly the total population $N(t)$ at time t is therefore given by

$$N(t) = \int_0^\omega n(x,t)dx \qquad (2.28)$$

where ω is the maximum possible age attainable by an individual in the population.

Next we wish to derive the equation of conservation of individuals in the population as time passes. This depends on the fact that in one unit of time, an individual in the population either ages by one unit of age, or else it drops out of the group of individuals under study. It is worth mentioning here that in more complex life cycles it might be more realistic to consider other variables as providing better information on the vital rates other than age. For example in stage structured populations stage specific vital rates might be of more interest than age specific ones. Better still a stage/age structured population model might be more realistic in this particular case. We mention this here because in the current work as earlier mentioned emphasis is placed on stage structured population models which we believe are a generalization of age structured ones. In particular we concentrate on vector populations such as ticks which are agents of animal diseases for example ***R.appendiculatus*** which is an agent for East Coast fever.

We thus define the derivative operator D of the population age density $n(x,t)$ by the expression

$$Dn(x,t) = \lim_{\delta t \to 0} \frac{n(x+\delta t, t+\delta t) - n(x,t)}{\delta t} \tag{2.29}$$

where δt denotes a small increament of time, t such that an individual aged x at time t will be aged $x+\delta t$ at time $t+\delta t$. Now Eq.(2.29) can be written in a more familiar notation as follows: Add and subtract $n(x+\delta t, t)$ on the right hand side and then take limits to obtain

$$\begin{aligned} Dn(x,t) &= \lim_{\delta t \to 0} \frac{n(x+\delta t, t+\delta t) - n(x+\delta t, t) + n(x+\delta t, t) - n(x,t)}{\delta t} \\ &= \lim_{\delta t \to 0} \frac{n(x+\delta t, t+\delta t) - n(x+\delta t, t)}{\delta t} + \lim_{\delta t \to 0} \frac{n(x+\delta t, t) - n(x,t)}{\delta t} \\ &= \frac{\partial n(x,t)}{\partial t} + \frac{\partial n(x,t)}{\partial x} \end{aligned}$$

Now as in Eq.(2.3a) and Eq.(2.3b) we have that

$$\mu(x,t)\delta t = Prob\,\{\text{dying between ages } x \text{ and } x+\delta t \mid \text{survival to age } x \text{ at time t}\} \tag{2.30}$$

The population exposed to risk of dying at age x at time t is $n(x,t)$; thus the number of individuals who die between age x at time t and age $x+\delta t$ at time

$t + \delta t$ is therefore given by

$$n(x,t) - n(x + \delta t, t + \delta t) = \mu(x,t)n(x,t)\delta t \tag{2.31}$$

assuming no births. Hence

$$n(x + \delta t, t + \delta t) = n(x,t) - \mu(x,t)n(x,t)\delta t \tag{2.32}$$

Equation (2.32) states that the number of individuals at time $t + \delta t$ is equal to the number present at time t less the number who die in the time interval $[t, t + \delta t)$. Rearranging Eq.(2.32) then dividing through by δt and taking the limit as $\delta t \rightarrow 0$ yields

$$Dn(x,t) + \mu(x,t)n(x,t) = 0$$

or

$$\frac{\partial n(x,t)}{\partial x} + \frac{\partial n(x,t)}{\partial t} + \mu(x,t)n(x,t) = 0 \tag{2.33}$$

where the operator D was defined in Eq.(2.29). Equation (2.33) is called the - McKendrick-von Foerster equation expressing the population dynamics under the process of aging and mortality. However since individuals age zero (new births) at time t are not accounted for in the equation we introduce this as a boundary condition or the birth law as

$$n(0,t) = \int_0^\infty m(x,t)n(x,t)dx = B(t) \tag{2.34a}$$

and the initial condition as

$$n(x,0) = n_0(x) \tag{2.34b}$$

Most of the time, it is assumed that the time dependence of both $\mu(x,.)$ and the maternity functions are related to the total population size at time t and not to time itself, such that the mortality and fertility functions are now in the form $\mu(x, N(t))$ and $m(x, N(t))$ where $N(t)$ is the total population at time t defined in Eq.(2.28). One can say that the functions depend on age x, time t and the total population $N(t)$.

In this case the analog to equation (2.6) is

$$E[n(x,t)] = \begin{cases} n_0(x-t)\pi(x-t, x, 0), & t < x \\ B(t-x)\pi(0, x, t-x), & t > x \end{cases} \tag{2.35}$$

where the function π is a generalization of the survivorship function defined in Eq.(2.4a). Next we consider the case of discrete time/age population model.

2.5 Discrete Age Structured Models

The requirements to the derivation of this model are the age specific vital rates obtainable from life table data. The life table in a sense deals only with death, as individuals in a cohort advance in age but in a broader manner it can be taken to include the maternity function, $m(x)$ to handle new entrants through reproduction. If the life table is not available then information on vital rates has to be estimated through census data or through a hypothetical functional relation between these rates and age as time passes.

2.5.1 The Survivorship Function

In this section we wish to explicitly show the relationship between the survival function $p(x)$ and the force of mortality $\mu(x)$ defined in Eq.(2.2a)-Eq.(2.3b). From the equation

$$F(x) = 1 - p(x)$$

it follows that

$$p'(x) = -F'(x) \tag{2.36}$$

where $F(x)$ is as defined in Eq.(2.2c). Then making the substitution of Eq.(2.36) in Eq.(2.3c) we get

$$\mu(x) = \frac{-p'(x)}{p(x)} \tag{2.37}$$

keeping in mind that

$$f(x) = F'(x) = -p'(x).$$

Thus

$$\mu(x) = -\frac{d}{dx} \ln p(x) \tag{2.38}$$

assuming $p(x)$ is a function of x alone otherwise we would replace the right hand side with its partial derivative analog. Solving equation (2.38) we obtain

$$p(x) = \exp\left[- \int_0^x \mu(\tau) d\tau\right] \tag{2.39}$$

Therefore,

$$Prob\{\text{an individual survives to age } x+\delta x \mid \text{survival upto age } x\}$$

$$\begin{aligned} &= \frac{p(x+\delta x)}{p(x)} \\ &= \exp\left[-\int_{x}^{x+\delta x} \mu(\tau)d\tau\right] \end{aligned} \tag{2.40}$$

and if we assume $\mu(x) = \mu$ in the age interval $[x, x+\delta x)$ then Eq.(2.39) becomes

$$P\,rob\{\text{an individual survives to age } x+\delta x \mid \text{survival to age x}\}$$

$$= e^{-\mu\delta x} \tag{2.41}$$

Thus equation (2.6) therefore becomes

$$E[n(x,t)] = \begin{cases} n_0(x-t)\exp[-\int_{x-t}^{x}\mu(\tau)d\tau], & t < x \\ B(t-x)\exp[-\int_0^x \mu(\tau)d\tau)], & t > x \end{cases} \tag{2.42}$$

If we have evidence that the vital rates are both age and time dependent then $\mu(.)$ is replaced by the appropriate function. From Eq.(2.39) it implies that we can write the characteristic equation in Eq.(2.11) as

$$1 = \int_{\alpha}^{\beta} \epsilon^{-rx}\exp\left[-\int_0^x \mu(\tau)d\tau\right] m(x)dx \tag{2.43a}$$

which was shown to posses exactly one(simple) real root $r = r_1$, and any other root is necessarily complex. We remark that the kernel of this characteristic equation is given by

$$k(x) = m(x)e^{-\int_0^x \mu(\tau)\,d\tau} \tag{2.43b}$$

therefore equation (2.43a) can be written more elegantly as

$$1 = \int_{\alpha}^{\beta} k(x)e^{-rx}\,dx. \tag{2.43c}$$

Thus if $l(x)$ is the continuos age life table function and the initial value is $l(0)$ then

$$l(x) = l(0)\exp\left[-\int_0^x \mu(\tau)d\tau\right]$$

where $l(x)$ was defined earlier on. The function $\mu(x)$ could be interpreted as the "instantaneous" death rate or force of mortality or the limiting value of the death rate when the age interval becomes very small.

Next we wish to formulate the discrete time matrix population model.

2.5.2 Formulation of the Matrix Model

A discrete version of the Lotka-Sharpe-McKendrick model was presented by Leslie(1945) which was also independently developed earlier by Lewis(1942). Consider a population of size $N(t)$ at time t that is closed to migration, and whose every individual is capable of reproducing. Let the population be composed of s distinct age classes of equal width say h, such that age class i corresponds to the interval $(i-1)h \leq x \leq ih$. The number h is defined appropriately depending on the maximum age, ω, which an individual may possibly attain or on the life cycle of the population. Let

$n_i(t)$ denote the number of individuals alive in age class i at time t

$p_{ij}(t)$ denote the probability that an individual in age class j at time t will transit to age class i at time $(t+1)$ or after one time interval, $i, j = 1, \dots, s$

$f_{1j}(t)$ denote the reproduction rate for an individual in age class j in the time interval t to $t+1$ (the offsprings who survive the interval join age class 1 at time t), $j = 1, \dots, s$

For simplicity we denote p_{ij} by $p_j(t)$ and $f_{1j}(t)$ by $f_j(t)$, $j = 1, \dots, s$. Assuming the width of a time interval equals h, the width of one age interval, then

$$n_i(t+1) = p_{i-1}(t)n_{i-1}, \quad i = 2, \dots, s \tag{2.44a}$$

and

$$n_1(t+1) = \sum_{i=1}^{s} f_i(t)n_i(t) \tag{2.44b}$$

In a population where individuals can be classified into male or female then a sex ratio $p : 1-p$ of *male:female* say, can be used to determine the number of each sex in each age class. If we let

$$\vec{n}(t) = \left(n_1(t), \dots, n_s(t)\right)'$$

denote the population distribution at time t, or a vector of dimension s by 1 whose i-th component is the number of individuals alive in age class i at time t. The s equations in Eq.(2.44a) and Eq.(2.44b) can be written compactly more in matrix notation as

$$\vec{n}(t+1) = M(t)\vec{n}(t) \tag{2.45}$$

where $M(t)$ is given by

$$M(t) = \begin{pmatrix} f_1(t) & f_2(t) & f_3(t) & \dots & f_{s-1} & f_s(t) \\ p_1(t) & 0 & 0 & \dots & 0 & 0 \\ 0 & p_2(t) & 0 & \dots & 0 & 0 \\ \vdots & \vdots & \vdots & \dots & \vdots & \vdots \\ 0 & 0 & 0 & \dots & p_{s-1}(t) & 0 \end{pmatrix} \tag{2.46}$$

Obviously $M(t)$ is square matrix of dimension s and $f_i(t) \geq 0$ because not all age classes are capable of reproducing. It is also clear that $0 < p_i(t) < 1, \quad i = 1, \dots, s-1$. Now equation (2.45) can be used recursively to generate the population distribution T time periods later as

$$n(t+T) = \left[\prod_{h=0}^{T-1} M(t+h)\right] n(t) \tag{2.47}$$

where the matrix product in the square brackets is explicitly written as

$$M(t+T-1)M(t+T-2)\dots\dots M(t+1)M(t) \qquad (2.48).$$

Given the matrix elements are time invariant then equation (2.47) becomes

$$\vec{n}(t+T) = M^T \vec{n}(t) \tag{2.49}$$

assuming M and $\vec{n}(t)$ are given. The main statistical problem in both the time dependent and time independent population systems is in the estimation of the matrix entries. This problem will be addressed in detail in later chapters. In the the current section our interest is to show the relationship between the continuous age and/or time models derived in sections 2.3 and 2.4 and the current model. The analysis of the homogeneous or time independent matrix model will be dealt with at length in chapter III.

Now consider the aging equation in Eq.(2.44a) where the survival probability, $p_{i-1}(t)$ is a function of both age and time. Now define

$$\delta n_i = n_i(t+1) - n_i(t)$$

that is

$$\delta n_i = p_{i-1} n_{i-1}(t) - n_i(t) \tag{2.50}$$

If we consider an infinitesmal value of h or time step then from the definition of the force of mortality, we can write $p_{i-1}(t)$ as

$$p_{i-1}(t) \approx 1 - \mu(i-1,t)$$

then substituting in Eq.(2.50) we obtain

$$\delta n_i = [1 - \mu(i-1,t)] n_{i-1}(t) - n_i(t)$$

and by rearrangement of terms we finally obtain the expression

$$\delta n_i + [n_i(t) - n_{i-1}(t)] = -\mu(i-1,t) n_{i-1}(t) \tag{2.51}$$

When we examine Eq.(2.51) we see that the first term on the L.H.S is change in numbers with respect to time while the second term in square brackets denotes the change in $n_i(t)$ with respect to age. Hence we can rewrite the above expression as

$$\frac{\delta n_i}{\delta t} + \frac{\delta n_i}{\delta x} = -\mu(i-1,t) n_{i-1}(t) \tag{2.52}$$

and letting $\delta t \rightarrow 0$ and $\delta x \rightarrow 0$ yields the time continuous population growth equation in Eq.(2.33), the McKendrick-von Foerster equation, showing the process of aging and mortality where age and time are both continuous variables.

It is important to understand the relationship between the continuous and discrete time population models because they often go hand in hand or supplement each other when developing other related models such as disease transmission or epideomological models. Thus it is important to have a sound population model before we could think of formulating a disease transmission model. For example to build a model for a vector transmitted disease model it is obviously important to have a sound model for the vector population and possibly for the host population. In chapter IV we derive a vector-host interaction compartmental model foı the brown ear tick or *R. appendiculatus* a vector for *Theileriosis* a disease for cattle in most parts of Africa.

Now the type of population under investigation in terms of its birth pattern is very important especially in the parametrization of the matrix elements. We now consider two types of populations according to their birth patterns namely birth flow and birth-pulse populaions and how to estimate the matrix elements for such types of populations.

2.6 Life Table Parametrization of the Matrix Model

The aim in this section is to find expressions for the matrix parameters f_i and p_i from the life table survival function $l(x)$ assumed to be continuous with respect to the age variable x.

2.6.1 Birth Flow Populations

Given an individual is in age class i at time t then such an individual will definitely enter age class $i+1$ at time $t+1$ if it survives that time interval. This is so if we assume that the projection interval $[t, t+1)$ is equal to the width of one age class. Let the i-th age class include all individuals with ages in the interval $i-1 \leq x < i$ and assume that $l(x)$ and $p(x)$ are defined as in Eq.(2.4a), as continuous functions of x.

Then since by definition $p(x) = l(x)/l(0)$ it follows that an estimate of p_i the probability that an individual in age class i, $(\{\text{ages}\, x : i-1 \leq x < i\})$, survives to age class $i+1$, $(\{\text{ages}\, x : i \leq x < i+1\})$ will be estimated by

$$\hat{p}_i = \frac{l(i) + l(i+1)}{l(i-1) + l(i)} \tag{2.53a}$$

which on dividing the numerator and denominator of the right hand side by $l(0)$ yields

$$\hat{p}_i = \frac{p(i) + p(i+1)}{p(i-1) + p(i)} \tag{2.53b}$$

Another alternative method is to calculate the probability of survival for each age

x then average over the entire age interval. This method gives

$$p_i = \int_{i-1}^{i} \frac{l(x+1)}{l(x)}dx$$
$$= \int_{i-1}^{i} \frac{p(x+1)}{p(x)}dx$$

which is discretely approximated by

$$\hat{p}_i = \frac{1}{2}\Big(\frac{p(i)}{p(i-1)} + \frac{p(i+1)}{p(i)}\Big) \qquad (2.54).$$

Formulae such as in Eq.(2.53a), Eq.(2.53b) and Eq.(2.54) are important because often values of the function $p(x)$ are only available at discrete points. $0, 1, 2, \ldots, i-1, i, i+1, \ldots,$. More alternative methods of estimation of the matrix elements are going to be considered in detail in chapter III where the life table need not be a pre-requisite.

Now to be able to estimate the $f_i^{\prime}s$ consider equation (2.44b) which states

$$n_1(t+1) = \sum_{i=1}^{s} f_i n_i(t).$$

We wish to find an estimate for f_i, $i = 1, \ldots, s$ from the maternity function $m(x)$ and the survivorship function $l(x)$.

Let $B(t, t+1)$ denote the total number of births recorded in the time interval $(t, t+1)$ and $n(x, t)$ possess the same meaning as before, then

$$B(t, t+1) = \int_{0}^{\infty}\int_{t}^{t+1} m(x)n(x, u)du dx \qquad (2.55).$$

Assuming $n(x, t)$ is known only at times t and $t+1$ then $B(t, t+1)$ can be expressed as

$$B(t, t+1) = \int_{0}^{\infty} m(x)\Big(\frac{n(x, t) + n(x, t+1)}{2}\Big)dx \qquad (2.56).$$

Now suppose that within an age interval $\{x : i-1 \leq x < i\}$; the functions $m(x)$ and $n(x, t)$ are fixed at m_i and $n_i(t)$ respectively then

$$B(t, t+1) = \frac{1}{2}\sum_{i=1}^{\infty} m_i\big(n_i(t) + n_i(t+1)\big) \qquad (2.57)$$

Now recall that

$$n_i(t+1) = p_{i-1}n_{i-1} \qquad i \geq 2$$

then it follows

$$\begin{aligned} B(t,t+1) &\approx \frac{1}{2}\Big\{\sum_{i=1}^{\infty} m_i(n_i(t) + p_{i-1}n_{i-1}(t))\Big\} \\ &= \frac{1}{2}\Big\{m_1n_1(t) + m_2(n_2(t) + p_1n_1(t)) + m_3(m_3(t) + p_2(t)) + \ldots\Big\} \\ &= \frac{1}{2}\Big\{\sum_{i=1}^{\infty}(m_i + p_im_{i+1})n_i(t)\Big\} \qquad (2.58) \end{aligned}$$

and by comparison of Eq.(2.58) with Eq.(2.44b) it follows that an estimate of the fecundity rate f_i is given by

$$\hat{f}_i = 1/2(m_i + p_im_{i+1}) \qquad (2.59)$$

However $B(t, t+1)$ is not quite the same as $n_1(t+1)$ because some of the members in $B(t, t+1)$ might not survive to time $t+1$. Individuals born just after time t are exposed to risk of mortality for a whole projection interval in order to be included in $n_1(t+1)$ while those born just before time $t+1$ are exposed to risk of mortality for only a negligible amount of time, and therefore have a high chance of being included in in $n_1(t+1)$. We therefore need to multiply the R.H.S. of Eq.(2.59) by $p(0.5h)$, the probability of an individual surviving to age $x = 0.5h$ from birth assuming deaths are uniformly distributed over the rate interval $[0, h)$. In case $p(x)$ is only available for integral values of x; $0, 1, \ldots,$ then $p(0.5h)$ can be estimated by method of interpolation between the values $p(0)$ and $p(h)$.

The intuitive meaning of Eq.(2.59) is that a typical individual in age class i produces offsprings at a rate that is the average of the rate for that age class and the next age class, the latter weighted by the appropriate survival probability. The offspring has to on average survive for one- half time unit for it to be counted in the population at time $t+1$. An alternative interpretation being that an individual aged $i - \frac{1}{2}$ spends half of the time interval producing offsprings at rate m_i and if it survives, enters the next age class and produces offsprings at the rate m_{i+1} for the rest of the time interval.

2.6.2 Birth-Pulse Populations

In this type of population, the functions $m(x)$ and $p(x)$ are discontinous. The age distribution at census time and formulae for p_i and f_i depend on when the pulse of breeding occurs relative to the census time. If θ $(0 < \theta < 1)$ denotes the fraction of a time interval that elapses between the pulse of reproduction and census, then at actual observation time, those who were age x will be age $x + \theta$ and therefore the age distribution at census time which we denote by $\vec{n}_{census}$ is give by

$$\vec{n}_{census} = (\theta, 1 + \theta, \ldots, i - 1 + \theta, i + \theta, \ldots, a_{max})'$$

where a_{max} denotes the maximum possible age an individual can attain. Remember we had defined individuals of age class i to be all those individuals aged x such that $\{(i - 1) \leq x < i\}$ hence these individuals are at census time assigned age $i - 1 + \theta$.

Now either $\theta \to 1$ corresponding to a pre-breeding census or $\theta \to 0$ corresponding to a post-breeding census. Thus

$$\begin{aligned} p_i &= Prob\{\text{individual transists to class } i + 1 \text{ at } t + 1 \mid \text{survived to class } i \text{ at } t\} \\ &= Prob\{\text{survival to age } i + \theta \mid \text{survival to age } i - 1 + \theta\} \\ &= \frac{p(i + \theta)}{p(i - 1 + \theta)} \end{aligned} \tag{2.60}$$

since by assumption individuals in age class i at reproduction time are assigned age $i - 1 + \theta$ at census time. To derive birth-pulse fertilities we require $f_i's$ satisfying equation (2.44b) with the understanding that all births within the time interval (t,t+1) occur at time $t + 1 - \theta$, thus we can write

$$B(t, t + 1) = B(t + 1 - \theta)$$

and

$$B(t + 1 - \theta) = \sum_{i=1}^{\omega} n_i(t) m_i \phi_i \tag{2.61}$$

where

m_i=the reproductive output of an individual of age class i upon reaching the i-th birth day(the individual is aged $i - 1 + \theta$ at census time)

ϕ_i=the probability of survival from age $i - 1 + \theta$ to age i.

Such individuals have to survive a fraction $1 - \theta$ of a time interval in order to reproduce; hence

$$\hat{\phi}_i \approx p_i^{1-\theta} \tag{2.62}$$

because these individuals have to survive a remaining fraction, $1-\theta$ of an age class. Detailed information on seasonal mortality rate within the unit time interval (say a year, week, day etcetera depending on the population species) can be useful. Now once reproduction has occured, the offspring must survive a fraction, θ, of time unit for it to be counted in $n_1(t+1)$. The probability of such an event is given by $p(\theta)$ according to the definition of the survival function $p(x)$ for continuous age variable x. If $p(\theta)$ cannot directly be obtained, then it can be estimated by interpolation between available values at inegral values of $p(x)$ namely $p(0)$ and $p(1)$. Thus substituting Eq.(2.62) into Eq.(2.61) we deduce that,

$$f_i = p(\theta)p_i^{1-\theta}m_i \tag{2.63}$$

and depending on whether dealing with a pre-breeding ($\theta \rightarrow 1$) or post-breeding ($\theta \rightarrow 0$) census;

$$f_i = \begin{cases} p_i m_i, & \theta \rightarrow 0 \\ p(1)m_i, & \theta \rightarrow 1 \end{cases} \tag{2.64}$$

To illustrate the difference between birth flow and birth-pulse populations we consider a mortality or life table for the larval stage for *R. appendiculatus*

SOURCE: From paper by Newson et al (1984); International Journal for Parasitology Vol.14 No.5 483-489

Table 1: Life Table Data For *R.Appendiculatus* Larvae

Age(x)	4	5	6	7	8	9
p(x)	1.000	0.724	0.505	0.091	0.028	0.000

Now using Eq.(2.53) the formula for p_i for birth-flow population and Eq.(2.60) for a birth pulse population gives p_i values for $i = 5, 6, 7, 8, 9$. We take a one month age and time interval. Results are tabulated in table below

Table 2: Age Specific Survival Probabilities for Two Reproduction Patterns.

	Birth Flow	Birth Pulse	Birth Pulse
i	p_i	$p_i(\theta \to 0)$	$p_i(\theta \to 1)$
5	0.713	0.724	0.698
6	0.485	0.698	0.180
7	0.200	0.180	0.308
8	0.235	0.308	0.000
9	0.000	0.000	-

Notice that in the pre-breeding census $(\theta \to 1), p_8 = 0$ because in the $9th$ age class, at the time of census individuals would be beginning to attain their $9th$ birth day but the mortality table indicates that none of them survive to do so. If considered as a post-breeding census $(\theta \to 0), p_8 > 0$ because individuals in the $9th$ age class have just attained their $8th$ birthday.

The table tells us that if such data was available for the complete life cycle for the species then the transition matrix could completely be parametrized. The $f_i's$ are calculated from the $m(x)$ functions using formulae (2.64).

To wind up this chapter we refer to the matrix equations (2.47) and (2.49) for the time dependent and time independent matrix elements. The fact that we can project forward the number of individuals in each age class, is an advantage of the matrix model over the continuous age/time population models in sections 2.2 to 2.4. We can follow the dynamics of the various age classes separately. Another advantage with the model is that other modes of classifications such as size, stage etcetera can be treated in a similar manner as the age classification and useful conclusions about the population dynamics derived. The other advantage with the discrete time/age matrix model, especially in the present computer age is that it can easily be computerized hence allowing simulations to be carried out on population dynamics to compare with observed information.

Finally it is seen from table 2 that the type of birth pattern of a population is crucial in the estimation of the matrix elements. It is clear that a wrong classification of the population greatly affects the estimates.

CHAPTER III

TIME HOMOGENEOUS MATRIX MODELS

3.1 Introduction

In this chapter we consider the analysis of the case when the elements of the population projection matrix $(m_{ij}(t))$ in Eq.(2.46) of chapter 2 are time independent or time invariant. This means that the fertility and mortality rates (vital rates) are constant over time. However in real life situations this is not exactly true for any given population species. The rates are bound to vary with time due to the influence of several factors such as environmental factors which in turn change with time. However the validity of time homogeneous models to study population dynamics lies in the distinction between forecasting future population structure and projecting the structure given the set of prevailing current conditions. The categorisation criteria depend on the population species and biology in question. For example when studying human populations, classification according to age is more appropriate. When dealing with tree populations size classification may be more appropriate than age classification while if it is an insect/arthropod and sometimes plant populations classification according to developmental stages is naturally the most suitable. A more complex mode of classification is that involving a combination of more than one classification attributes say age and stage of development. We shall attempt to present a more general mode of classification. In order to do this we will refer to the various classes in which an individual in the population may belong at time t as simply states or stages.

It will be shown that as $t \to \infty$ the population structure $\vec{n}(t)$ becomes proportional to the stable population structure. The concept of strong and weak ergodicity is brought out clearly. Finally we discuss the problem of estimating the matrix elements under various assumptions that of time homogeneity being one of them.

3.2 The Model

Consider a population composed of s age classes $1, \ldots, s$. If the width of a typical age class is h, then the i-th age class is composed of all those individuals or organisms with age x in the interval $(i-1)h \leq x < i\,h$. We also consider time scale in units of length h such that in real sense a time interval $(t, t+1)$ means the interval $[t, t+h)$. Let the time independent(invariant) fertility and survival rates for individuals in the i-th age class be f_i and p_i respectively for $i = 1, \ldots, s$. Then the population disribution vector at time t is given by

$$\vec{n}_t = (n_1(t), \ldots, n_s(t))' \tag{3.1}$$

where $n_i(t)$ denotes the number of individuals in age class i. It is important to note that $f_i \geq 0$ and $0 < p_i \leq 1$. That is an individual is either fertile or not fertile at all $(f_i = 0)$ and if the individual survives the interval $[t, t+1)$ then it has to transit to the next age class. From these definitions it is clear that the number entering the lowest age class(offsprings) is given by

$$n_1(t+1) = \sum_{i=1}^{s} n_i(t) f_i. \tag{3.2}$$

and $n_i(t+1)$ is given by

$$n_i(t+1) = p_{i-1} n_{i-1}(t), \quad i = 2, \ldots, s. \tag{3.3}$$

Equations (3.2) and (3.3) can be written in matrix notation as

$$\vec{n}(t+1) = M \vec{n}(t) \tag{3.4}$$

where the elements of the matrix M are given by

$$m_{ij} = \begin{cases} f_j, & i = 1 \quad j = 1, \ldots, s \\ p_j, & j = i-1, \quad i = 2, \ldots, s \\ 0, & \text{elsewhere} \end{cases} \tag{3.5}$$

The matrix M above is referred to as the complete time homogeneous population projection matrix. It is called complete because it caters for the entire population. It has elements (non-zero) in the leading subdiagonal and in the first row. It is square of dimension s and it is a non-negative matrix meaning $m_{ij} \geq 0$ for all (i, j). It is also worth noting at this point that given $\vec{n}(t)$, then the distribution or structure after τ time periods is given by

$$\vec{n}(t+\tau) = M^{\tau} \vec{n}(t) \tag{3.6}$$

If we set $t = 0$ then the above equation becomes

$$\vec{n}(\tau) = M^{\tau}\vec{n}(0), \quad \tau = 1, 2, \ldots,$$

which shows that if we start observing the population at time zero then, the structure at time t is

$$\vec{n}(t) = M^{t}\vec{n}(0) \tag{3.7}$$

The column vector $\vec{n}(0)$ is known as the initial population vector. We stress here that the structure of the the matrix M depends on the population species under investigation and other examples will be considered later. However there is no loss of generality in sticking to age classification.

It is not really necessary to deal with the complete population projection matrix, because if the fertility rates are such that; $f_j \geq 0, \quad i = 1, \ldots, k-1; f_k > 0$ and $f_j = 0$ for $j = k+1, k+2, \ldots, s$ then the matrix M can be partioned as follows

$$M = \begin{pmatrix} A & O \\ B & C \end{pmatrix} \tag{3.8}$$

where the elements of the matrix A are

$$a_{ij} = \begin{cases} f_j, & i = 1, j = 1, \ldots, k \\ p_j, & j = i-1, i = 2, \ldots, k \\ 0, & \text{elsewhere} \end{cases} \tag{3.8b}$$

This means that the set of age classes can be partioned into pre-reproductive and reproductive age classes which is the set $S_1 = \{1, \ldots, k\}$ and post reproductive age classes which is the set $S_2 = \{k+1, \ldots, s\}$ with $|S_1| = k$ and $|S_2| = s - k$, where $|S|$ denotes cardinality of the set S. Another observation as a result of this partitioning is that

$$Det\, M = 0\left(\prod_{i=1}^{s-1} p_i\right) = 0$$

hence M is singular. The most important conclusion out of the above partitioning of the age classes is that the matrix M can now be partitioned symmetrically as

$$M = \begin{pmatrix} A & O \\ B & C \end{pmatrix} \tag{3.9}$$

where

A is kxk with its only non-zero terms in the first row and along the main sub-diagonal

B is $(s-k)$xk with all its elements zero except in the upper right corner

C is $(s-k)$x$(s-k)$ with its only non-zero terms in the upper right corner

and

O is kx$(s-k)$ matrix of zeroes.

In the same manner we can write the population distribution vector as

$$\vec{n}(t) = \begin{pmatrix} \vec{n}_1(t) \\ \vec{n}_2(t) \end{pmatrix} \tag{3.10}$$

where

$$\vec{n}_1(t) = (n_1(t), \ldots, n_k(t))'$$

and

$$\vec{n}_2(t) = (n_{k+1}(t), \ldots, n_s(t))'.$$

By repeated multiplication we can show that

$$M^t = \begin{pmatrix} A^t & O \\ B_{(t)} & C^t \end{pmatrix} \tag{3.11a}$$

where

$$B_{(t)} = \sum_{i=0}^{t-1} C^i \, B \, A^{t-i-1}, \quad t = 1, 2, \ldots \tag{3.11b}$$

Therefore given $\vec{n}(0)$,

$$\vec{n}(t) = \begin{pmatrix} \vec{n}_1(t) \\ \vec{n}_2(t) \end{pmatrix} = \begin{pmatrix} A^t & O \\ B_{(t)} & C^t \end{pmatrix} \begin{pmatrix} \vec{n}_1(0) \\ \vec{n}_2(0) \end{pmatrix} \tag{3.12}$$

which implies that,

$$\vec{n}_1(t) = A^t \vec{n}_1(0) \tag{3.13a}$$

and

$$\vec{n}_2(t) = B_{(t)} \vec{n}_1(0) + C^t \vec{n}_2(0) \tag{3.13b}$$

We notice that from Eqs.(3.13a,b) the components of $\vec{n}_1(t)$ are independent of $\vec{n}_2(0)$ while those of $\vec{n}_2(t)$ are dependent on $\vec{n}_1(0)$. This simply means that the population in the reproductive phase does not depend on the population past the reproductive phase. The converse is obviously not true. Infact intuitively $C^{s-k} = O$ so that M^t, $t \geq s-k$ has all its last $s-k$ columns equal to $\vec{0}$. This is because once an individual enters the post reproductive phase of the system it is already of age $\geq k$ units and the maximum possible attainable age is s thus it follows that this individual will remain in the system for at most $s-k$ units of age hence the result.

What this means is that once the system has been in operation for s units of time the effect of the post-reproductive sub-cohort of individuals is immaterial and can therefore be forgotten as far as system renewal is concerned. The matrix A remains the only one which is principally of interest because it involves the set S_1 of the pre-reproductive and reproductive age classes. The matrix A can explicitly be written as

$$A = \begin{pmatrix} f_1 & f_2 & f_3 & \cdots & f_{k-1} & f_k \\ p_1 & 0 & 0 & \ldots & 0 & 0 \\ 0 & p_2 & 0 & \ldots & 0 & 0 \\ 0 & 0 & p_3 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ldots & \vdots & \vdots \\ 0 & 0 & 0 & \ldots & p_{k-1} & 0 \end{pmatrix} \tag{3.14a}$$

such that

$$\begin{aligned} Det\, A &= (-1)^{k+1} p_1 p_2 \cdots p_{k-1} f_k \\ &= (-1)^{k+1} \left(\prod_{i=1}^{k-1} p_i \right) f_k, \quad p_i > 0 \, \forall i. \end{aligned} \tag{3.14b}$$

Therefore as opposed to matrix M, A is non-singular hence it possesses an inverse. Thus given an initial age distribution vector $\vec{n}(0)$, we can in addition to the forward series $\{A^t \vec{n}(0)\}$, also consider the backward series namely $\{A^{-t} \vec{n}(0)\}$, $t = 1, 2, \ldots$. In practice the latter does not find much use hence our attention will be focussed more on the forward series as time elapses. The matrix A will in the sequel be referred to as the population projection matrix.

It is very much dependent on the population species and the classification criteria used. For example considering a tree species with k size classes, then an individual in size class i at time t may by time $t+1$ have moved to the next class, $i+1$, remained in the same class or died. Let p_i, π_i and $1 - p_i - \pi_i$ denote the probabilities of the above events. Then for such population species the matrix A is given by

$$(a_{ij}) = \begin{cases} \pi_1 + f_1, & \text{for } i = j = 1 \\ f_j, & i = 1 \quad j = 2, \dots, k \\ \pi_i, & i = j = 2, \dots, k \\ p_j, & j = i - 1 \quad i = 2, \dots, k \end{cases} \tag{3.15a}$$

where f_i denotes the reproduction rate for the *ith* size class. In full the matrix A is given by

$$A = \begin{pmatrix} \pi_1 + f_1 & f_2 & f_3 & \dots & f_{k-1} & f_k \\ p_1 & \pi_2 & 0 & \dots & 0 & 0 \\ 0 & p_2 & \pi_3 & \dots & 0 & 0 \\ 0 & 0 & p_3 & \ddots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \dots & p_{k-1} & \pi_k \end{pmatrix} \tag{3.15b}$$

Such kind of classification is or would be appropriate for a population model meant for the management of renewable resources such as forests. The aim would be to develop a sustainable harvesting strategy or policy. The question of appropriate classification will be revisited in section 3.4 for a general stage structured population such as insect or arthropod populations.

In order to understand and analyse the time homogeneous model fully we study some of the relevant definitions and theorems in matrix algebra in the next section.

3.3 Properties of the Population Projection Matrix

From the discussion in the preceeding sections it is clear that both the complete population projection matrix, M, and the population projection matrix A, are non-negative that is $m_{ij} \geq 0$ and $a_{ij} \geq 0$. The matrix is said to be positive if its elements are strictly positive. Negative elements for M and A are not feasible because this would suggest a possibility of a negative number of individuals in a stage which is in practice not realistic. The matrices are square and the dimensions will depend on the number of age classes, hence the smaller the size of an age class the higher the dimension and vice versa. An interesting subclass of square non- negative matrices is that of stochastic matrices which have either all row or all column sums equal to unity, and which have an important role in the study of Markov chains. It is possible to break down the population projection matrix into a stochastic matrix which gives the transition probabilities and a second matrix that gives the reproductive data for all the classes. We next present a series of important definitons, theorems and corollaries on nonnegative matrices as in Horn and Johnson(1985). However the structure of the projection matrix in the present study requires certain modifications in the proofs of some of the theorems , to bring them into context. Thus we briefly present some of the proofs and definitions. Their importance comes in when we present several properties of the population projection matrix in the sequel.

Definition 1: An nxn matrix P is called a permutation matrix if exactly one entry in each row and column is equal to 1, and all other entries are 0. Multiplication by such a matrix effects a permutation of rows or columns of the matrix multiplied.

The simplest example of a permutation matrix P has $p_{ij} = p_{ji} = 1$ for some fixed i, j and has all other nondiagonal entries 0. In general, left multiplication of an mxn matrix, A by an mxm permutation matrix P, permutes the rows of A, while right multiplication of A by an nxn matrix P permutes the columns of A. The determinant of a permutation matrix is $\pm$ which implies that permutation matrices are necessarily nonsingular. Although permutation matrices do not, in general commute under multiplication, the product of two permutation matrices is again a permutation matrix. Since the identity is a permutation matrix and $P^T = P^{-1}$ for every permutation matrix P, it follows the permutation matrices constitute a subgroup of the group of nonsingular matrices. Further, from the definition of a permutation matrix, it follows that such a matrix is unitary, hence orthogonal($P^T = P^{-1}$). Since $P^T = P^{-1}$ permutes columns in the same way that the nxn permutation matrix P permutes rows, the transformation $A \rightarrow PAP^T$ permutes the rows and columns of an nxn matrix A in the same way. Thus, if P is a permutation matrix, the similarity PAP^T is obtained from A by a suitable permutation of rows and colmns of A.

Definition 2: A matrix $A = (a_{ij})$ is said to have the *property* SC(strong connected) if for every pair of distinct integers p, q with $1 \leq p, q \leq n$ there is a sequence of distinct integers $k_1 = p, k_2, k_3, \ldots, k_{m-1}, k_m = q$, $1 \leq m \leq n$, such that all of the matrix entries $a_{k_1k_2}, a_{k_2k_3}, \ldots, a_{k_{m-1}k_m}$ are non zero.

Definition 3: If $A = (a_{ij}) \in M_{m,n}$ (the set of m-by- n complex matrices) we set $|A| = (|a_{ij}|)$ and $M(A) = (\mu_{ij})$, where $\mu_{ij} = 1$ if $a_{ij} \neq 0$ and $\mu_{ij} = 0$ if $a_{ij} = 0$. The matrix $M(A)$ is called the indicator or incidence matrix of A.

Definition 4: The directed graph of $A \in M_n$ (the set of n-by-n square matrices), denoted by $\Gamma(A)$, is the directed graph on nodes $P_1, P_2, \ldots, P_n$ such that there is a directed arc in $\Gamma(A)$ from P_i to P_j if and only if $a_{ij} \neq 0(\mu_{ij} \neq 0)$

Definition 5: A directed path γ in a graph Γ is a sequence of arcs $P_{i_1}P_{i_2}, P_{i_2}P_{i_3}$,-$P_{i_3}P_{i_4}, \ldots$ in Γ. The ordered list of nodes in the directed path γ is $P_{i_1}, P_{i_2}, \ldots$. The *length* of a directed path is the number of successive arcs in the directed path if the number is finite; otherwise, the directed path is said to have infinite length. A *cycle* is a directed path that begins and ends at the same node; this node occurs exactly twice in the ordered list of nodes in the path, and no other node occurs more than once in the list. A cycle of length one is called a loop.

Definition 6: A directed graph Γ is strongly connected if between every pair of distinct nodes P_i, P_j in Γ there is a directed path of finite length that begins at P_i and ends at P_j.

Theorem 3.1: Let $A \in M_n$. Then A has the property SC if and only if the directed graph $\Gamma(A)$ is strongly connected.

As a remark let Γ be a directed graph on n nodes. If there is a directed path in Γ between two nodes , then between these nodes there is a directed path that has length not more than $n-1$. The question is how one can tell if a given matrix A has property SC. This amounts to checking whether $\Gamma(A)$ is strongly connected. If n is not large or if $M(A)$ has a special structure, then one can just inspect $\Gamma(A)$ and trace out paths between all pairs of nodes. However, this is not practical in general, thus we need some computational method.

Theorem 3.2: Let $A \in M_n$ be given, and let P_i and P_j be given nodes in $\Gamma(A)$. There exists a directed path of length m in $\Gamma(A)$ between P_i and P_j if and only if $(|A|^m)_{ij} \neq 0$, or equivalently, if $[M(A)^m]_{ij} \neq 0$.

Proof: We proceed by induction. For $m = 1$ the assertion is trivial. For $m = 2$ we compute

$$\begin{aligned}(|A|^2)_{ij} &= \sum_{k=1}^{n} [|A|]_{ik}[|A|]_{kj} \\ &= \sum_{k=1}^{n} |a_{ik}|\,|a_{kj}|\end{aligned} \tag{3.16a}$$

so that $[|A|^2]_{ij} \neq 0$ if and only if for at least one value of k, a_{ik} and a_{kj} are both nonzero. But this is the case if and only if there exists a path of length 2 in $\Gamma(A)$ from P_i and P_j. Assume the assertion is true for $m = q$. Then

$$\begin{aligned}[|A|^{q+1}]_{ij} &= \sum_{k=1}^{n} [|A|^q]_{ik}[|A|]_{kj} \\ &= \sum_{k=1}^{n} [|A|^q]_{ik}|a_{kj}| \neq 0\end{aligned} \tag{3.16b}$$

if and only if for at least one value of k, $[|A|^q]_{ik}$ and a_{kj} are both nonzero. This is equivalent to having a path from P_i to P_k of length q and from P_k to P_j of length 1, and this is the case if and only if there is a path from P_i to P_j of length $q + 1$. The same argument works for $M(A)$.

Definition 7: Let $A = (a_{ij}) \in M_n$. We say that $A \geq 0$ (A is nonnegative) if all its entries a_{ij} are real and nonnegative. We say $A > 0$(A is positive) if all its entries a_{ij} are real and positive.

Corollary 1: Let $A \in M_n$. Then $|A|^m > 0$ if and only if from each node P_i to each node P_j in $\Gamma(A)$ there is a directed path of length exactly m. The same is true for $M(A)^m$.

Corollary 2: Let $A \in M_n$. Then A has property SC if and only if $(I+|A|)^{n-1} > 0$ or equivalently if $[I + M(A)]^{n-1} > 0$.

Proof:

$$(I + |A|)^{n-1} = I + (n-1)|A| + \binom{n-1}{2}|A|^2 + \ldots + \binom{n-1}{n-2}|A|^{n-2} + |A|^{n-1} > 0 \tag{3.17}$$

if and only if for each pair (i,j) of nodes with $i \neq j$ at least one of the terms $|A|, |A|^2, \ldots, |A|^{n-1}$ has a positive (i,j) entry. But Theorem (3.2) says this happens if and only if there is some directed path in $\Gamma(A)$ from P_i to P_j. This is equivalent to $\Gamma(A)$ being strongly connected, which is equivalent to A having property SC.

Corollary 3: There is a path in $\Gamma(A)$ from P_i to P_j if and only if $[(I+|A|)^{n-1}]_{ij} \neq 0$.

We finally introduce one more equivalent characterisation of the property SC. It is based on the fact that strong connectivity of $\Gamma(A)$ is just a topological property of $\Gamma(A)$ and has nothing to do with the labeling assigned to the nodes of $\Gamma(A)$. If we permute the labels of the nodes, the graph stays either strongly connected or not strongly connected. It is important to note that if we interchange the i-th and j-th rows of A as well as the i-th and j-th columns this has the effect on $\Gamma(A)$ of interchanging the labels on nodes P_i and P_j and vice-versa. Thus it is important to know whether some permutation of rows of A can be found that brings A into the following special block form.

Definition 8: A square non-negative matrix M of order n is said to be reducible if there exists a permutation matrix P such that

$$PMP^{-1} = \begin{pmatrix} A & O \\ B & C \end{pmatrix} \tag{3.18}$$

where A and C are square matrices of order r and $n-r$ respectively for some integer r with $1 \leq r \leq n-1$. The matrices O and B are of dimensions $r\text{x}(n-r)$ and $(n-r)\text{x}r$ respectively.

Notice that the definition does not insist that the blocks A, B and C have nonzero entries, but only that we should be able to get an $r\text{x}(n-r)$ block of 0 entries in the indicated position by some sequence of row and column interchanges. If $|M| > 0$, clearly M is not reducible, and if M is reducible, it must have at least (n-1) 0 entries.

Definition 9: A matrix $A \in M_n$ is irreducible if it is not reducible.

Theorem 3.3: A matrix $A \in M_n$ is irreducible if and only if

$$(I+A)^{n-1} > 0 \tag{3.19a}$$

or, equivalently, if

$$[I + M(A)]^{n-1} > 0. \tag{3.19b}$$

Proof: We shall actually prove that A is reducible if and only if $(I + |A|)^{n-1}$ has at least one 0 entry. Suppose that A is reducible such that for some permutation matrix P

$$PAP^{-1} = \begin{pmatrix} A & O \\ B & C \end{pmatrix}$$

which implies that

$$A = P^{-1} \begin{pmatrix} A & O \\ B & C \end{pmatrix} P = P^{-1} \tilde{A} P \tag{3.20a}$$

where A, B, O, and C are block matrices as in definition (8) above. Now it follows that

$$|A| = |P^{-1} \tilde{A} P| = P^{-1} |\tilde{A}| P \tag{3.20b}$$

since the effect of P is only to permute rows and columns, also we notice that $|\tilde{A}|^2$, $|\tilde{A}|^3, \ldots, |\tilde{A}|^{n-1}$ all have the same r by $(n-r)$ block of zeroes in the upper right corner as $\tilde{A}$. Thus

$$\begin{aligned} (I + |A|)^{n-1} &= (I + P^{-1}|\tilde{A}|P)^{n-1} \\ &= (P^{-1}[I + |\tilde{A}|]P)^{n-1} \\ &= P^{-1}(I + |\tilde{A}|)^{n-1}P \\ &= P^{-1}[I + |\tilde{A}| + \binom{n-1}{2}|\tilde{A}|^2 + \ldots + \binom{n-1}{n-1}|\tilde{A}|^{n-1}]P \end{aligned} \tag{3.20c}$$

and all the terms in the square brackets have an r-by-$(n-r)$ block of $0's$ in the upper right corner. Thus $(I + |A|)^{n-1}$ is reducible and hence it cannot have all nonzero entries.

Conversely, suppose for some $p \neq q$ that the (p, q) entry of $(I + |A|)^{n-1}$ is 0. Then we know that there is no directed path in $\Gamma(A)$ from P_p to P_q. Define the sets of nodes

$$S_1 = \{P_i : P_i = P_q \text{ or there is a path in } \Gamma(A) \text{ from } P_i \text{ to } P_q\} \tag{3.21a}$$

and let S_2 contain all nodes of $\Gamma(A)$ that are not in S_1. We notice that

$$S_1 \cup S_2 = \{P_1, \ldots, P_n\} \tag{3.21b}$$

and

$$P_q \in S_1 \neq \emptyset \text{ so } S_2 \neq \{P_1, \dots, P_n\} \tag{3.21c}$$

If there were a path from one node P_i of S_2 to some node P_j of S_1, then (by definition of S_1) there would be a path from P_i to P_q and so P_i would already be in S_1 which is a contradiction. Thus, there can be no path from any node of S_2 to any node of S_1. Now we relable the nodes so that

$$S_1 = \{\tilde{P}_1, \dots, \tilde{P}_r\} \text{ and } S_2 = \{\tilde{P}_{r+1}, \dots, \tilde{P}_{r+n-r}\} \tag{3.21d}$$

and hence

$$\tilde{A} = PAP^{-1} = \begin{pmatrix} B & O \\ C & D \end{pmatrix} \quad B \in M_r, O \in Mr, n-r \tag{3.21e}$$

so that A is reducible. The argument for $[I + M(A)]^{n-1}$ is similar.

Let us summarize the results as follows

Theorem 3.4: Let $A \in M_n$. The following are equivalent

(a) A is irreducible

(b) $(I + |A|)^{n-1} > 0$

(c) $[I + M(A)]^{n-1} > 0$

(d) $\Gamma(A)$ is strongly connected

(e) A has property SC

From definitions 8 and 9 we conclude that an age classified matrix with pre-reproductive and post-reproductive age classes or simply the complete population projection matrix given in Eq.(3.8) is reducible. In this case we can take $P = I$. A matrix is irreducible if it is not reducible. Sometimes the terms decomposable and indecomposable are used instead of reducible and irreducible especially in the study of stochastic matrices. Next we show that the population projection matrix written in full in Eq.(3.14) is irreducible. Let us call this property 1 of matrix A

Property 1: A is irreducible.

This property follows from the following argument. The matrix A in Eq.(3.14) can in general be written as a sum of two matrices given by

$$A = A_0 + B \tag{3.22a}$$

where the the matrix $A_0 = (a^0_{ij})$ has elements only in its first row given by

$$a^0_{1j} = f_j = 0, \quad j = 1, \ldots, k-1 \text{ and } a^0_{1k} = f_k > 0$$

and in the leading sub-diagonal given by

$$a^0_{i,i-1} = p_{i-1} \quad i = 2, \ldots, k$$

and zero elsewhere. The matrix $B = (b_{ij})$ has all its elements zero except possibly in the first row since by assumption

$$b_{1j} = f_j \geq 0 \quad j = 1, \ldots, k-1 \text{ and } b_{1k} = f_k = 0.$$

We claim that if A_0 is irreducible then so is the more general matrix, A. Suppose that this is not the case. Then there exist a permutation matrix P such that

$$\begin{aligned} PAP^{-1} &= P(A_0 + B)P^{-1} \\ &= PA_0P^{-1} + PBP^{-1} \\ &= \begin{pmatrix} F & O \\ G & H \end{pmatrix} \end{aligned} \tag{3.22b}$$

where F and H are square. Since the inverse of a permutation matrix is again a permutation matrix then $B \geq 0 \Rightarrow PBP^{-1} \geq 0$. But PA_0P^{-1} cannot be of the form given in Eq.(3.22b) by hypothesis, hence A is irreducible, since the addition of the non-negative matrix PBP^{-1} cannot result in a sum of the form in Eq.(3.22b). One can also see that by definition $\Gamma(A)$ is strongly connected and by Theorem 3.4 it follows that A is irreducible.

Next we state the fundamental Perron-Frobenius theorem which is vital in the study of both discrete and continuous time matrix population models. In what follows, therefore, we deal with square nonnegative matrices $A = (a_{ij}) \quad i, j = i, \ldots, n$; that is $a_{ij} \geq 0 \quad \forall i, j$, in which case we use the notation $A \geq 0$. If in fact $a_{ij} > 0 \quad \forall i, j$ we write $A > 0$. This definition and notation extends in an obvious way to row vectors $\vec{y}^T$ and column vectors $\vec{x}$ also to expressions such as

$$A \geq B \iff A - B \geq 0 \tag{3.23}$$

where A, B and O are square nonnegative matrices of compatible dimensions. We use the notation $\vec{y}^T = (y_i)$, $\vec{x} = (x_i)$ for row and column vectors respectively and $A^k = (a^k_{ij})$ for kth powers of matrices.

Definition 10: A square non-negative matrix is said to be primitive if there exists a positive integer k such that $A^k > 0$.

It is clear that if any other matrix B has the same dimensions as A, and has positive entries and zero entries in the same positions of A, then this will also be true for powers A^k, B^k of the two matrices. As incidence matrices $\tilde{A}$ corresponding to a given matrix A replaces all positive entries of A by ones clearly $\tilde{A}$ is primitive iff A is. We now state without proof the two forms of the Perron-Frobenius Theorem first for strictly primitive matrices then secondly for general irreducible matrices. The proofs can be found in any of the books by Gantmacher(1959), Seneta(1981) or Horn and Johnson(1985).

Theorem 3.5: Perron-Frobenius Theorem for Primitive Matrices: Suppose L is an nxn non-negative primitive matrix. Then there exists an eigenvalue λ_1 such that

(a) λ_1 is real and > 0;

(b) with λ_1 can be associated strictly positive left and right eigenvectos $\vec{y}^T$ and $\vec{x}$ respectively;

(c) $\lambda_1 > |\lambda|$ for any eigenvalue $\lambda \neq \lambda_1$ of L;

(d) the eigenvectors associated with λ_1 are unique to constant multiples.

(e) If $O \leq B \leq L$ and β is an eigenvalue of B, then $|\beta| \leq \lambda_1$. Moreover, $|\beta| = \lambda_1 \Rightarrow B = L$. Here O denotes a matrix of zero elements only.

(f) λ_1 is a simple root of the characteristic equation of L.

Theorem 3.6: Perron-Frobenius for Irreducible Matrices: Suppose L is an nxn irreducible non-negative matrix. Then all of the assertions (a)-(f) of Theorem 3.5 hold except (c) is replaced by the weaker statement: $\lambda_1 \geq |\lambda|$ for any eigenvalue λ of L.

From the structures of M and A given in Eq.(3.8) and Eq.(3.14a) together with the size classsified case of Eq.(3.15b) it is clear that these matrices are nonnegative square matrices. We had already indicated from Eq.(3.9), definition 8 and property 1 of matrix A that matrix M is reducible while A, the population projection matrix is irreducible. Next we state the relevant definitions and rules to guide us on primitivity of a matrix.

Definition 11: The index of imprimitivity τ of an irreducible non-negative matrix A is the algebraic multiplicity of its eigenvalues of modulus λ_1 that is τ is the number of eigenvalues λ_i of A such that $|\lambda_i| = \lambda_1$.

Definition 12: An irreducible non-negative matrix A is said to be primitive if the index of imprimitivity $\tau = 1$. Some books refer to the corresponding eigenvalue as a root of multiplicity one.

Now suppose the characteristic equation of a matrix B is given by

$$|\lambda I - B| = 0 \tag{3.24a}$$

then by the Descarte's rule of signs, the number of positive roots of the equation is equal to the number of changes of signs in it. We also comment here that the terms 'aperiodic' and 'periodic' are used instead of 'primitive' and 'imprimitive' and a stochastic matrix that is both irreducible and primitive is said to be 'regular' or ergodic. More precisely the corresponding Markov chain is said to be regular or an ergodic chain. The property of ergodicity in population dynamics will be revisited later in the work. Next we study the population projection matrix in relation to the above definitions and theorems as a discrete time homogeneous process.

3.3.1 Discrete Stable Population Theory

We now continue studying the properties of the matrix A in (3.14a) and the sequence $\{n(t+1) = An(t)\}_{t\in N}$ as $t \to \infty$.

Property 2: The projection matrix A has a positive eigenvalue λ_1 which is a simple root (root of multiplicity one).

We know that the eigenvalues of the matrix A satisfy the homogeneous equation

$$A\vec{x} = \lambda\vec{x}$$

$$\Rightarrow (A - \lambda I)\vec{x} = 0$$

$$\Rightarrow |A - \lambda I| = 0$$

and from the structure of matrix A in Eq.(3.14a) it follows that

$$|A - \lambda I| = \lambda^k - f_1\lambda^{k-1} - p_1 f_2\lambda^{k-2} - \ldots - f_k \prod_{i=1}^{k-1} p_i = 0 \tag{3.24b}$$

Since $p_i > 0, \quad i = 1, \ldots, k-1$ and $f_i \geq 0$ for $i = 1, 2, \ldots, k-1$ and $f_k > 0$ then

$$f_k \prod_{i=1}^{k-1} p_i > 0 \tag{3.24c}$$

so A has no 0 eigenvalue. Further dividing the characteristic equation in Eq.(3.19) by λ^k and rearranging gives

$$f(\lambda) = \frac{f_1}{\lambda} + \frac{p_1 f_2}{\lambda^2} + \ldots + \frac{f_k}{\lambda^k} \prod_{i=1}^{k-1} p_i = 1 \tag{3.25a}$$

from which it is clear that

(i)

$$\lim_{\lambda \to 0} f(\lambda) = \infty$$

(ii)

$$\lim_{\lambda \to \infty} f(\lambda) = 0$$

hence $f(\lambda)$ is a monotonic decreasing function of λ. This means that there is only one value of $\lambda = \lambda_1$ say which satisfies $f(\lambda) = 1$. Another intuitive interpretation of (3.25a) is that given an individual is initially in age class one at time zero, then after one time interval we expect it to produce f_1 individuals, $p_1 f_2$ after two time periods, $p_1 p_2 f_3$ after three time intervals and so on. That is, if we let $E_F(j)$ denote the number of offsprings from such an individual after j time periods then

$$E_F(j) = f_j \prod_{i=1}^{j-1} p_i \tag{3.25b}$$

Property 3: All remaining eigenvalues of A are smaller in magnitude than the one real positive eigenvalue λ_1 above.

Let λ_j, $j = 2, \ldots, k$ represent the remaining $k-1$ eigenvalues of the population projection matrix. Then in general we can write or represent, λ_j as

$$\lambda_j = u_j + iv_j, \quad j = 2, \ldots, k-1 \; u_j, \, v_j \in R$$

as a complex number (i=$\sqrt{-1}$) or in polar coordinates form as

$$\lambda_j = |\lambda_j|(cos\theta + isin\theta) = |\lambda_j|e^{i\theta}$$

where,

$$|\lambda_j| = \sqrt{(}u_j^2 + v_j^2)$$

and

$$\theta = tan^{-1}(v_j/u_j)$$

It follows that

$$\begin{aligned} \lambda_j^{-1} &= |\lambda_j|^{-1}(cos\theta - isin\theta) \\ &= \exp(\alpha + i\beta), \end{aligned} \qquad (3.25c)$$

where α is real, β is real and positive. Further $\beta \neq 2\pi, 4\pi, 6\pi, \ldots$, because if this was the case λ_j would be real and positive which was shown to be impossible from property 2 otherwise we have more than one positive real roots. Even from Descarte's rule of signs it follows from Eq.(3.24b) that there is only one change of signs hence only one positive root exists.

Substituting λ_j from Eq.(3.25c) in Eq.(3.25a) then equating the real parts we get

$$f_1 e^{\alpha} cos\beta + p_1 f_2 e^{2\alpha} cos2\beta + \ldots + f_k e^{k\alpha} cosk\beta \prod_{i=1}^{k-1} p_i = 1 \qquad (3.26a)$$

Since λ_1 is real, then we can express it as $\lambda_1^{-1} = e^r$ for some $r \in R$. Further since λ_1 satisfies $f(\lambda_1) = 1$ then it follows by substituting $\lambda = \lambda_1 = e^{-r}$ in Eq.(3.25a) that

$$f_1 e^r + p_1 f_2 e^{2r} + \ldots + f_k e^{kr} \prod_{i=1}^{k-1} p_i = 1 \qquad (3.26b)$$

where $\beta = 0$ in this case. But we know that $|cos m\beta| \leq 1$ thus for some j, the coefficient e^{α} in Eq.(3.26a) is greater than the corresponding coefficient in Eq.(3.26b) so that for that j

$$e^{\alpha} > e^{r} \iff e^{-\alpha} < e^{-r} \iff |\lambda_j| < \lambda_1 \tag{3.26c}$$

This shows that for an age classified population projection matrix defined in Eq.(3.14a) there exists a dominant eigenvalue λ_1 which exceeds the modulus of all other eigenvalues.

Property 4: The population projection matrix A has a right eigenvector $\vec{x}_1$, of dimension k corresponding to λ_1 such that all its components $x_i, \quad i = 1, 2, \ldots, k$ are positive.

To show this we let $\vec{x}_1 = (x_1, \ldots, x_k)'$. Then $\vec{x}_1$ satisfies the homogeneous equation

$$\lambda_1 \vec{x}_1 = A\vec{x}_1 \tag{3.27a}$$

which is a system of k simultaneous equations given by

$$\begin{aligned} \lambda_1 x_1 &= \sum_{i=1}^{k} f_i x_i \\ \lambda_1 x_i &= p_{i-1} x_{i-1}, \quad i = 2, \ldots, k \end{aligned} \tag{3.27b}$$

without loss of generality let $x_1 = 1$ such that from the second of the k linear equations x_2 is given by

$$x_2 = p_1 / \lambda_1$$

and then from the third equation we get

$$x_3 = \frac{p_2}{\lambda_1} x_2 = \frac{p_1 p_2}{\lambda_1^2}$$

and continuing recursively in a similar manner we get the general expression for x_j as

$$x_j = \prod_{j=1}^{j-1} \frac{p_j}{\lambda_1}, \quad j = 2, \ldots, k. \tag{3.27c}$$

From the definition of A we know that $p_i > 0, \quad i = 1, \ldots, k-1$ and clearly $\lambda_1 > 0$ thus from Eq.(3.27c) above each $x_i > 0, \quad i = 1, \ldots, k$ hence the conclusion $\vec{x}_1 > 0$.

The components of the eigenvector $\vec{x}_1$ characterise the stable age distribution. This is true because in all the above derivations in this subsection we assume the system has attained stability.

Property 5: The matrix A has a left eigenvector $\vec{y}_1 = (y_1, \ldots, y_k)'$ corresponding to λ_1 such that all its components are positive.

Again without loss of generality we let $y_1 = 1$. But $\vec{y}_1$ satisfies the matrix equation

$$\vec{y}_1^T A = \lambda \vec{y}^T$$

which again gives a system of k homogeneous equations given by

$$\begin{aligned} y_1 f_1 + y_2 p_1 &= \lambda_1 y_1 \\ y_1 f_2 + y_3 p_2 &= \lambda_1 y_2 \\ &\cdots\cdots \\ y_1 f_i + y_{i+1} p_i &= \lambda_1 y_i \qquad (3.28a) \\ &\cdots\cdots \\ y_1 f_{k-1} + y_k p_{k-1} &= \lambda_1 y_{k-1} \\ y_1 f_k &= \lambda_1 y_k \end{aligned}$$

Now from the last of these equations we see that

$$y_k = f_k / \lambda_1 \quad \text{since } y_1 = 1 \tag{3.28b}$$

and from the second last equation in the system Eq.(3.28a) and using the value for y_k above we get

$$\lambda_1 y_{k-1} = f_{k-1} + \frac{f_k p_{k-1}}{\lambda_1}$$

or

$$y_{k-1} = \frac{f_{k-1}}{\lambda_1} + \frac{f_k p_{k-1}}{\lambda_1^2} \tag{3.28c}$$

and in general we have

$$y_j = \sum_{i=j}^{k} \left(\prod_{h=j}^{i-1} p_h \right) f_i \lambda_1^{j-i-1}, \quad j = 2, \ldots, k \tag{3.28d}$$

We adopt the condition $\prod_{h=i}^{i-1} p_h = 1$ to avoid ambiguity in Eq.(3.28d). Clearly $y_j > 0, \quad j = 1, 2, \ldots, k$. The quantities can be interpreted to measure the reproductive potential of an individual in age class $j = 1, 2. \ldots k$. Thus the quantity y_j will be called the reproductive value of an individual aged j. It gives the expected total number of offsprings an individual currently in age class j would give in the remaining expected life span, Caswell(1982,1983).

Propery 6: For an initial population distribution vector $\vec{n}(0)$ not identically zero, there exists a constant c_1, which depends upon the vector such that

$$\lim_{T\to\infty} \frac{A^T \vec{n}(0)}{\lambda_1^T} = c_1 \vec{x}_1 \tag{3.29a}$$

where λ_1 is the dorminant eigenvalue and $\vec{x}_1$ its corresponding right eigenvector. To derive this property let $\lambda_i, \quad i = 1, 2, \ldots, k$ denote the k eigenvalues of the population projection matrix A. Then,

$$A\vec{x}_i = \lambda_i \vec{x}_i, \quad i = 0, 1, \ldots, k-1 \tag{3.29b}$$

and

$$\vec{y}_i^T A = \lambda_i \vec{y}_i^T \quad i = 1, 2, \ldots, k \tag{3.29c}$$

where $\vec{x}_i$ and $\vec{y}_i$ are respectively the right and left eigenvectors corresponding to λ_i. Further let,

$$D = diag(\lambda_i) \tag{3.29d}$$

denote the Jordan canonical matrix representation of A. We assume that the population's life cycle is such that the $\lambda_i's$ are distinct. Without loss of generality assume that

$$|\lambda_1| > |\lambda_2| \geq \cdots \geq |\lambda_k|.$$

Next we define, the two matrices X and Y given by

$$X = (\vec{x}_1, \vec{x}_2, \ldots, \vec{x}_k) \tag{3.30a}$$

and

$$Y = (\vec{y}_1, \vec{y}_2, \cdots, \vec{y}_k)' \tag{3.30b}$$

We adopt the condition $\prod_{h=i}^{i-1} p_h = 1$ to avoid ambiguity in Eq.(3.28d). Clearly $y_j > 0, \quad j = 1, 2, \ldots, k$. The quantities can be interpreted to measure the reproductive potential of an individual in age class $j = 1, 2. \ldots k$. Thus the quantity y_j will be called the reproductive value of an individual aged j. It gives the expected total number of offsprings an individual currently in age class j would give in the remaining expected life span, Caswell(1982,1983).

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and

$$Y = (\vec{y}_1, \vec{y}_2, \ldots, \vec{y}_k)' \tag{3.30b}$$

Then it follows that the matrix equation in Eq.(3.29b) and Eq.(3.29c) can be written compactly as

$$AX = XD \tag{3.31a}$$

and

$$YA = DY. \tag{3.31b}$$

Assuming that X and Y are invertible then,

$$A = XDX^{-1} = Y^{-1}DY$$

which means that as a consequence of uniqueness

$$X = Y^{-1} \iff Y = X^{-1}$$

thus

$$XY = XX^{-1} = Y^{-1}Y = I$$

and

$$\begin{aligned} A &= XDX^{-1} \\ &= XDY \\ &= \lambda_1 \vec{x}_1 \vec{y}_1^T + \lambda_1 \vec{x}_2 \vec{y}_2^T + \ldots + \lambda_k \vec{x}_k y_k^T \\ &= \sum_{i=1}^{k} \lambda_i \vec{x}_i \vec{y}_i^T \\ &= \sum_{i=1}^{k} \lambda_i H_i \end{aligned} \tag{3.31c}$$

where

$$H_i = \vec{x}_i \vec{y}_i^T \quad i = 1, 2, \ldots, k \tag{3.31d}$$

are k by k matrices called the spectral components of A and posses the special property that they are idempotent. To see this note that

$$A^N = XD^N X^{-1}$$

but since

$$X^{-1} = Y$$

then

$$\begin{aligned} A^N &= XD^NY \\ &= \sum_{i=1}^{k} \lambda_i^N H_i, \end{aligned} \tag{3.31e}$$

where N is a non-negative integer. Now compare this with,

$$A^N = [\lambda_1 H_1 + \lambda_2 H_2 + \ldots + \lambda_k H_k]^N$$

thus we conclude

$$H_i^N = H_i \tag{3.32}$$

and

$$H_i H_j = 0 \quad for\ i \neq j. \tag{3.32b}$$

It follows that for $N = t$

$$\frac{A^t}{\lambda_1^t} = H_1 + \left(\frac{\lambda_2}{\lambda_1}\right)^t H_2 + \ldots + \left(\frac{\lambda_k}{\lambda_1}\right)^t H_k \tag{3.32c}$$

and given

$$\lambda_1 > |\lambda_2| \geq \ldots \geq |\lambda_k|$$

then

$$\lim_{t\to\infty} \left(\frac{\lambda_i}{\lambda_1}\right)^t = 0, \quad 2 = 1, \ldots, k$$

Hence

$$\lim_{t\to\infty} \frac{A^t}{\lambda_1^t} = H_1 = \vec{x}_1 \vec{y}_1^T \tag{3.33a}$$

which on post-multiplying both sides by $\vec{n}(0)$ gives

$$\lim_{t\to\infty} \frac{A^t \vec{n}(0)}{\lambda_1^t} = \vec{x}_1 \vec{y}_1^T \vec{n}(0) = c_1 \vec{x}_1 \tag{3.33b}$$

where

$$c_1 = \vec{y}_1^T \vec{n}(0) > 0. \tag{3.33c}$$

The results obtained above allow us to make concrete conclusions about an age structured time homogeneous model. Given $\vec{n}(0)$ then the structure at time t is given by

$$\begin{aligned}\vec{n}(t) &= A^t\vec{n}(0)\\ &= \sum_{i=1}^{k} c_i\lambda_i^t\vec{x}_i \end{aligned} \tag{3.34a}$$

where

$$c_i = \vec{y}_i^T\vec{n}(0) \tag{3.34b}.$$

For large t,

$$\vec{n}(t) \rightarrow c_1\lambda_1^t\vec{x}_1 \tag{3.35}$$

Thus an indication that the population has attained stability is achieved when

$$\vec{n}(t+1) = \lambda_1\vec{n}(t) \tag{3.36a}$$

or

$$A\vec{n}(t) = \lambda_1\vec{n}(t) \tag{3.36b}$$

holds.

After the population attains stability the initial age structure $\vec{n}(0)$ becomes irrelevant, while Eq.(3.34a) tells us that the growth of the classified population is decomposed into a set of exponential contributions one for each eigenvalue. The value λ_1 is called the true rate of population growth and it is related to the intrinsic rate of natural increase r, by the relation

$$\log_e \lambda_1 = r \tag{3.36c}$$

If $|\lambda_i| < 1$ its contribution decays, either smoothly if $\lambda_i > 0$ or with damped oscillations if in addition $\lambda_i < 0$ or complex. If $|\lambda_i| > 1$, then its contribution to population growth grows exponentially, either smoothly if $\lambda_i > 0$ (positive and real) or with oscillations if $\lambda_i < 0$ or complex.

As t becomes large λ_1, the dominant eigenvalue of A becomes the determining rate of growth and we notice that for a particular age class i

$$\lim_{t\rightarrow\infty} \frac{n_i(t+1)}{n_i(t)} = \lambda_1 \tag{3.37a}$$

and $\vec{n}(t)$ becomes proportional to $\vec{x}_1$ the eigenvector associated with λ_1. Also it can be shown that for two consecutive age classes i and $i+1$ the following relation holds:

$$\lim_{t \to \infty} \frac{n_i}{n_{i+1}(t)} = \frac{x_i}{x_{i+1}} = \frac{\lambda_1}{p_i} \quad i = 1, 2, \ldots, k-1 \tag{3.37b}$$

where the final equality is as a result of the expression for the stable distribution obtained for the $x_i's$ in Eq.(3.27c).

3.4 Generalized Stage-Age Structured Matrix Model

The classical age classified Leslie matrix for population dynamics was stated in Eq.(3.5) for the complete population projection matrix and in Eq.(3.14a) for the pre-reproductive and reproductive population. In this model we assume that all individuals in age class i, say, advance(transit) at the same rate and that the age of an individual carries all the vital information. The model also requires the classification to be such that the size of one age class be equal to the projection interval, or time step $(t, t+h)$.

In general a population's life cycle may consist of k developmental stages of variable residence times T_i, $i = 1, 2, \ldots, k$. By residence time we mean the expected length of time an individual waits in a stage before transiting to the next stage. Depending on the magnitude of T_i and h, we can further classify individuals in stage i into $t_i = T_i/h$ age classes of size h each. We make the following assumptions regarding an individual in class j, $j = 1, \ldots, t_i$ of stage i within a unit time interval say $[t, t+h) \equiv [t, t+1)$;

A1. It survives to time $t+1$ with probability s_{ij}.

A2. (i) Given it survives to time $t+1$ it either transits to age group 1 of the next stage $i+1$ with probability γ^i_{1j}, $i = 1, \ldots, k$; $j = 1, \ldots, t_i$.

(ii) or transits to the next age group of the same stage with probability, $(1 - \gamma^i_{1j})$

A3. Such an individual produces f^i_{1j} offsprings who survive and enter age group 1 of stage one just before or at time $t+1$.

Now even for fixed or persistent environmental conditions, individuals in a particular stage may develope at different rates. Let

$S_{ij}(t)$ = event that an individual of age j in stage i at time t will survive to time $t+1$

$T_j^i(t)$ = event that an individual transits to the next stage, $i+1$, during the time interval [t,t+1) and

$\gamma_{1j}^i(t)$ = the transition probability from age group j in stage i at time t to the next stage, $i+1$.

Now, γ_{1j}^i is a conditional probability because an indvidual will transit to the next stage only if it survives to time $t+1$. Therefore we can write, especially for the independent case,

$$\gamma_{1j}^i = P(T_j^i(t)|S_{ij}(t)) \tag{3.38a}$$

Therefore the probability that an individual of age j in stage i at time t will transit to the next stage during the time interval $[t, t+1)$ denoted by p_{1j}^i is given by;

$$\begin{aligned} p_{1j}^i &= P(T_j^i(t) \cap S_{ij}(t)) \\ &= P(S_{ij}(t))P(T_j^i(t)|S_{ij}(t)) \end{aligned}$$

That is,

$$p_{1j}^i = s_{ij}\gamma_{1j}^i \tag{3.38b}$$

If an individual survives the interval $[t, t+1)$ but does not transit to the next stage, $i+1$, it will definitely transit to age class $j+1$ within the same stage with probability $\pi_{j+1,j}^i$ given by

$$\begin{aligned} \pi_{j+1,j}^i &= P(T_j^i(t)^c \cap S_{ij}(t)) \\ &= P(S_{ij}(t))P(T_j^i(t)^c|S_{ij}(t)). \qquad (3.38c) \\ &= s_{ij}(1-\gamma_{1j}^i) \end{aligned}$$

From equations (3.38b) and (3.38c) it follows that the probability that an individual in age class j of stage i dies within the time interval $(t, t+1)$ is given by

$$q_{dj}^i = 1 - p_{1j}^i - \pi_{j+1,j}^i = 1 - s_{ij} \tag{3.39}$$

as expected. Now let $n_j^i(t)$ denote the numbers of individuals in age class j of stage i. Then the vector representation of the population distribution for stage i is

$$\vec{n}_i(t) = (n_1^i(t), \ldots, n_{t_i}^i(t))' \quad i = 1, \ldots, k \tag{3.40}$$

and for the entire population,

$$\vec{n}(t) = (\vec{n}_1(t), \ldots, \vec{n}_i(t), \ldots, \vec{n}_k(t))' \tag{3.41}$$

which is a partitioned column vector of dimension $\sum_{i=1}^{k} t_i$ by 1. Since newly born offsprings enter age class one of stage one on survival, it follows that

$$n_1^1(t+1) = \sum_{i=1}^{k} \sum_{j=1}^{t_i} f_{1j}^i \, n_j^i(t) \tag{3.42}$$

This equation defines the renewal process of the system.

Next consider the aging process which involves transitions within and between stages. It follows from Eq.(3.38c) that the transitions within stage i is governed by the equation

$$n_{j+1}^i(t+1) = \pi_{j+1,j}^i n_j^i(t), \quad j = 1, 2, \ldots, t_i - 1, \quad i = 1, 2, \ldots, k. \tag{3.43}$$

while the between stage dynamics are given by the equation

$$n_1^{i+1}(t+1) = \sum_{j=1}^{t_i} p_{1j}^i \, n_j^i(t), \quad i = 1, 2, \ldots, k-1 \tag{3.44}$$

where p_{1j} and $\pi_{j+1,j}^i$ were derived from Eq.(3.38a), Eq.(3.38b) and Eq.(3.38c) and assumptions $A2(i)$ and $A2(ii)$ as stated in page 76.

Now equations Eq.(3.42), Eq.(3.43) and Eq.(3.44) can be linked together in matrix notation as

$$\vec{n}(t+1) = A^* \vec{n}(t) \tag{3.45}$$

where $\vec{n}(t)$ was stated in Eq.(3.40) and Eq.(3.41). The matrix A^* will be called the generalized stage-age classified matrix and is written explicitly as;

$$\begin{pmatrix}
f^1_{11} & \cdots & f^1_{1,t_1-1} & f^1_{1t_1} & \cdots & f^i_{11} & \cdots & f^i_{1,t_i-1} & f^i_{1t_i} & \cdots & f^k_{1,t_k-1} & f^k_{1,t_k} \\
\pi^1_{21} & \cdots & 0 & 0 & \cdots & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \\
\vdots & \ddots & \vdots & \vdots & \cdots & \vdots & \cdots & \vdots & \vdots & \cdots & \vdots & \vdots \\
0 & \cdots & \pi^1_{t_i,t_1-1} & 0 & \cdots & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \\
p^1_{1,1} & \cdots & p^1_{1,t_1-1} & p^1_{1,t_1} & \cdots & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \\
0 & \cdots & 0 & 0 & \cdots & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \\
\vdots & \cdots & \vdots & \vdots & \cdots & \vdots & \cdots & \vdots & \vdots & \cdots & \vdots & \vdots \\
0 & \cdots & 0 & 0 & \cdots & \pi^i_{21} & \cdots & 0 & 0 & \cdots & 0 & 0 \\
\vdots & \cdots & \vdots & \vdots & \cdots & \vdots & \ddots & \vdots & \vdots & \cdots & \vdots & \vdots \\
0 & \cdots & 0 & 0 & \cdots & 0 & \cdots & \pi^i_{t_i,t_i-1} & 0 & \cdots & 0 & 0 \\
0 & \cdots & 0 & 0 & \cdots & p^i_{11} & \cdots & p^i_{1,t_i-1} & p^i_{1,t_i} & \cdots & 0 & 0 \\
\vdots & \cdots & \vdots & \vdots & \cdots & \vdots & \cdots & \vdots & \vdots & \cdots & \vdots & \vdots \\
0 & \cdots & 0 & 0 & \cdots & 0 & \cdots & 0 & 0 & \cdots & \pi_{t_k,t_k-1} & 0
\end{pmatrix} \tag{3.46}$$

A special observation here is that $p^i_{1t_i} = s_{ij}$ because given that an individual of age t_i in stage i survives the time interval $[t, t+1)$ the only transition at its disposal is age class one of stage $i+1$, that is $\gamma^i_{1t_i} = 1$. A^* is more conveniently written as a partitioned matrix as

$$A^* = \begin{pmatrix}
(F_1 + A_1) & F_2 & F_3 & \cdots & F_{k-1} & F_k \\
P_1 & A_2 & O & \cdots & O & O \\
O & P_2 & A_3 & \cdots & O & O \\
\vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\
O & O & O & \cdots & A_{k-1} & 0 \\
O & O & O & \cdots & P_{k-1} & A_k
\end{pmatrix} \tag{3.47}$$

where, the matrix,

$$F_i = (f^i_{hl}) \quad i = 1, 2, \ldots, k \tag{3.48a}$$

which we call the fertility matrix for stage i may have positive elements only in the first row and zeroes elsewhere and is of dimension $t_1 x t_i$. That is

$$f^i_{hl} = \begin{cases} f^i_{1l} & l = 1, 2, \ldots, t_i \\ 0 & \text{elsewhere} \end{cases} \tag{3.48b}$$

where for completeness f^i_{1l} denotes the number of offsprings born to an individual in age class l of stage i who survive to be counted in $n_{11}(t+1)$ at time $t+1$.

The matrix

$$A_i = (a^i_{hl}), \quad i = 1, \ldots, k \quad h, l = 1, \ldots, t_i \tag{3.49a}$$

is square of order t_i with positive elements only in the leading subdiagonal and zeroes elsewhere. That is

$$a^i_{hl} = \begin{cases} \pi^i_{h,h-1} \geq 0, & h = 2, \ldots, t_i \\ 0 & \text{elsewhere} \end{cases} \tag{3.49b}$$

The matrix represents within stage dynamics in the sense that $\pi^i_{h,h-1}$ denotes the probability that an individual in age class $h-1$ of stage i at time t will transit to age class h of the same stage at time $t+1$.

Finally the matrix

$$P_i = (p^i_{hj}) \quad i = 1, \ldots, k-1 \tag{3.50a}$$

represents the between stage dynamics with positive elements only in the first row by virtue of assumption $A2(i)$. Thus

$$P^i_{hj} = \begin{cases} p^i_{1j} \geq 0 & j = 1, \ldots, t_i \\ 0 & \text{elsewhere} \end{cases} \tag{3.50b}$$

It is of order t_{i+1} by t_i. In particular p^i_{1j} denotes the probability that an individual in age class j of stage i at time t will transit to age class 1 of stage $i+1$ by time $t+1$.

The elegance of the partitioned matrix in Eq.(3.47) is that we can explicitly see the within and between stage dynamics for the entire population. That is, at a glance, the array of matrices on the leading subdiagonal represent the between stage dynamics while those on the main diagonal represent the within stage dynamics. The first row of the F matrices represent the stage-age specific fertilities within a unit time interval. Their outputs end up in age class one of stage one causing a change in the value $n^1_1(t)$ to $n^1_1(t+1)$. Thus the entire system represented by matrix A^* can be looked at as an integration of k modules which define the life cycle of the particular population which may be under study.

3.5 Estimation of the Matrix Elements

In this section we consider the problem of estimation of the elements of the population projection matrix in Eq.(3.14a) and its generalized version in Eq.(3.46). The data requirements in the methods are (i) availability of census data observed for a defined period of time or (ii) experimental data obtained under a given set of environmental conditions. Under the time homogeneous model the given set of environmental conditions are assumed to remain the same with time. However this is not the case in a real system. This requires the development of time dependent and stochastic models to study such types of systems. The problem with such kind of models however is the availability of relevant data to estimate some of the matrix or model input parameters.

3.5.1 Estimation from Transition Frequency Data

The entries in the projection matrix M or A in Eq.(3.8) and Eq.(3.14a) respectively reflect both the transition probabilities for the aging process and the fecundities for the reproducing individuals. If individuals can be monitored and identified as time elapses, the transition probabilities can be estimated by simply recording the state of individuals at time t and time $t+1$ respectively. State variables include age, size, developmental stages or even a combination of any two or more attributes depending on the classification criteria. The state "dead" is trivial because a dead individual at time t is still dead at any later time $\tau > t$ say $t+1$.

Now let $n_{ij}(t+1)$ denote the number of individuals who transit from state j to state i within a unit time interval where $i, j = 1, \ldots, k$. Let "d" denote the death state. Then out of $n_j(t)$ individuals initially present in state j at time t, $n_{ij}(t)$ transit to state $i = 1, \ldots, k$ with probability a_{ij} say. Let $n_{dj}(t+1)$ denote those who die between times t and $t+1$. Then it follows that

$$n_j(t) = \sum_{i=1}^{k+1} n_{ij}(t+1) \tag{3.51a}$$

giving a multinomial model for the process and the estimate of a_{ij} in the matrix A is given by

$$\hat{a}_{ij} = \frac{n_{ij}(t+1)}{\sum_{i=1}^{k+1} n_{ij}(t+1)} = \frac{n_{ij}(t+1)}{n_j(t)}. \tag{3.51b}$$

If observations are repeatedly made at time $t, t+1, \ldots, t+\tau$ then an improved estimate of the transition probability a_{ij} can be found because now more information is available. This improved estimate is precisely given by

$$\begin{aligned} \hat{a}_{ij} &= \frac{\sum_{r=1}^{\tau} n_{ij}(t+r)}{\sum_{r=0}^{\tau-1} \sum_{i=1}^{k+1} n_{ij}(t+r)} \\ &= \frac{\sum_{r=1}^{\tau} n_{ij}(t+r)}{\sum_{r=0}^{\tau-1} n_j(t+r)} \end{aligned} \tag{3.52}$$

Note that in all we have $k+1$ states including the death state because we need to account for every individual that was present at the beginning of each time interval. The case for the time interval $(t, t+1)$ is shown in equation Eq.(3.51a). For an age classified population where the projection interval or model time step is equal to the size of one age class, transitions are possible only from age class (state) j to state $j+1$ so that for all $j = 1, \ldots, k-1$ we only estimate $a_{j+1,j}$. Now let $b_{1j}(t+1)$ be the number of offsprings who are born to an individual in state j and these offsprings survive to time $t+1$, then if data is available for τ time periods we have

$$\hat{f}_j = \frac{\sum_{r=1}^{\tau} b_{1j}(t+r)}{\tau} \qquad j = 1, \ldots, k \tag{3.53}$$

Thus $\hat{f}_j$ denotes the estimate of the fecundity rate for individuals in age class or state j. We assume observations are made at times $t, \ldots, t+\tau$ under homogeneous conditions. Thus from Eq.(3.52) and Eq.(3.53) one is able to estimate the entire matrix shown in Eq.(3.14a).

3.5.2 Estimation from Stage Duration Distributions

Recall from Eq.(3.38a) and Eq.(3.38b) that for stage classified populations with k stages one can generally assume that the i-th stage is of duration T_i due to both biotic and abiotic factors acting on individuals in that stage. This being the case, we can classify individuals in stage i into $t_i = T_i/h$ age classes of size h each of which is also equal to one time step in the population model. We know from Eq.(3.38b) and Eq.(3.38c) that;

$$p^i_{1j} = s_{ij}\gamma^i_{1j}$$

and

$$\pi^i_{j+1,j} = s_{ij}(1 - \gamma^i_{1j})$$

Let us assume that $\gamma^i_{1j} = \gamma^i$ for all individuals in stage i, $i = 1, \ldots, k$. Then the two equations above become

$$p^i_{1j} = s_{ij}\gamma^i \tag{3.54a}$$

and

$$\pi^i_{j+1,j} = s_{ij}(1 - \gamma^i). \tag{3.54b}$$

Here γ^i denotes the probability that an individual in stage i at time t grows or transits to stage $i+1$ by time $t+1$. We know the stage duration is T_i for individuals in stage i which we can take as a random variable. Thus T_i can take values $1, 2, \ldots$ time intervals. Thus the probability that $T_i = r$ time intervals is;

$$P(T_i = r) = \gamma^i(1 - \gamma^i)^{r-1}, \quad r = 1, 2, \ldots$$

which is a geometric distribution with parameter γ^i. Thus

$$E(T_i) = \frac{1}{\gamma^i}$$

or

$$\hat{\gamma}^i = \frac{1}{\tilde{T}_i} = \tilde{T}_i^{-1} \tag{3.54c}$$

where $\tilde{T}_i$ is the average residence time for stage i obtained from experimental data. The intuitive interpretation of Eq.(3.54c) is that after each time interval a fraction equal to the reciprocal of the average residence time transits to the next stage.

Another useful approximation is based on within stage dynamics of the population. We had earlier stated that stage i is composed of t_i age classes of equal size ($t_i = T_i/h$) depending on the stage duration time T_i. Assuming equal survival probabilities for all age classes in stage i say s_i we propose that the stable age distribution in stage i is given by

$$\vec{w}_i = (1,\ s_i/\lambda,\ (s_i/\lambda)^2,\ \ldots,\ (s_i/\lambda)^{t_i-1})'. \tag{3.55a}$$

To see this assume the within stage population dynamics are governed by an underlying stage specific projection matrix A_i. It follows that if the stage i population structure at time t is $\vec{w}(t)$ then the structure one time period later is given by

$$\vec{w}_i(t+1) = A_i\vec{w}_i(t), \quad i = 1, \ldots, k \tag{3.55b}$$

where

$$\vec{w}_i(t) = (w_1^i(t), w_2^i(t), \ldots, w_{t_i}^i(t))' \tag{3.55c}$$

It therefore means that once the population attains stability, there exists a time independent stable stage i age distribution vector $\vec{w}_i$ which satisfies the equation

$$A_i\vec{w}_i = \lambda\vec{w}_i, \quad i = 1, \ldots, k \tag{3.55d}$$

where

$$\vec{w}_i = (w_1^i, \ldots, w_{t_i}^i)', \quad i = 1, \ldots, k. \tag{3.55e}$$

and λ is the dominant eigenvalue for the stage specific projection matrix A_i. Expanding Eq.(3.55d) we obtain the system of equations given by

$$\begin{aligned} s_i w_1^i &= \lambda w_2^i \\ s_i w_2^i &= \lambda w_3^i \\ &\vdots \\ s_i w_j^i &= \lambda w_{j+1}^i \\ &\vdots \\ s_i w_{t_i-1}^i &= \lambda w_{t_i} \end{aligned} \tag{3.56a}$$

Without loss of generality assume $w_1^i = 1$ then from the first equation in the system of equations Eq.(3.56a) we get

$$w_2^i = s_i/\lambda \tag{3.56b}$$

then substituting for w_2^i in the second equation of the same system we get

$$w_3^i = (s_i/\lambda)^2. \tag{3.56c}$$

Continuing recursively in this manner we get the general equation

$$w_j^i = (s_i/\lambda)^{j-1} \quad j = 2, \ldots, t_i. \tag{3.56d}$$

Substituting for these quantities in $\vec{w}_i$ we arrive at

$$\vec{w}_i = (1,\ s_i/\lambda,\ (s_i/\lambda)^2,\ \ldots,\ (s_i/\lambda)^{t_i-1})' \tag{3.56e}$$

as required. Now since stage i sojourn time is T_i it means that an individual currently in this stage i will transit to the next stage $i+1$ only after reaching the last age class namely t_i. Thus once the population has attained stability, then after every time step $(s_i/\lambda)^{t_i-1}$ individuals will always graduate to the next stage $i+1$. We know that in the stage individuals are distributed according to the stable vector $\vec{w}_i$. Therefore

$$\hat{\gamma}^i = \frac{(s_i/\lambda)^{t_i-1}}{1 + (s_i/\lambda) + \ldots + (s_i/\lambda)^{t_i-1}} \tag{3.57a}$$

and since the denominator is a geometric series with common ratio $r = s_i/\lambda$ it follows that if $r < 1$,

$$\hat{\gamma}^i = \frac{(s_i/\lambda)^{t_i} - (s_i/\lambda)^{t_i-1}}{(s_i/\lambda)^{t_i} - 1} \tag{3.57b}$$

If $r = 1$ expression Eq.(3.57a) reduces to Eq.(3.54c). We note that for a given value of λ and assuming s_i is known one can use equation Eq.(3.57a) to estimate γ^i. Then using this estimate in Eq.(3.38b) and Eq.(3.38c) we can estimate within and between transition probabilities hence be able to parametrize the entire stage-age population projection matrix A^* displayed in Eq.(3.46).

To further generalise the above considerations, let us assume that an individual currently in stage i can graduate into the next stage, $i+1$ from any age class $j = 1, \ldots, t_i$ within stage i. It is more realistic to assume that stage duration varies among individuals with mean $\bar{T}_i$ and the variance σ_i. It follows that the proportion of individuals that graduate into stage $i+1$ from stage i in the time interval $(t, t+1)$ depends on the within stage age distribution.

Now given an individual survives the time interval $(t, t+1)$ with probability s_i let

γ_j^i denote the probability that an individual of age j in stage i graduates to the next stage, $i+1$, within the time interval $(t, t+1)$;

g_j denote the probability that an individual in stage i at time t graduates into the next stage, $i+1$, at age j given it did not transit at any age $l \leq j-1, \quad j = 1, \ldots, t_i$ assuming it survives;

h_j denote the probability of not having graduated by age j given it survives in the interval (t, t+1).

Clearly the set $g_j, \quad j = 1, \ldots, t_i$ gives the probability density of age at graduation to the next stage from stage i. Then the following relations hold. First we observe that the probability density can be obtained from the exit probabilities, $g_1 = \gamma_1^i$, $g_2 = \gamma_2^i(1-\gamma_1^i)$, and in general

$$g_j = \gamma_j^i \prod_{k=1}^{j-1}(1-\gamma_k^i). \tag{3.58a}$$

Note that

$$g_{t_i} = \prod_{k=1}^{t_i-1}(1-\gamma_k^i).$$

Then $h_0 = 1$, $h_1 = 1-\gamma_1^i$, $h_2 = (1-\gamma_2^i)(1-\gamma_1^i)$, and in general

$$h_j = (1-\gamma_j^i)\prod_{k=1}^{j-1}(1-\gamma_k^i) = \prod_{k=1}^{j}(1-\gamma_k^i). \tag{3.58b}$$

As a consequence we find

$$\gamma_j^i = g_j/h_{j-1}. \tag{3.58c}$$

Since by definition of γ_j^i if an individual graduates at age j, then it means it did not graduate at any age before age j. In this setting, in the absence of (true) mortality, graduation can be seen as a mortality, and thus a life table and stable age distribution can be computed, of course (h_j) replaces the survival function, γ_j^i replaces the mortality, and g_j the probability of death at any given age $j = 1, 2, \ldots, t_i$. Assume once again that the true within stage age distribution is $\vec{w}_i(t)$. Then it follows from Eq.(3.55b) that,

$$\vec{w}_i(t+1) = A_i\vec{w}_i(t) \tag{3.59a}$$

where the A_i is a submatrix extracted from Eq.(3.47) to represent the aging process within stage i. Now assuming the population has attained stability then the following equation, same as in Eq.(3.55d) holds

$$A_i \vec{w}_i = \lambda \vec{w}_i \tag{3.59b}$$

where as before $\vec{w}_i$ is the stable stage i age distribution vector given by Eq.(3.55e). Thus given this stable distribution, then the mean of the proportion of graduating individuals is

$$\gamma_i = \frac{\sum_{j=1}^{t_i} \gamma_j^i w_j^i}{\sum_{j=1}^{t_i} w_j^i}. \tag{3.59c}$$

Now we have to find the stable stage i age distribution itself. To do this we have to take into account true mortality and population growth or assume a stage specific survival probability s_i over the time interval (t, t+1). We next expand the matrix equation (3.59a) to get the system of equations

$$\begin{aligned}
s_i(1-\gamma_1^i)w_1^i &= \lambda w_2^i \\
s_i(1-\gamma_2^i)w_2^i &= \lambda w_3^i \\
&\vdots \\
s_i(1-\gamma_{j-1}^i)w_{j-1}^i &= \lambda w_j^i \\
&\vdots \\
s_i(1-\gamma_{t_i-1}^i)w_{t_i-1}^i &= \lambda w_{t_i}
\end{aligned} \tag{3.59d}$$

From the first equation in the system (3.59d) w_2^i is given by

$$w_2^i = (1-\gamma_1^i)s_i/\lambda \tag{3.60a}$$

then from the second equation we get w_3^i as

$$w_3^i = (1-\gamma_2^i)(s_i/\lambda)w_2^i \tag{3.60b}$$

which on substituting for the expression for w_2^i becomes

$$w_3^i = (1-\gamma_1^i)(1-\gamma_2^i)(s_i/\lambda)^2 \tag{3.60c}$$

We continue solving the system recursively and in general

$$w_j^i = \prod_{k=1}^{j-1}(1-\gamma_k^i)(s_i/\lambda)^{j-1}, \quad j = 2, \ldots, t_i. \tag{3.60d}$$

It follows that the stable distribution $\vec{w}_i$ is explicitly given by

$$\vec{w}_i = \begin{pmatrix} 1 \\ (1-\gamma_1^i)(s_i/\lambda) \\ (1-\gamma_1^i)(1-\gamma_2^i)(s_i/\lambda)^2 \\ \vdots \\ \prod_{k=1}^{t_i-1}(1-\gamma_k^i)(s_i/\lambda)^{t_i-1} \end{pmatrix}. \tag{3.61a}$$

Introducing this distribution into the expression for the mean proportion who graduate to stage $i+1$ from stage i we get

$$\begin{aligned}\gamma_i &= \frac{\sum_{j=1}^{t_i}\gamma_j^i\prod_{k=1}^{j-1}(1-\gamma_k^i)(s_i/\lambda)^{j-1}}{\sum_{j=1}^{t_i}\prod_{k=1}^{j-1}(1-\gamma_k^i)(s_i/\lambda)^{j-1}} \\ &= \frac{\lambda/s_i\sum_{j=1}^{t_i}g_j(\lambda/s_i)^{-j}}{\lambda/s_i\sum_{j=0}^{t_i-1}h_j(\lambda/s_i)^{-j}}.\end{aligned} \tag{3.61b}$$

Now from here we want to extract an appplicable formula connecting γ_i and the mean and the variance of T_i. Define

$$a = \ln(\lambda/s_i). \tag{3.62a}$$

Then take logarithms in Eq.(3.61b)

$$\ln\gamma_i = \ln\left(\sum_{j=1}^{t_i}g_je^{-aj}\right) - \ln\left(\sum_{j=0}^{t_i-1}h_je^{-aj}\right). \tag{3.62b}$$

The first term on the right hand side is the cumulant generating function of the g_j. The second term can be seen as the cumulant generating function of the appropriately normalized numbers h_j. Thus writing

$$\hat{h}_j = \frac{h_j}{\sum_j h_j}, \tag{3.62c}$$

we find

$$\ln\gamma_i = \ln\left(\sum_{j=1}^{t_i}g_je^{-aj}\right) - \ln\left(\sum_{j=0}^{t_i-1}\hat{h}_je^{-aj}\right) - \ln\bar{T}_i. \tag{3.62d}$$

where of course, $\bar{T}_i = \sum_j h_j$ is the expected stage duration. We expand both cumulants into power series in a (see Kendall and Stuart 1958), to obtain,

$$\ln \gamma_i = 1 - ak_1(g) + \frac{a^2}{2!}k_2(g) - \cdots - 1 + ak_1(\hat{h}) - \frac{a^2}{2!}k_2(\hat{h}) + \cdots - \ln \bar{T}_i. \quad (3.63a)$$

Here

$$\begin{aligned} k_1(g) &= \bar{T}_i \\ k_2(g) &= \sigma_i \\ k_1(\hat{h}) &= \frac{\sigma_i + \bar{T}_i^2}{2\bar{T}_i}. \end{aligned} \quad (3.63b)$$

Thus, to first order in a,

$$\ln \gamma_i = -a\left(\frac{\bar{T}_i}{2} - \frac{\sigma_i}{2\bar{T}_i}\right) - \ln \bar{T}_i \quad (3.63c)$$

or

$$\gamma_i \simeq (1/\bar{T}_i)exp\left[-a\left(\frac{\bar{T}_i}{2} - \frac{\sigma_i}{2\bar{T}_i}\right)\right]. \quad (3.63d)$$

The second expression gives

$$\gamma_i \simeq \bar{T}_i^{-1} \quad (3.63e)$$

for sufficiently small values of a. When $a = \ln(\lambda/s_i) > 0$, it is obvious that the estimate $\gamma_i \simeq 1/T_i$ overestimates γ_i, because it overestimates the abundance of old individuals within the stage by neglecting the effects of mortality and population growth in shifting the age distribution towards young individuals. The smaller the variance σ_i in stage duration, and the larger the average duration $\bar{T}_i$, the greater the overestimate of γ_i. It is important to note that these estimates depend on the value of λ. However λ is an estimate to be made and cannot be known until the projection matrix is first estimated. One can however assume the value of λ say $\lambda = 1$ and use an iterative method to calculate γ_i. The idea is to choose a value λ then calculate the entries of A, the projection matrix. The eigenvalues of A yield a second estimate of λ. If repeated the process usually converges to the matrix A whose entries are compatible with its own eigenvalues.

Another approach is to relax the assumption of stable within-stage age distribution and assume that the stage duration distribution is negative binomial with mean and variance $E(T)$ and $V(T)$ respectively. As before we let T_i denote the residence time for stage i. There are k stages in the entire life cycle with a common probability γ of moving from stage i to the next stage, $i+1$. The time T required to grow through all the k stages is equal to the k-th success in a series of identically distributed Bernoulli trials with probability of success γ; that is

$$P(T=x) = \binom{x-1}{k-1}\gamma^k(1-\gamma)^{x-k} \tag{3.64a}$$

where

$$E(T) = \tilde{T} = \frac{k}{\gamma} \tag{3.64b}$$

and

$$V(T) = \frac{k(1-\gamma)}{\gamma^2}) \tag{3.64c}$$

To imitate such a situation for stage dynamics we divide a typical stage say i into a series of k identical but invisible "pseudostages" as in Longstaff(1984). These are supposed to slow down individuals proceeding through the stages so as to produce a distribution of stage durations with specified mean and variance. The assumption here is that mortalities and fertility are identical for all pseudostages within a stage. Thus each transition within the stage is conditional on stage-specific survival probability s_i and is given the same specific fertility coefficient f_i which is set to zero for non adult stages in the current model. Solving for γ in the two expressions for $E(T)$ and $V(T)$ yields

$$\hat{\gamma}^i = \frac{\tilde{T}_i}{V(\hat{T}_i) + \tilde{T}_i} \tag{3.64d}$$

and

$$\hat{k}_i = \frac{\tilde{T}_i^2}{v(\tilde{T}_i) + \tilde{T}_i} \tag{3.64e}$$

where $\tilde{T}_i$ and $V(\hat{T}_i)$ are estimates for $E(T)$ and $V(T)$. Thus using $\hat{\gamma}^i$ in Eq.(3.64d) we can estimate p^i_{1j} and $\pi^i_{j+1,j}$ in Eq.(3.38b) and Eq.(3.38c) respectively. Thus if from observed data we can estimate the mean and variance of stage duration then γ_i and k_i can be estimated from the equations above. The estimate k_i can be interpreted as the waiting time before an individual transits to the next stage.

3.5.3 Estimation from Experimental Cumulative Distributions

Assume that an experiment is conducted at time t_0. Let us focus our attention on a particular stage say $i = 1, \ldots, k$ and on a specific cohort of individuals at time t_0. Since there are t_i age classes of equal size then at any time $t \in [t_0, t_0 + t_i)$, any individual still in this cohort is of age $j = t - t_0 + 1$. Let

M = total number of individuals which will transit to the next stage $i + 1$.

$F(t)$ = proportion of the M individuals that have transited to stage $i + 1$ by time t

t_1 = time just prior to the transition (to stage $i + 1$) of the first individual

t_2 = the time at which the last individual transits to stage $i + 1$.

Then obviously $F(t)$ is monotonic increasing namely $0 \leq F(t) \leq 1$. It is called the experimental cumulative distribution. It follows that given an individual survives to stage $i + 1$, the probability that it transits to the next stage within $[t, t + 1)$ is given by the expression

$$p^i_{1j} = F(t + 1) - F(t) \tag{3.65}$$

The event that an individual transits during $[t, t + 1)$ is the same as that it transits at age $j = t - t_0 + 1$.

Given that an individual is in age $j = t - t_0 + 1$ and it will survive to the next stage the conditional probability that it transits to the next stage during the time interval $[t, t + 1)$, is given by the expression

$$\tilde{\gamma}^i_{1j} = \begin{cases} \frac{F(t+1)-F(t)}{1-F(t)} & t < t_2 \\ 1 & t \geq t_2 \end{cases} \tag{3.66}$$

That is if we let U_{ij} denote the event that an individual of age j in stage i will survive to stage $i + 1$ then

$$P(T(t)|U_{ij}) = \begin{cases} \frac{F(t+1)-F(t)}{1-F(t)} & t < t_2 \\ 1 & t \geq t_2 \end{cases} \tag{3.67}$$

that is

$$\tilde{\gamma}^i_{1j} = P(T(t)|U_{ij}) \tag{3.68}$$

where $T(t)|U_{ij}$ denotes the event that an individual transits to stage $i+1$ in the interval $[t, t+1)$ given it survives to that stage. The event $T(t)$ had already been defined in section 3.4. That is if we can work out a functional expression for $F(t)$ we can use Eq.(3.68) to estimate γ_{ij}^{i} then using it together with information on survival probabilities in Eq.(3.37b) and Eq.(3.38c) one is able to parametrize the matrix A^*.

All the methods of estimation highlighted above are based on the assumption of homogeneity. In chapter VI we will revisit the problem of estimation of the elements of matrix A and its generalized counterpart, A^*. The effect of seasonality and vegetation type to the vital rates is incorporated into the system.

3.6 Classical Leslie and Experimental Transition Probabilites

In this section we wish to derive the relationship between the two probabilities given in Eq.(3.38a) and Eq.(3.68). The difference between the two probabilities is in the condition. $S_{ij}(t)$ is the event that the individual will survive to time $t+1$, but we do not know whether it will stay in the same stage or transit to the next stage. $S_{ij}(t)$ is only related to the time interval $[t, t+1)$. On the other hand U_{ij} is the event that an individual will survive to the next stage, but we do not know when it will transit. U_{ij} is related to the time interval $[t, t+t_i-j+1)$. In fact we deduce that

$$U_{ij} \subseteq S_{ij}(t) \tag{3.69}$$

The relationship between the transition probabilities in the classical Leslie model and those from experimental cumulative distributions is contained in the following two theorems. The theorems are proved elsewhere by Yanan *et al* (1990) but we present modified proofs relating to the current work. However before we state and prove the theorems we present some useful statements and notations:

$S_{ij}(t, t+m)$ =the event that an individual at age j in stage i at time t will survive to time $t+m$, and $S_{ij}(t) = S_{ij}(t, t+1)$ for simplicity and

$T(t, t+m)$ = the event that an individual will transit to the next stage during the time interval $[t, t+m)$, and $T(t) = T(t, t+1)$ for simplicity.

Theorem 3.7 If the following Markov-like property holds,

$$P(S_{ij}(t,t+r+1) \cap T(t+r,t+r+1))$$
$$= P(S_{ij}(t,t+r) \cap T^c(t,t+r))P(S_{i,j+r}(t+r,t+r+1) \cap T(t+r,t+r+1)) \tag{3.71a}$$

and

$$P(S_{ij}(t,t+r+1) \cap T^c(t+r,t+r+1))$$
$$= P(S_{ij}(t,t+r) \cap T^c(t,t+r))P(S_{i,j+r}(t+r,t+r+1) \cap T^c(t+r,t+r+1)) \tag{3.71b}$$

then the transition probabilities in the Leslie model can be obtained from experimental cumulative distributions by the following formulae:

$$\gamma^i_{1t_i} = \tilde{\gamma}^i_{1t_i} = 1, \tag{3.72a}$$

and

$$\gamma_{ij} = \frac{\phi(j)\tilde{\gamma}_{ij}}{1-[1-\phi(j)]\tilde{\gamma}_{ij}}, \quad j = 1,\ldots,t_i - 1 \tag{3.72b}$$

where

$$\phi(j) = \sum_{r=1}^{t_i-j}(\prod_{m=1}^{r-1} s_{i,j+m}(1-\gamma_{i,j+m}))s_{i,j+r}\gamma_{i,j+r}, \tag{3.72c}$$

$$s_{i,j+m} = P(S_{i,j+m}(t+m)),$$

and the conventions

$$\prod_{r_1}^{-1} a(r_1) = \prod_{r_1=1}^{0} a(r_1) = 1$$

is always assumed. Further, if $s_{ij} = s_i \;\; \forall j = 1,\ldots,t_i$, say, then Eq.(3.72d) becomes

$$\phi(j) = \sum_{r=1}^{t_i-j} s_i^r \left\{ \prod_{r_1=1}^{r-1} (1-\gamma_{i,j+r_1} \right\} \gamma_{i,j+r}. \tag{3.72e}$$

Proof: By definition of the event U_{ij}, we have

$$U_{ij} = \bigcup_{r=0}^{t_i-j}(S_{ij}(t,t+r+1) \cap T(t+r,t+r+1))$$

Since

$$T(t+r,t+r+1), \quad r = 0,1,\ldots,t_i - j,$$

are mutually exclusive events

$$(S_{ij}(t,t+r+1)\cap T(t+r,t+r+1)),\quad r=0,1,\ldots,t_i-j$$

are also mutually exclusive. Hence

$$\begin{aligned}P(U_{ij}) &= P\left\{\bigcup_{r=0}^{t_i-j}(S_{i,j}(t,t+r+1)\cap T(t+r,t+r+1))\right\}\\ &= \sum_{r=0}^{t_i-j}P\left\{S_{i,j}(t,t+r+1)\cap T(t+r,t+r+1)\right\}.\end{aligned}$$

From Eq.(3.71a)

$$P(U_{ij})=\sum_{r=0}^{t_i-j}P\Big(S_{ij}(t,t+r)\cap T^c(t,t+r)\Big)P\Big(S_{i,j+r}(t+r)\cap T(t+r)\Big)$$

where

$$S_{i,j+r}=S_{i,j+r}(t+r,t+r+1)\quad\text{and}\quad T(t+r)=T(t+r,t+r+1)$$

for simplicity. Using Eq.(3.71b) repeatedly we have

$$P(U_{ij})=\sum_{r=0}^{t_i-j}\left\{\prod_{m=0}^{r-1}P\Big(S_{i,j+m}(t+m)\cap T^c(t+m)\Big)\right\}P\Big(S_{i,j+r}(t+r)\cap T(t+r)\Big). \tag{3.73a}$$

By definition of $s_{i,j+m}$ and $\gamma_{i,j+m}$ we have

$$\begin{aligned}P\Big(S_{i,j+m}(t+m)\cap T^c(t+m)\Big) &= P\Big(S_{i,j+m}(t+m)\Big)P\Big(T^c(t+m)|S_{i,j+m}(t+m)\Big)\\ &= s_{i,j+m}(1-\gamma_{i,j+m})\end{aligned} \tag{3.73b}$$

for $m=0,1,\ldots,r-1$, and

$$\begin{aligned}P(S_{i,j+r}(t+r)\cap T(t+r) &= P\Big(S_{i,j+r}(t+r)\Big)P\Big(T(t+r)|S_{i,j+r}(t+r)\Big)\\ &= s_{i,j+r}\gamma_{i,j+r}.\end{aligned} \tag{3.73c}$$

Using equations (3.73a), (3.73b) and (3.73c) we get

$$\begin{aligned}P(U_{ij}) &= \sum_{r=0}^{t_i-j}\left\{\prod_{m=0}^{r-1}s_{i,j+m}(1-\gamma_{i,j+m})\right\}s_{i,j+r}\gamma_{i,j+r}\\ &= s_{ij}\gamma_{ij}+s_{ij}(1-\gamma_{ij})\sum_{r=1}^{t_i-j}\Big(\prod_{m=1}^{r-1}s_{i,j+m}(1-\gamma_{i,j+m})\Big)s_{i,j+r}\gamma_{i,j+r}\\ &= s_{ij}\gamma_{ij}+s_{ij}(1-\gamma_{ij})\phi(j)\\ &= s_{ij}\gamma_{ij}(1-\phi(j))+s_{ij}\phi(j),\end{aligned} \tag{3.74a}$$

where

$$\phi(j) = \sum_{r=1}^{t_i-j} \Big(\prod_{m=1}^{r-1} s_{i,j+m}(1-\gamma_{i,j+m}) \Big) s_{i,j+r}\gamma_{i,j+r}$$

Now we show that

$$T(t) \cap U_{ij} = T(t) \cap S_{ij}(t)$$

Note that

$$U_{ij} = \bigcup_{r=0}^{t_i-j} (S_{ij}(t, t+r+1) \cap T(t+r, t+r+1))$$

Hence

$$\begin{aligned} T(t) \cap U_{ij} &= \bigcup_{r=0}^{t_i-j} T(t) \cap (S_{ij}(t, t+r+1) \cap T(t+r, t+r+1)) \\ &= T(t) \cap [S_{i,j}(t) \cap T(t)] \\ &= S_{i,j}(t) \cap T(t). \end{aligned}$$

Thus we have

$$P(T(t) \cap U_{ij}) = P(T(t) \cap S_{ij}(t)) \tag{3.74b}$$

Now note that

$$\gamma_{ij} = \frac{P(T(t) \cap S_{ij}(t)}{P(S_{ij}(t)}$$

thus

$$s_{ij}\gamma_{ij} = P(T(t) \cap S_{ij})$$

and from Eq.(3.74b)

$$\begin{aligned} s_{ij}\gamma_{ij} &= P(T(t) \cap U_{ij}) \\ &= P(U_{ij}) \frac{P(T(t) \cap U_{ij})}{P(U_{ij})} \cdot \end{aligned}$$

We now use the expression for $P(U_{ij})$ to get

$$s_{ij}\gamma_{ij} = [s_{ij}\gamma_{ij}(1-\phi(j)) + s_{ij}\phi(j)]\tilde{\gamma}_{ij}$$

and solving for γ_{ij} we have

$$\gamma_{ij} = \frac{\phi(j)\tilde{\gamma}_{ij}}{1-[1-\phi(j)]\tilde{\gamma}_{ij}}, \quad j = 1, \ldots, t_i - 1.$$

Theorem 3.8: Under the condition that Eq.(3.71) and Eq.(3.71b) hold,

$$\gamma_{ij} = \tilde{\gamma}_{ij}, \quad j = 1, \ldots, t_i - 1 \quad \text{iff} \quad s_{ij} = 1, \forall j = 1, 2, \ldots, t_i$$

That is, for a given stage i, the two transition probabilites are identical if and only if the survival rate for any age group of the stage is 1.

Proof. (1) Sufficiency: Suppose that

$$s_{ij} = 1 \quad \forall j = 1, \ldots, t_i.$$

Then

$$\begin{aligned}\phi(j) &= \sum_{r=1}^{t_i-1}\left(\prod_{m=1}^{r-1}(1-\gamma_{i,j+m})\right)\gamma_{i,j+r} \\ &= \gamma_{i,j+1} + (1-\gamma_{i,j+1})\gamma_{i,j+2} + (1-\gamma_{i,j+1})(1-\gamma_{i,j+2})\gamma_{i,j+3} + \ldots \\ &+ (1-\gamma_{i,j+1})\cdots(1-\gamma_{i,t_i-2})\gamma_{i,t_i-1} \\ &+ (1-\gamma_{i,j+1})\cdots(1-\gamma_{i,t_i-2})(1-\gamma_{i,t_i-1})\gamma_{i,t_i}.\end{aligned}$$

Now since

$$\gamma_{i,t_i} = 1$$

combining the last two terms in the just concluded expression gives

$$\begin{aligned}\phi(j) &= \gamma_{i,j+1} + (1-\gamma_{i,j+1})\gamma_{i,j+2} + (1-\gamma_{i,j+1})(1-\gamma_{i,j+2})\gamma_{i,j+3} + \cdots \\ &+ (1-\gamma_{i,j+1})\cdots(1-\gamma_{i,t_i-2}).\end{aligned}$$

Continuing in this manner we finally get

$$\phi(j) = 1$$

and by substituting this result into Eq.(3.72b) we get

$$\gamma_{ij} = \tilde{\gamma}_{ij} \quad j = 1, \ldots, t_i - 1.$$

(2) Necessity: Suppose

$$\gamma_{ij} = \tilde{\gamma}_{ij} \quad j = 1, \ldots, t_i - 1$$

then from Theorem 3.7

$$\gamma_{ij} = \frac{\phi(j)\gamma_{ij}}{1 - [1 - \phi(j)]\gamma_{ij}} \quad , j = 1, \ldots, t_i - 1$$

which implies that

$$1 - [1 - \phi(j)]\gamma_{ij} = \phi(j)$$

or

$$[1 - \phi(j)](1 - \gamma_{ij}) = 0$$

and since

$$\gamma_{ij} < 1 \quad \forall j = 1, \ldots, t_i - 1$$

then

$$\phi(j) = 1 \quad j = 1, \ldots, t_i - 1. \tag{3.74c}$$

On the other hand if $\exists$ some m_1 with $0 \leq m_1 \leq t_i - j$ such that

$$s_{i,j+m_1} < 1 \tag{3.74d}$$

then we can show that

$$\phi(j) < 1 \tag{3.74e}$$

which contradicts Eq.(3.74c). Then we have

$$s_{ij} = 1, \quad j = 1, \ldots, t_i.$$

So all that is left to do is to show that Eq.(3.74d) implies Eq.(3.74e). From Theorem 3.7

$$\begin{aligned}
\phi(j) &= \sum_{r=1}^{t_i - 1} \left(\prod_{m=1}^{r-1} s_{i,j+m}(1 - \gamma_{i,j+m}) \right) s_{i,j+r}\gamma_{i,j+r} \\
&= \sum_{r=1}^{m_1 - 1} \left(\prod_{m=1}^{r-1} s_{i,j+m}(1 - \gamma_{i,j+m}) \right) s_{i,j+r}\gamma_{i,j+r} \\
&+ \sum_{r=m_1}^{t_i - j} \left(\prod_{m=1}^{r-1} s_{i,j+m}(1 - \gamma_{i,j+m}) \right) s_{i,j+r}\gamma_{i,j+r}.
\end{aligned}$$

Now let all $s_{i,j+m}$ be replaced by 1 except $s_{i,j+m_1}$, then

$$\phi(j) \le \sum_{r=1}^{m_1-1}\left(\prod_{m=1}^{r-1}(1-\gamma_{i,j+m})\right)\gamma_{i,j+r}$$
$$+\sum_{r=m_1}^{t_i-j} s_{i,j+m_1}\left(\prod_{m=1}^{r-1}(1-\gamma_{i,j+m})\right)\gamma_{i,j+r}.$$

Since $\gamma_{i,j+m} < 1, \quad m = 1, 2, \dots, t_i - j - 1$, and $\gamma_{i,t_i} = 1$

$$\prod_{m=1}^{t_i-j-1}(1-\gamma_{i,j+m})\gamma_{i,t_i} > 0$$

and from eq.(3.74d)

$$s_{i,j+m_1}\left(\prod_{m=1}^{t_i-j-1}(1-\gamma_{i,j+m})\right)\gamma_{i,t_i} < \left(\prod_{m=1}^{t_i-j-1}(1-\gamma_{i,j+m}\right)\gamma_{i,t_i}.$$

Therefore

$$\phi(j) < \sum_{r=1}^{m_1-1}\left(\prod_{m=1}^{r-1}(1-\gamma_{i,j+m})\right)\gamma_{i,j+r}$$
$$+\sum_{r=m_1}^{t_i-1}\left(\prod_{m=1}^{r-1}(1-\gamma_{i,j+m})\right)\gamma_{i,j+r}$$
$$=\sum_{r=1}^{t_i-j}\left(\prod_{m=1}^{r-1}(1-\gamma_{i,j+m})\right)\gamma_{i,j+r}$$
$$=1.$$

That is

$$\phi(j) < 1.$$

Since Eq.(3.74e) contradicts Eq.(3.74c) it follows that Eq.(3.74d) is false. Therefore we have

$$s_{ij} = 1 \quad \forall j = 1, \dots, t_i.$$

The practical implication of these two theorems is that the two kinds of transition probabilities are very different for lower survival rates. This means that the difference will be significant for those stages where survival is generally low due to say high sensitivity to unfavourable conditions.

It is important to note that while the experiments are often conducted under conditions which lead to high survival, the Leslie model is often used to simulate real environmental conditions, such as seasonality, diapause, predation, chemical treatment and so on. For example Stinner(1975) studies the effect of temperature on development rates of a beetle population. From Theorem 3.8 we know that the two kinds of transition probabilities are identical if and only if the survival rates in the experiment are 1. It follows that when the experimental survival rates are high, making the function $\phi(j)$ close to 1, then the cumulative distribution provides a close approximation to the Leslie transition probabilities. The results described provide a connection between the two kinds of probabilities, and we expect will assist in more accurate model construction and use.

A simulation model for the brown ear tick (*R. appendiculatus*) population is presented in chapter VI to validate and clarify some of these ideas. The simulation is based on the data by Short *et al*(1989a,b) collected in Zimbabwe. It is a multiple matrix product simulation model where variability in the matrix inputs is due to seasonality and vegetation type.

CHAPTER IV

A VECTOR-HOST INTERACTION MODEL

4.1 Modeling approaches

Terminology and Definitions

We start by giving some basic definitions and terminologies.

1.) Fecundity means the number of eggs per female based on a 1:1 sex ratio. This may vary with female body size and saturation.

2.) Pre-oviposition period: This is the period in the female adult, from completion of engorgement to first day of egg laying.

3.) Egg development period: This is the period from first day of egg laying to first day of hatching.

4.) Moulting period: Applies to engorged larvae and nymph.

Different types of models

We shall design a sequence of models of increasing complexity in a building block fashion. The simplest model will be a linear stage model for the tick population only. Here the first modeling problem arises. Each individual undergoes development from egg through larva, nymph and adult whereby the duration of stages is subject to variation and external factors such as temperature and humidity. There are basically four different ways to describe such a situation.

1.) Discrete time compartment model of the form

$$x_j^{t+1} = a_{j-1} x_{j-1}^t, \quad j = 1, ..., n \tag{4.1}$$

with subscripts taken cyclically. In general x_j^t denotes the number of individuals in compartment j while the constant a_j denotes the proportion transiting into compartment $j+1$ from compartment j in one time step. Then the time step t has to be interpreted either as a generation (which does not make sense in any field study) or as a chronological time step, for example t could be counting weeks or months. Then the different compartments x_j have to be attributed to certain developmental stages. This amounts to an implicit coupling of the lengths of these stages to the time steps.

2.) Continuous time compartment model in the form of

$$\dot{x}_j(t) = \alpha_{j-1}x_{j-1} - \mu_j x_j, \quad j = 1, ..., n, \tag{4.2}$$

again subscripts taken cyclically. The variable x_j carries the same meaning as above while $\dot{x}_j(t)$ denotes its derivative with respect to time. This approach seems more flexible and suitable to describe overlapping generations. The rate α_{j-1} describes the transitions at which individuals enter the j-th compartment, and μ_j is the rate at which they leave the compartment. Again, the model structure implies an assumption on the underlying process: Individuals leave the j-th compartment according to a Poisson process with parameter μ_j. The probability for an individual to stay in compartment j decreases as $\exp(-\mu_j t)$. If T is the exit time from stage j, then

$$Pr\{T \geq t\} = e^{-\mu_j t}. \tag{4.3}$$

Then the probability distribution function is

$$F(t) = \begin{cases} 1 - e^{-\mu_j t}, & \text{if } t \geq 0 \\ 0, & \text{if } t < 0. \end{cases} \tag{4.4}$$

and the probability density is:

$$f(t) = \begin{cases} \mu_j e^{-\mu_j t}, & \text{if } t \geq 0 \\ 0, & \text{if } t < 0. \end{cases} \tag{4.5}$$

Thus the mean and variance are;

$$\begin{aligned} E(T) &= \textstyle\int_0^\infty \mu_j e^{-\mu_j t} t dt = 1/\mu_j \\ V(T) &= E(T^2) - (E(T))^2 = 1/\mu_j^2 \end{aligned} \tag{4.6}$$

Thus the compartment model assumes that the sojourn time in compartment j is on the average, $1/\mu_j$.

3.) A third possibility would be a structured model along the lines of the physiologically structured population models of Metz and Diekmann (1986). These authors test their models for *Daphnia* populations. Then the model would take the form

$$\frac{\partial u(t,x)}{\partial t} + \frac{\partial (g(x)u(t,x))}{\partial x} = -\mu(x)u(t,x) \tag{4.7}$$

with an appropriate recruitment condition, namely

$$u(t,0) = \int_0^\infty b(x)u(t,x)dx. \tag{4.8}$$

The continuous parameter x describes the stage, the function $\mu(x)$ is the stage dependent mortality and $g(x)$ is the rate at which the individuals pass through the stages with reference to chronological time. Corresponding to the partial differential equation(4.7) there is an associated system of "characteristic" ordinary differential equations(see John 1978)

$$\frac{dt}{ds} = 1, \quad \frac{dx}{ds} = g(x), \quad \frac{du}{ds} = -(g'(x) + \mu(x)). \tag{4.9}$$

Since $t = t_0 + s$ with some constant t_0, the second characteristic equation $dx/dt = g(x)$ describes how the different stages are passed in time. Notice that this law is again deterministic in the sense that the stage is uniquely determined by the time. Of course discontinuities such as transitions between entirely different stages such as larva and nymph can be incorporated by appropriately replacing the single equation by a system of equations.

4.) Finally one can try to incorporate maturation periods, diapause periods and so on in the form of delays. In a general sense delay equations can be considered as special cases of the hyperbolic systems mentioned in Eq.(4.9) above where coefficients are step functions.

It appears that there is a problem in comparing these approaches. As indicated earlier, the Leslie type models described in Eq.(4.1) have a fixed time scale. The time step must be defined, for example as a period of one year, one month, or one week. Equation of the form (4.1), can more generally be expressed as

$$x_i^{t+1} = \sum_k a_{ik} x_k^t, \tag{4.10}$$

where a_{ik} denotes the proportion of individuals from the k-th class that move into the i-th class during one time step. If the sum

$$\sum_i a_{ik}$$

is less than 1 then not all individuals of the k class are distributed to other stages, that is a mortality after the k-th stage is implicitly modelled. A more detailed description can be obtained with time dependent transition matrices. In the general system (4.10) the types or classes need not be consecutive stages in the life of an individual. As in the model of Sandberg *et al.* (1992) where the classes were determined by whether an individual is in its 1-st or 2-nd year or whether fall-fed or spring-fed thus in a model the types or states may be different life histories apart from consecutive stages in the life of an individual.

In the ordinary differential equations model (4.2), or more generally

$$\dot{x}_i = \sum_k b_{ik} x_k, \tag{4.11a}$$

there is also an implicit time scale, because, if properly connected to data, the coefficients are rates, that is transitions per time unit. Typically the diagonal elements are negative numbers. Since for each stage the exit time from that stage is modeled by a Poisson process, the expected residence time in the ith stage is $-1/b_{ii}$, where $b_{ii} < 0$ since it denotes the rate which individuals leave stage i. For example in Eq.(4.2) the average residence time in the j-th compartment is $1/\mu_j$. The residence time so computed is the residence time for all individuals independent of whether these move to the next stage or just die. Note that equation (4.11a) can be written in matrix notation as

$$\dot{\vec{x}} = B\vec{x} \tag{4.11b}$$

where

$$B = (b_{ik}) \quad i, k = 1, \ldots, n. \tag{4.11c}$$

Usually it is easy to condition on survival to the next stage. Suppose, for example the i-th and $(i+1)$-st equations posses the form

$$\dot{x}_i = \ldots - a_i x_i - \mu_i x_i,$$

$$\dot{x}_{i+1} = \ldots + a_i x_i \ldots,$$

where a_i is the trasition rate from stage i into stage $i+1$ and μ_i the mortality rate for individuals in stage i then it follows that the residence time in the i-th stage of those who continue to the next stage is $1/a_i$.

Now we consider the transition between the continuous time system (4.11a) and the discrete time system (4.10). The mathematical procedure we apply is the Euler one step method for the differential equation

$$\dot{u} = F(u) \tag{4.12}$$

where the variable u is a function of time and in general u could be vector valued. If we discretize time in small time steps of size h such that

$$t_{i+1} = t_i + h$$

then we can approximately write

$$u(t_{i+1}) = hF(u(t_i)) + u(t_i). \tag{4.13}$$

Thus if we discretize Eq.(4.11a) by the Euler one step method then we arrive formally at a discrete time system

$$y_i^{m+1} = y_i^m + h\sum_k b_{ik} y_k^m, \qquad (4.13)$$

thus formally

$$a_{ik} = \delta_{ik} + hb_{ik} \tag{4.14}$$

or, in matrix form,

$$A = I + hB \qquad (4.15).$$

Here y_i^m denotes the number of individuals in class i after m time steps or at time $t = mxh$ thus y_i^m must be seen as an approximation to $x_i(t)$. Of course one time step of the discrete system correponds to a time interval of length h in the continuous system. If we just interpret $I + hB$ as the matrix of a discrete time stage model then we must bear in mind that the rates are adapted to a time step h.

This is clear if we suppose in the expansion

$$\sum_{j=0}^{\infty} \frac{(hB)^j}{j!} = \exp\{hB\} \tag{4.16}$$

h is small such that we can ignore powers of h of order two and above, so that we can write

$$\exp\{hB\} \simeq I + hB \qquad (4.17).$$

Thus the above considerations are (approximately) correct only for small h that is as long as $I + hB$ is a good approximation for $\exp\{hB\}$. If h is too large then $I + hB$ becomes meaningless as a matrix of a discrete time model.

The converse is even more difficult. Suppose we are given a discrete time system (4.10) then we can artificially make a transition to a continuous time system by introducing the length $h = 1$ of the time step that underlies the data, and write

$$x^{m+1} - x^m = h(A - I)x^m. \qquad (4.18)$$

If $h = 1$ can be considered small in relation to the changes in the x^m then one can replace the difference quotient $(x^{m+1} - x^m)/h$ by the derivative $\dot{x}$ and thus arrive at Eq.(4.11b) with $B = A - I$. The asymmetry between the two problems arises from the fact that a derivative (differential quotient) by definition is the limit of difference quotients, but a difference quotient in general cannot be approximated (in a unique way) by derivatives.

Finally we try to etablish the connection between the partial differential equations in model (4.7) and Leslie models. We discretize the time and space variable with equidistant steps Δt and Δx, respectively. The solution $u(t, x)$ is then approximated by u_i^k, when $x = i\Delta x$, $t = k\Delta t$. That is u_i^k denotes the number of individuals who are in stage class i after k time periods. In a similar manner we can discretize the continuous function $g(x)$ such that g_i represents the rate at which individuals pass through stage class i. Let us now closely consider individuals in stage class i at time t who by definition are denoted by u_i^k. Clearly the fate of an individual in the $(i + 1)$-th class after one time step is determined by one of the following;

(i) grow or mature into class $i + 2$ at rate determined by g_{i+1}

(ii) remain in the same stage or

(iii) exit the system through natural mortality at a rate of μ_{i+1}.

Thus the discretized equation corresponding to Eq.(4.7) results in the following balance equation

$$u_{i+1}^{k+1} = u_{i+1}^{k} - (\Delta t/\Delta x)(g_{i+1}u_{i+1}^{k} - g_i u_i^k) - \Delta t \mu_{i+1} u_{i+1}^{k}, \tag{4.19a}$$

which by re-arrangements of terms gives

$$u_{i+1}^{k+1} = (1 - (\Delta t/\Delta x)g_{i+1})u_{i+1}^{k} + (\Delta t/\Delta x)g_i u_i^k - \Delta t \mu_{i+1} u_{i+1}^{k}. \tag{4.19b}$$

Then replacing i by $i-1$ we get

$$u_i^{k+1} = (1 - (\Delta t/\Delta x)g_i)u_i^k + (\Delta t/\Delta x)g_{i-1}u_{i-1}^{k} - \Delta t \mu_i u_i^k. \tag{4.19c}$$

This system says that at the time step from t to $t+1$ a certain proportion $(1-(\Delta t/\Delta x)g_i)$ of individuals stay in the ith compartment, and a proportion of $(\Delta t/\Delta x)g_{i-1}$ move from the $(i-1)$-st to the i-th, whereas $\Delta t \mu_i$ exit the system through natural mortality. The recruitment condition (4.8) is discretized as

$$u_0^{k+1} = \sum_{i=0}^{N} b_i u_i^k. \tag{4.20}$$

where we assume the system is structured into N compartments and b_i denotes the fecundity of the i-th compartment or stage class. Thus, formally, we obtain a Leslie model.

So far we have attempted to reconcile the two types of population models namely the continuous and discrete population models. This is important because in most cases the two model approaches are used together or ideas in one can help to understand the other better and vice versa.

4.2 The Compartment Model

Let the variables $x_1, x_2, \ldots, x_n$ with $(n = 10)$ denote the numbers of individuals in the stages 1 to n. Let p_i, $i = 1, \ldots, n-1$, be the rate of transition from stage i to stage $i+1$. For the moment we assume that the p_i are constants, later we can let these quantities depend on external parameters such as temperature or host abundance. In each stage there is a natural mortality μ_i, $i = 1, \ldots, n$.

The model is a cyclic chain model of n linear differential equations with constant coefficients,

$$\begin{aligned}
\dot{x}_1 &= f x_n - p_1 x_1 - \mu_1 x_1 \\
\dot{x}_2 &= p_1 x_1 - p_2 x_2 - \mu_2 x_2 \\
&\cdots \\
\dot{x}_i &= p_{i-1} x_{i-1} - p_i x_i - \mu_i x_i \\
&\cdots \\
\dot{x}_{n-1} &= p_{n-2} x_{n-2} - p_{n-1} x_{n-1} - \mu_{n-1} x_{n-1} \\
\dot{x}_n &= p_{n-1} x_{n-1} - \mu_n x_n .
\end{aligned} \tag{4.21}$$

The p_j, $j = 1, 2, \ldots, n-1$ are defined as follows:

p_1: rate of egg hatching

p_2: rate of larval attachment onto a host

p_3: rate of drop offs from a host by larva

p_4: rate of moulting by developing larva

p_5: rate of attachment by questing nymph

p_6: rate of drop offs from host by nymph

p_7: rate of moulting by developing nymph

p_8: rate of host attachment by questing adult

p_9: rate of drop off from host by engorged adults

f: fecundity of the adult stage

Now, system (4.21) can be written in matrix notation as shown below,

$$\begin{pmatrix} \dot{x}_1 \\ \dot{x}_2 \\ \vdots \\ \dot{x}_{n-1} \\ \dot{x}_n \end{pmatrix} = \begin{pmatrix} -a_1 & 0 & 0 & \cdots & 0 & f \\ p_1 & -a_2 & 0 & \cdots & 0 & 0 \\ 0 & p_2 & -a_3 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \cdots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & p_{n-1} & -a_n \end{pmatrix} \begin{pmatrix} x_1 \\ x_2 \\ \vdots \\ x_{n-1} \\ x_n \end{pmatrix} \tag{4.22}$$

where $a_i = p_i + \mu_i$, $i = 1, 2, \ldots, n-1$ and $a_n = \mu_n$. More compactly the system (4.22) can be writen as

$$\dot{\vec{x}} = A\vec{x} \tag{4.23}$$

where A is the matrix in Eq.(4.22).

A discretized version of Eq.(4.23) is given by;

$$\vec{x}_{t+1} - \vec{x}_t = hA\vec{x}_t$$

or

$$\vec{x}_{t+1} = (I + hA)\vec{x}_t = L\vec{x}_t$$

where $L = I + hA$ for small h is a discrete type Leslie matrix, as derived in section 4.1 and h measures the time step.

The matrix $A = (a_{ij})$ is of a type that is called essentially nonnegative, that is the off-diagonal elements are nonnegative while the diagonal elements may be of either sign (nonpositive in the present case). In case the p_i and f are all positive, the matrix is irreducible. Thus to this matrix the theorem of Perron-Frobenius can be applied. For any matrix A, define the spectral bound as the least upper bound of the real parts of the eigenvalues. In other words, the spectral bound is the maximum taken over the real parts of all eigenvalues. In general, the spectral bound need not be an eigenvalue itself. But in the case of an essentially nonnegative matrix, the spectral bound is a (real) eigenvalue. Furthermore, if the essentially nonnegative matrix is irreducible then the spectral bound is a simple root of the characteristic polynomial and all other eigenvalues have strictly smaller real parts. Corresponding to the spectral bound there is a positive eigenvector. There are no positive eigenvectors to any other eigenvalues. Thus the spectral bound governs the stability of the zero solution of the differential equation. If the spectral bound is postive then the population will grow exponentially; if it is negative, then it will decay.

Of course, the spectral bound is a zero of the characteristic polynomial. This is because the matrix A we are dealing with in Eq.(4.22) is essentially nonnegative and irreducible. We analyse the properties of the matrix A by first getting a compact expression for the characteristic polynomial. In general the characteristic polynomial can be obtained by expanding the determinant $|A - \lambda I|$.

In the case of the matrix A in Eq.(4.23) the characteristic polynomial can most conveniently be obtained from the corresponding linear system rather than by expanding determinants, this is clear from the fact that the characteristic polynomial is a function of λ only. Thus to obtain the polynomial from $A\vec{x} = \lambda\vec{x}$ we have to eliminate the x_i's from the equation which is explicitly given by

$$\begin{aligned}
\lambda x_1 &= f x_n - p_1 x_1 - \mu_1 x_1 \\
\lambda x_2 &= p_1 x_1 - p_2 x_2 - \mu_2 x_2 \\
&\ldots\ldots \\
\lambda x_i &= p_{i-1} x_{i-1} - p_i x_i - \mu_i x_i \\
&\ldots\ldots \\
\lambda x_{n-1} &= p_{n-2} x_{n-2} - p_{n-1} x_{n-1} - \mu_{n-1} x_{n-1} \\
\lambda x_n &= p_{n-1} x_{n-1} - \mu_n x_n.
\end{aligned} \tag{4.24}$$

From the last equation

$$x_{n-1} = \frac{a_n + \lambda}{p_{n-1}} x_n, \tag{4.25}$$

and from the second last equation

$$\begin{aligned}
x_{n-2} &= \frac{a_{n-1} + \lambda}{p_{n-2}} x_{n-1} \\
&= \frac{(a_{n-1} + \lambda)(a_n + \lambda)}{p_{n-2} p_{n-1}} x_n,
\end{aligned} \tag{4.26}$$

where $a_i = p_i + \mu_i \quad , i = 2, \ldots, n-1$ and $a_n = \mu_n$. Continuing in this manner we get a general expression for x_i as,

$$x_i = x_n \prod_{j=i+1}^{n} (a_j + \lambda) / \prod_{j=i}^{n-1} p_j. \tag{4.27}$$

In particular

$$x_1 = x_n \prod_{j=2}^{n} (a_j + \lambda) / \prod_{j=1}^{n-1} p_j. \tag{4.28}$$

From the first of the equations in Eq.(4.24) we get that,

$$x_n = \frac{a_1 + \lambda}{f} x_1. \tag{4.29}$$

Substituting this expression in the above formula for x_1 and eliminating $x_1 \neq 0$ we finally get the characteristic polynomial in the form

$$P(\lambda) = \prod_{i=1}^{n}(a_i + \lambda) - f \prod_{i=1}^{n-1} p_i, \tag{4.30a}$$

that is

$$P(\lambda) = \prod_{i=1}^{n}(p_i + \mu_i + \lambda) - f \prod_{i=1}^{n-1} p_i, \tag{4.30b}$$

(with $p_n = 0$) since in general p_i denotes the rate of moving from compartment i to compartment $i+1$ and according to the model specification, compartment n is the last in the system therefore p_n is set to zero. It is assumed individuals can only leave the last compartment through death. These individuals reproduce at a rate f when still surviving. At this point we wish to discuss the relationship of the current system to the discrete case particularly in relation to the Perron-Frobenius Theorem and Cauchy polynomials.

Remark 4.1: The Discrete Time Case.

Consider any nonnegative matrix $A = (a_{ij})$. Then the Perron-Frobenius theorem (classical version) applies. In particular one can look at matrices of Leslie type.

Also one can consider the class of stochastic matrices, and the class of stochastic companion matrices. The stochastic companion matrices have characteristic polynomials of the form

$$P(\lambda) = \lambda^n - \sum_{i=0}^{n-1} a_i \lambda^i \tag{4.31a}$$

where

$$a_i \geq 0, \quad \sum_{i=0}^{n-1} a_i = 1. \tag{4.31b}$$

A polynomial of the form (4.31a) with the property (4.31b) is called a Cauchy polynomial. Cauchy polynomials have several interesting properties. Trivially all their eigenvalues lie in the unit disc $\{\lambda : |\lambda| \leq 1\}$, and 1 is an eigenvalue. Furthermore on the unit circle only those numbers can be eigenvalue of any Cauchy polynomial of order n that are roots of unity of some order $m \leq n$. Except 1, no positive number can be a root of any Cauchy polynomial. For given n, the set of all eigenvalues of all Cauchy polynomials is a compact subset of the unit circle that has two connected components: the isolated point $\{1\}$ and a compact star-shaped domain.

In the present case of matrices related to the continuous time evolution we have probably quite similar properties that have to be discussed. At this moment one sees that depending on the sign of the expression

$$D = \prod_{i=1}^{n} a_i - f_n \prod_{i=1}^{n-1} p_i \tag{4.31c}$$

either all coefficients are positive ($D > 0$) or all coefficients are positive with the exception of the absolute term ($D < 0$), where

$$a_i = p_i + \mu_i \tag{4.31d}$$

Since $P(\lambda)$ is an increasing function for positive λ, the sign of $D = P(0)$ determines the sign of the spectral bound. If $D > 0$ then the spectral bound is negative, the solutions decay. If $D < 0$ then the spectral bound is positive, the population grows exponentially.

If $D < 0$ then $Q(\lambda) = \lambda^n P(1/\lambda)$ is a polynomial with all coefficients nonnegative except the leading coefficient that is negative. Thus, up to a simple scaling, $Q(\lambda)$ is a Cauchy polynomial.

Now if $P(\lambda)$ is expanded in the form

$$P(\lambda) = \sum_{i=1}^{n} c_i \lambda^i \tag{4.32}$$

then all coefficients except c_0 are positive, in particular $c_n = 1$, and by substituting $\lambda = 0$ in equation (4.30b) or 4.32 we get

$$c_0 = P(0) = \prod_{i=1}^{n} (p_i + \mu_i) - f \prod_{i=1}^{n-1} p_i. \tag{4.33a}$$

Clearly the condition $c_0 < 0$ holds if in the equation above

$$f \prod_{i=1}^{n-1} p_i > \prod_{i=1}^{n} (p_i + \mu_i) \tag{4.33b}$$

and of course $f > 0$. Now define

$$m = \min_{1 \le i \le n} (p_i + \mu_i). \tag{4.34}$$

In view of

$$\dot{P}(\lambda) = \sum_{i=1}^{n} \prod_{\substack{j=1 \\ j \ne i}}^{n} (p_j + \mu_j + \lambda) \tag{4.35}$$

the function $P(\lambda)$ is strictly increasing, as long as

$$\lambda > -m. \tag{4.36}$$

If from the above remark $P(0) = D < 0$ and $m > 0$ we have $P(-m) < 0$ and $P(\lambda) > 0$ for $\lambda >> 0$. Hence the spectral bound s_0 is the unique zero of $P(\lambda)$ in the interval $(-m, +\infty)$.

The sign of c_0 determines that of s_0. If $c_0 < 0$ then $P(0) < 0$ and it follows $s_0 > 0$. Thus from Eq.(4.33b) the tick population is exponentially increasing (with exponent s_0) if and only if

$$f > \prod_{i=1}^{n} (p_i + \mu_i) / \prod_{i=1}^{n-1} p_i, \tag{4.37}$$

or, equivalently, if

$$f > \mu_n \prod_{i=1}^{n-1} \frac{p_i + \mu_i}{p_i} = \mu_n \prod_{i=1}^{n-1} (1 + \frac{\mu_i}{p_i}). \tag{4.38a}$$

In biological terms this inequality says that the tick population persists if the egg production rate exceeds the product

$$\mu_n \prod_{i=1}^{n-1} (1 + \mu_i / p_i). \tag{4.38b}$$

This product measures the mortalities against the average sojourn times in the corresponding compartments. To interprete this more recall that we had shown in section 4.1 that if in general the rate of leaving a stage i to the next stage is a_i then the average sojourn time in that stage is $1/a_i$. In the current model specification this rate is p_i and the mortality rate is μ_i thus the ratio μ_i/p_i is a measure of mortality against the average sojourn time in stage i. We can get some more information on the dependence of s_0 on the parameters through the implicit function theorem which is crucial in such kind of analysis. The general form of the theorem is stated below.

Theorem 4.1: The Implicit Function Theorem

Let E, F, G be three Banach spaces, f a continuously differentiable mapping (i.e continuous and its first derivative also continuous) of an open subset A of E x F into G. Let (x_0, y_0) be a point of A such that $f(x_0, y_0) = 0$ and that the partial derivative $D_2 f(x_0, y_0)$ of f with respect to second variable be a linear homeomorphism of F onto G. Then, there is an open neighborhood U_0 of x_0 in E such that, for every open connected neighborhood U of x_0, contained in U_0, there is a unique continuous mapping u of U into F such that $u(x_0) = y_0$, $(x, u(x)) \in A$ and $f(x, u(x)) = 0$ for any $x \in U$. Furthermore, u is continuously differentiable in U, and its derivative is given by

$$u'(x) = -(D_2 f(x, u(x)))^{-1}(D_1 f(x, u(x))), \tag{4.39a}$$

where $D_1 f(x, u(x))$ denotes the partial derivative of f with respect to the first variable.

From the implicit function theorem applied to the equation $P(\lambda) = 0$ we get

$$\frac{\partial s_0}{\partial \mu_i} = -\left.\frac{\partial P(\lambda, \mu_i)/\partial \mu_i}{\partial P(\lambda, \mu_i)/\partial \lambda}\right|_{\lambda = s_0} = -\frac{\prod_{\substack{j=1 \\ j \neq i}}^{n} (p_j + \mu_j + s_0)}{\dot{P}(s_0)} < 0. \tag{4.39b}$$

where a general expression for $\dot{P}(\lambda)$ is given in Eq.(4.35). Thus the spectral bound s_0 is a decreasing function of the mortalities, as it should be. Similarly one shows that s_0 is an increasing function of f. The dependence of s_0 on the transitions p_i is more involved. Again by the implicit function theorem, for $j \leq n-1$,

$$\frac{\partial s_0}{\partial p_i} = -\left.\frac{\partial P(\lambda, p_i)/\partial p_i}{\partial P(\lambda, p_i)/\partial \lambda}\right|_{\lambda = s_0} = -\frac{\prod_{\substack{j=1 \\ j \neq i}}^{n} (p_j + \mu_i + s_0) - f \prod_{\substack{j=1 \\ j \neq i}}^{n} p_j}{\dot{P}(s_0)}. \tag{4.40}$$

Hence $\partial s_0/\partial p_i$ is positive if and only if

$$\prod_{\substack{j=1\\ j\neq i}}^{n}(p_j+\mu_j+s_0) < f\prod_{\substack{j=1\\ j\neq i}} p_j. \tag{4.41a}$$

Using the fact that s_0 is a root of the characteristic polynomial $P(\lambda)$ given by Eq.(4.30b) the expression $P(s_0)=0$ implies that

$$\prod_{j=1}^{n}(p_j+\mu_j+s_0) = f\prod_{j=1}^{n-1} p_j. \tag{4.41b}$$

Now it follows that inequality (4.41a) can be written as

$$\frac{\prod_{j=1}^{n}(p_j+\mu_j+s_0)}{p_i+\mu_i+s_0} < \frac{f\prod_{j=1}^{n-1} p_j}{p_i} \tag{4.41c}$$

which implies that

$$p_i+\mu_i+s_0 > p_i \tag{4.42a}$$

using equality (4.41b). Thus we find that inequality (4.41a) is equivalent to

$$s_0 > -\mu_i. \tag{4.42b}$$

Thus for an increasing tick population increasing any p_i leads to an increase of s_0. In biological terms, accelerating the development process increases the rate of exponential growth.

The eigenvector of the matrix A corresponding to the eigenvalue s_0 describes the "persistent" stage distribution at exponential growth (or decay). From - Eq.(4.27) we find, by normalizing the adults to $x_n = 1$,

$$x_i = \prod_{j=i+1}^{n}(p_j+\mu_j+s_0)/\prod_{j=i}^{n-1} p_j \tag{4.43}$$

where by persistent stage distribution we mean that stage distribution attained when the system reaches stability. This stage distribution determines the future population structure and its growth rate is governed by the spectral bound s_0 of the matrix A in Eq.(4.22). These numbers give the relative proportions of the different stages in the persistent stage distribution. Of course we also could normalize x_1 but this choice is not appropriate from a practical point of view since adults can be counted more easily.

As indicated earlier this model is the first building block for subsequent more realistic models. But the simplified model can already be used. Assume the tick population is in factical equilibrium with respect to the environment, in particular with the host population. Then s_0 is close to 1 and we can try to fit the coefficients, based on realistic biological assumptions, to the observed frequencies of eggs, larvae, nymphs and adults. In this case the rates μ_j, p_j are factical rates given the environment.

4.3 Vector Host Interaction

Model (4.21) is a stage structured model for the vector population only. It does not incorporate any factors that would limit population growth, in particular host abundance and availability has not been considered. In this section we introduce a variable y that describes the number of available natural (wild) hosts such as (wild) ungulates and also a quantity z that counts the domestic animals serving as hosts for the ticks. We assume that the rate of transition from an off-host stage to an on-host stage is proportional to the numbers of hosts available, that is of the form $q_i(y+z)$. What we mean here is that the rate p_i in system (4.21) can in general be denoted more precisely as $p_i + q_i(y+z)$ where for an off host questing tick searching for a host $p_i = 0$ and $q_i(y+z) \geq 0$ since such a tick has some positive rate of attaching to a host. On the other hand if the transition is that to a non-host state then $p_i \geq 0$ and $q_i(y+z)$ is zero. At low host densities $y+z$, these transitions become bottlenecks for the development of the vector population.

This is because such host densities might be too low to support the vector population. In otherwords there is a possibility of a critical host density below which the vector population is threatened with extinction. It is important to know what conditions will limit the number of vectors (tick population). Limiting effects could be related to intraspecific competition for hosts or a detrimental effect of the ticks (or the disease transmitted by them) to the hosts. One could imagine that hosts avoid heavily tick infested areas. This would mean that if tick abundance goes up then host density goes down, in specific grazing areas. Thus we get something like or similar to a predator prey model. The host equation is therefore given by

$$\dot{y} = r - dy - \vec{c}^T \vec{x} y \tag{4.44a}$$

where r is the inflow of hosts due to immigration of hosts into a given grazing area or renewal of hosts within that area. The constant (row) vector

$$\vec{c}^T = (c_1, c_2 \ldots, c_n) \tag{4.44b}$$

measures the effects of the different stages of the vectors present in the area on the host population. We assume that $c_i \geq 0$ and $c_i > 0$ only if i is a questing stage. The vector $\vec{x}$ has the same meaning as before. Here competition effects have not been incorporated.

We assume that the quantity z describing the available cattle population is not a dynamic variable but a parameter, simply for the reason that cattle density will be controlled by actions not within the framework of the model.

At this moment we do not incorporate the aspect of host preference for each of the three questing tick stages. That is a questing tick can either attach onto a domestic host z or a wild host y if it is lucky to find one. The transition rates are $q_i(y + z)$ for the ith stage. Thus the new set of equations giving between stage interactions are given by

$$\begin{aligned}
\dot{x}_1 &= f x_n - (p_1 + hq_1)x_1 - \mu x_1 \\
\dot{x}_2 &= (p_1 + hq_1)x_1 - (p_2 + hq_2)x_2 - \mu_2 x_2 \\
&\ldots\ldots \\
\dot{x}_j &= (p_{j-1} + hq_{j-1})x_{j-1} - (p_j + hq_j)x_j - \mu_j x_j \\
&\ldots\ldots \\
\dot{x}_{n-1} &= (p_{n-2} + hq_{n-2})x_{n-2} - (p_{n-1} + hq_{n-1})x_{n-1} - \mu_{n-1} x_{n-1} \\
\dot{x}_n &= (p_{n-1} + hq_{n-1})x_{n-1} - \mu_n x_n \\
\dot{y} &= r - dy - \vec{c}^T \vec{x} y
\end{aligned} \tag{4.45a}$$

Here the term describing the transition from the i-th stage to the $(i+1)$-st stage is $p_i + hq_i$, with $h = y + z$, where, of course, $p_i = 0$ if i is a questing stage and

$q_i = 0$ if i is a non questing stage. The system (4.45a) is exactly the same as the original system (4.21) except that here we attempt to express p_i as a function of host density given by $p_i(y+z)$ where the variables y and z represent the natural wild hosts and cattle hosts respectively. As a first approximation we let

$$p_i(y+z) = p_i + hq_i, \quad i = 1, \ldots, n-1 \tag{4.45b}$$

which takes specific forms determined by whether a tick is questing or not. For a questing tick $p_i = 0$ and $q_i \geq 0$ since the transition to state $i+1$ is host dependent while for non-questing tick $q_i = 0$ and $p_i \geq 0$ since the transition to state $i+1$ for this tick is host independent. In our case $n = 10$ since we have 10 distinct developmental stages in the life cycle. Here the questing stages are 2, 5, and 8, corresponding to questing larvae, nymphs, and adults. Together with the host equation (4.44a) we have a system of altogether $n+1$ equations, 11 in the particular case.

We now wish to express the system (4.45a) in matrix notation but first we define the following set of matrices. Let matrices F, D, P, Q, M have the following structures. The stage transition matrix is

$$D = \begin{pmatrix} -1 & 0 & 0 & \cdots & 0 & 0 \\ 1 & -1 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \cdots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & 1 & 0 \end{pmatrix}. \tag{4.46}$$

The fecundity matrix F contains a single nonzero element, at the right top corner i.e

$$F = \begin{pmatrix} 0 & 0 & 0 & \cdots & f_n \\ 0 & 0 & 0 & \cdots & 0 \\ \vdots & \vdots & \vdots & \cdots & \vdots \\ 0 & 0 & 0 & \cdots & 0 \end{pmatrix}. \tag{4.47}$$

The matrices P, Q, and M, are the diagonal matrices given by

$$P = (p_i\delta_{ij}), \quad Q = (q_i\delta_{ij}), \quad M = (\mu_i\delta_{ij}) \tag{4.48}$$

of transitions to off host stages, to on host stages, and of stage specific mortalities. Thus in matrix notation the system of equations (4.45a) may be written as

$$\begin{aligned} \dot{\vec{x}} &= F\vec{x} + D(P + (y+z)Q)\vec{x} - M\vec{x} \\ \dot{y} &= r - dy - \vec{c}^T\vec{x}y \end{aligned} \tag{4.49a}$$

Putting

$$A = F + DP - M, \quad B = DQ \tag{4.49b}$$

this system assumes the form

$$\begin{aligned} \dot{\vec{x}} &= (A + (y+z)B)\vec{x} \\ \dot{y} &= r - dy - \vec{c}^T \vec{x} y \end{aligned} \tag{4.50}$$

where A can be looked at as a matrix denoting the survival and birth process of the tick population, while B denotes the matrix of interaction between the tick population and its host.

Before entering the analysis of the model we discuss a two-dimensional caricature where x is just one compartment and consequently A, B, C, are numbers. We choose $b = B > 0$, $c > 0$ and $A = -a < 0$ negative because ticks do not survive in the absence of any hosts. In this case the system reads

$$\begin{aligned} \dot{x} &= -ax + b(y+z)x \\ \dot{y} &= r - dy - cxy \end{aligned} \tag{4.51}$$

There is always a tick free equilibrium given by

$$x = 0, \quad y = r/d \tag{4.52}$$

Now assume there is a stationary state where ticks are present, that is $x > 0$. Then the conditions

$$b(y+z) = a \tag{4.53}$$

and

$$r - dy = cxy \tag{4.54}$$

must hold.

Case 1: $z > a/b$.

Then the first equation (4.53) cannot be satisfied with positive y. In this situation there is so much cattle present (at a fixed density) that all the three species z, y and x do not persist together. Thus the wildlife will be expelled, the ticks persist on cattle alone and their population density is exponentially increasing. Factically this would suggest that also the cattle density cannot be maintained.

Case 2: $z < a/b$.

Then the equation (4.53) can be solved with $y > 0$, given by

$$\bar{y} = a/b - z. \tag{4.55}$$

Thus we get formally

$$\bar{x} = \frac{r - d\bar{y}}{c\bar{y}}. \tag{4.56}$$

Hence there are again two subcases.

Case 2a): $\bar{y} > r/d$ or $r < d\,\bar{y}$.

In this case there is no coexistence of all three species, the tick density would become negative.

Case 2b): $\bar{y} < r/d$ or $r > d\,\bar{y}$.

In this case there is a coexistence point $(\bar{x}, \bar{y})$ with $\bar{y} < r/d$. To have something concrete at hand we keep a, b, c and d fixed and draw a (z, r) parameter plane. Briefly this plane can be divided into three regions namely region I, II and III. In region I we get coexistence between z and y without ticks. In region II there is coexistence of all three species x, y and z while in region III the parameter space can only allow coexistence between ticks and cattle but no wildlife. A further property with region III is that the tick density is such that it will explode and ultimately cattle cannot be maintained.

Now we discuss the situation where all points are fixed except z, i.e the situation that a particular cattle breeder considers to exploit a certain region. There are two cases again.

case I: $r < ad/b$ or $r/d < a/b$.

Then at $z = 0$ one finds no ticks. Introducing cattle at low densities still makes the biotope not feasible for ticks. This is from the fact that condition (4.53) for the host population is not satisfied that is we have a situation where there are no cattle and the existing natural wild host population is not feasible the existence of ticks. If cattle density is increased then there is a first theshold at which the biotope becomes feasible for first time. This threshold value is

$$z_1 = a/b - r/d. \tag{4.57a}$$

Figure 3: System of Wild Hosts, Cattle and Ticks

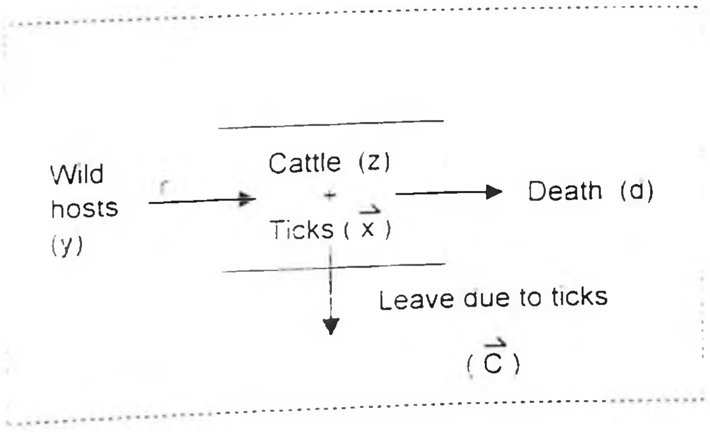
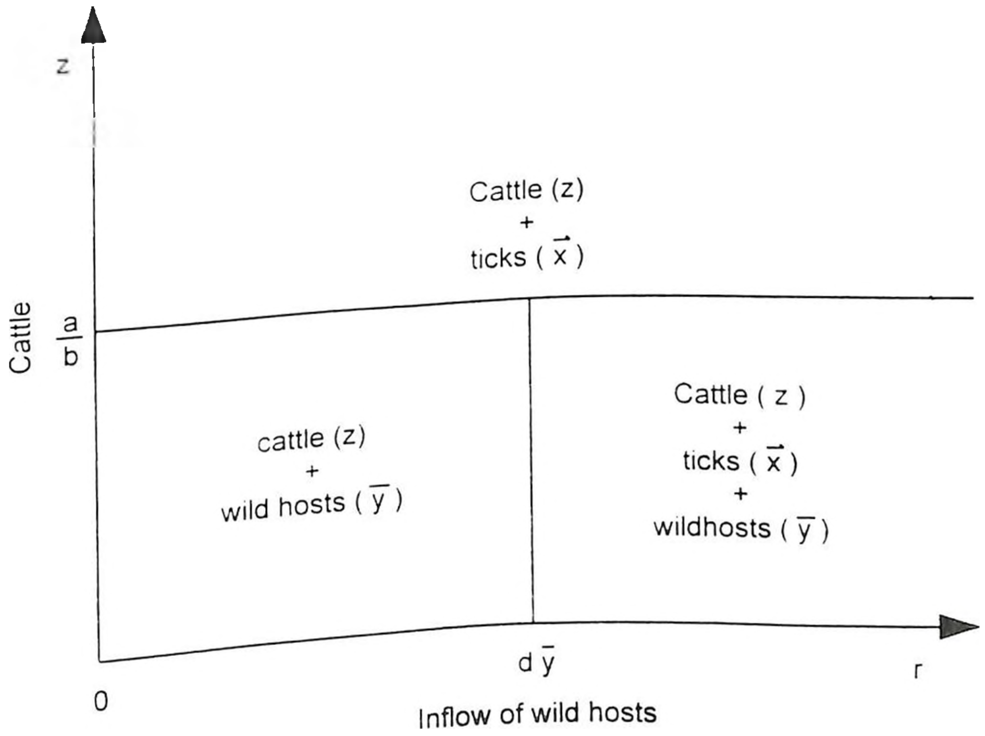


Figure 4: A (z, r) parameter plane



At this threshold

$$z_1 + \bar{y} = a/b \tag{4.57b}$$

and equation (4.53) is satisfied. Beyond this ($z = z_1$) cattle, wildlife and ticks co-exist. But as z is further increased beyond

$$z_2 = a/b \tag{4.58}$$

the wildlife will vanish and ticks explode same as the situation described in case 1 above.

case II: $r > ad/b$ or $r/d > a/b$.

In this case a possible cattle breeder will introduce some cattle into an already infected area. The cattle will result in an increase in the tick density. More precisely the situation here is that before the breeder introduces cattle in this region, the natural wild host population is already enough to support a tick population. However the stationary total host population is supposed to be a/b by condition (4.53) thus the introduction of cattle in this region means disturbing the stationary state of the system. Thus after the threshold $z_2 = a/b$ the wildlife will continuously fall and eventually vanish and the tick population will explode.

Now we return to the discussion of system (4.49a). We find similar phenomena as in the caricature, but in addition we find the stage distribution of the ticks. The first step in the analysis of this system will be the determination of stationary states. At a stationary state $(\vec{x}, y)$ the following equations must hold

$$\begin{aligned} 0 &= (A + (y+z)B)\vec{x} \\ 0 &= r - dy - \vec{c}^T \vec{x} y. \end{aligned} \tag{4.59}$$

For fixed $y + z$, the first equation is a homogeneous linear system for the vector $\vec{x}$. Thus a necessary condition for the existence of a nonzero $\vec{x}$ is that the determinant of the matrix

$$A + (y+z)B \tag{4.60a}$$

vanishes, that is

$$\det(A + (y+z)B) = 0. \tag{4.60b}$$

Thus consider the equation

$$\det(A + hB) = 0. \tag{4.61}$$

We compare the linear system

$$\begin{aligned}
0 &= fx_n - (p_1 + hq_1)x_1 - \mu_1 x_1 \\
0 &= (p_1 + hq_1)x_1 - (p_2 + hq_2)x_2 - \mu_2 x_2 \\
&\ldots\ldots \\
0 &= (p_{j-1} + hq_{j-1})x_{j-1} - (p_j + hq_j)x_j - \mu_j x_j \\
&\ldots\ldots \\
0 &= (p_{n-2} + hq_{n-2})x_{n-2} - (p_{n-1} + hq_{n-1})x_{n-1} - \mu_{n-1}x_{n-1} \\
0 &= (p_{n-1} + hq_{n-1})x_{n-1} - \mu_n x_n
\end{aligned} \tag{4.62}$$

to sytem (4.24) with $\lambda = 0$ and p_i replaced by $p_i + hq_i$. Then from Eq.(4.30b) one sees that the quantity h must be a zero of the polynomial

$$\tilde{P}(h) = \prod_{i=1}^{n}(p_i + hq_i + \mu_i) - f\prod_{i=1}^{n-1}(p_i + hq_i). \tag{4.63}$$

This polynomial can also be written in the the form

$$\tilde{P}(h) = \mu_n \prod_{i\notin E}(p_i + \mu_i)\prod_{i\in E}(hq_i + \mu_i) - h^m f \prod_{i\notin E} p_i \prod_{i\in E} q_i \tag{4.64}$$

where $E \subset \{1, 2, \ldots, n\}$ and m is the number of questing stages in the system. In otherwords we group the product terms in the right hand side of Eq.(4.63) according to parameters associated to questing stages (indices in the set E) and non questing tick stages (indices not in E). Now we define the quantity

$$R_0(h) = \frac{f}{\mu_n}\prod_{i\notin E}\frac{p_i}{p_i + \mu_i}\prod_{i\in E}\frac{hq_i}{hq_i + \mu_i}, \tag{4.65}$$

which is the average number of ticks produced by one adult female tick in its life time. This number $R_0(h)$ is the basic reproduction number of the tick population on a host population of density h. We see that

$$R_0(\infty) = \frac{f}{\mu_n}\prod_{i\notin E}\frac{p_i}{p_i + \mu_i}. \tag{4.66}$$

If $R_0(\infty) > 1$ then the tick can persist on sufficiently dense host populations. The critical host density is h_0, where h_0 is the unique positive root of the equation $R_0(h) = 1$. Thus the tick can persist on host populations with density $> h_0$ and cannot persist on host populations with density $< h_0$. Notice that h_0 depends only on the parameters p_i, q_i, μ_i and f. This conclusion is in agreement with what is expected in the field. Norval *et al* (1992) concluded that the most important factors affecting the abundance of *R. appendiculatus* in wildlife reserves in Zimbabwe are host density and climate. The authors suggest that in a given environment the tick can only become established if the host density exceeds a certain threshold level. Norval *et al* (1992) state that this level is low when a high proportion of host population is comprised of tick-susceptible animals and becomes higher as the suitability of the environment for tick survival decreases. They further state that the most severe tick problems occur in wildlife reserves with highest host densities. The model so far seems to be in the right direction as far as tick dynamics are concerned. At any nontrivial equilibrium we would have $R(h) = 1$, thus $h = h_0$. Then the non-normalized tick distribution, according to stage is

$$\bar{x}_i = x_n \prod_{j=i+1}^{n} (p_j + h_0 q_j + \mu_j) / \prod_{j=i}^{n-1} (p_j + h_0 q_j), \quad i = 1, \dots, n-1. \tag{4.67}$$

Furthermore the three populations of wildlife, cattle and ticks must satisfy

$$r - dy - \vec{c}^T \vec{x} y = 0 \quad \text{and} \quad y + z = h_0. \tag{4.68}$$

Case 1: When $z > h_0$ then the equation $y + z = h_0$ cannot be satisfied with $y > 0$. We have $R_0(z) > 1$. Thus, at the given level of domestic animals, the tick population can survive on cattle alone, the tick population grows exponentially, and the wild animals disappear. Factically, cattle breeding at this density (with the given transition rates) is impossible.

Case 2: When $z < h_0$ then at equilibrium $y = \bar{y}$, where

$$\bar{y} = h_0 - z.$$

For the tick population $\tilde{\vec{x}}$, we get the equation

$$r - d\bar{y} = \vec{c}^T \tilde{\vec{x}}.$$

Hence there are again two cases.

Case 2a): $\bar{y} > r/d$ or $r < d\,\bar{y}$.

In this case

$$\bar{y} = h_0 - z > r/d$$

or

$$h_0 > z + r/d.$$

Then

$$(z + r/d) < h_0.$$

Thus the tick population cannot survive on the joint wild and domestic animals.

Case 2b): $\bar{y} < r/d$ or $r > d\,\bar{y}$.

In this case

$$\bar{y} = h_0 - z < r/d$$

or

$$h_0 < z + r/d.$$

Then

$$z + r/d > h_0.$$

Thus, due to the assumed possibility that wild animals avoid heavily tick infested areas, an equilibrium density of wild animals $\bar{y}$ establishes itself. The cattle density is z, the density of wildlife animals is $\bar{y} = h_0 - z$ and the total population size of ticks is determined from

$$c^T\vec{x} = \frac{r - d\bar{y}}{\bar{y}} \tag{4.69}$$

The right hand side of Eq.(4.69) is positive, since $r/d > h_0 - z = \bar{y}$.

4.4 Stability Analysis

We have just found that there are at most two stationary states. It remains to investigate the conditions under which these states are stable or unstable, respectively. In order to perform a stability analysis we have to linearise at the stationary state, that is we have to form the Jacobian at the stationary state. We start by forming the Jacobian at any state $(\vec{x}, y)$. We do not form the Jacobian, as usual, by computing partial derivatives, but we introduce small u, v variations in the equations and drop terms of order greater than 1. Thus we enter $\vec{x}+\vec{u}$, $y+v$ in equation (4.49a) to obtain the following equations

$$\begin{aligned}(\vec{x}+\vec{u})^{\cdot} &= F(\vec{x}+\vec{u}) + D(P+(y+v+z)Q)(\vec{x}+\vec{u}) - M(\vec{x}+\vec{u})\\ (y+v)^{\cdot} &= r - d(y+v) - \vec{c}^T(\vec{x}+\vec{u})(y+v)\end{aligned} \tag{4.70}$$

Expanding the two equations above and ignoring terms of order 2 we get,

$$\begin{aligned}\dot{\vec{u}} &= (F+DP+(y+z)DQ-M)\vec{u} + vDQ\vec{x}\\ \dot{v} &= -yc^T u - \vec{c}^T\vec{x}v - dv\end{aligned} \tag{4.71}$$

where $\vec{u}$ is a column vector of length n and v is a scalar variable. The two equations above may be written in matrix notation as;

$$\begin{pmatrix}\dot{\vec{u}}\\ \dot{v}\end{pmatrix} = \begin{pmatrix}F+DP+(y+z)DQ-M & DQ\vec{x}\\ -y\vec{c}^T & -d-c^T\vec{x}\end{pmatrix}\begin{pmatrix}\vec{u}\\ v\end{pmatrix}. \tag{4.72}$$

In coordinate notation the system reads

$$\begin{aligned}\dot{u}_1 &= fu_n - (p_1+(y+z)q_1)u_1 - vq_1x_1 - \mu_1x_1\\ \dot{u}_2 &= (p_1+(y+z)q_1)u_1 - (p_2+(y+z)q_2)u_2 + vq_1x_1 - vq_2x_2 - \mu_2x_2\\ &\cdots\cdots\\ \dot{u}_i &= (p_{i-1}+(y+z)q_{i-1})u_{i-1} - (p_i+(y+z)q_i)u_i + vq_1x_i - vq_ix_i - \mu_ix_i\\ &\cdots\cdots\\ \dot{u}_n &= (p_{n-1}+(y+z)q_{n-1})u_{n-1} + vq_{n-1}x_{n-1} - \mu_nx_n\\ \dot{v} &= -y\vec{c}^T u - \vec{c}^T\vec{x}v - dv\end{aligned} \tag{4.73}$$

In the special case of the equilibrium the coefficients of v have a well-defined sign, negative for a questing stage equation and positive for a post questing stage equation (a stage following a questing stage)

First we look at the uninfected stationary state. The stability analysis will show whether the tick can invade a tick-free area. Then $y = r/d$ and $\vec{x} = 0$. In this case the Jacobian becomes

$$J_0 = \begin{pmatrix}F+DP+(y_0+z)DQ-M & 0\\ -y_0c^T & -d\end{pmatrix}. \tag{4.74}$$

The matrix splits. There is one eigenvalue $\lambda_0 = -d$. The remaining eigenvalues are those of the matrix

$$A_0 = F + DP + (y_0 + z)DQ - M. \tag{4.75}$$

Thus we find that the uninfected stationary state is stable if the spectral bound satisfies

$$s(A_0) < 0.$$

This condition is equivalent to the inequality

$$R_0 < 1.$$

This means that the uninfected stationary state is stable meaning that a tick population invading a tick free area declines exponentially with time. Now consider the infected state $(\tilde{\bar{x}}, \bar{y})$ where we have the Jacobian

$$J(\tilde{\bar{x}}, \bar{y}) = \begin{pmatrix} F + DP + (\bar{y} + z)DQ - M & DQ\tilde{\bar{x}} \\ -y\bar{c}^T & -d - c^T\tilde{\bar{x}} \end{pmatrix}. \tag{4.76}$$

Here the matrix does not split, and the problem gets exceedingly more difficult. To demonstrate the structure of this problem we see that in general the matrix above is of the form

$$J(\tilde{\bar{x}}, y) = \begin{pmatrix} A & B \\ C & D \end{pmatrix}$$

the matrix A is exponentially positive, C is a nonpositive row vector, D is a negative scalar, and B is a column with entries of either sign. Although these matrices have such structures it is not obvious that, under the condition that $R_0 > 1$, this matrix is in fact stable. If it were unstable then we would expect secondary bifurcations of the infected stationary state $(\tilde{\bar{x}}, \bar{y})$.

4.5 Competition of Ticks

As Branagan (1969) observed in a series of experiments involving *R. appendiculatus*, it is evident that there is competition when ticks attach onto a host for a blood meal. It was observed that on host nymphs tend to detach earlier than expected when nymphal density on the host is high. The resultant obvious effect is that ticks do not get enough blood share, hence their chances of survival in the next stage is reduced to some extent. We wish to consider an extension of the model (4.45a) where the observed competition effects are incorporated. It is not obvious how this should be done. If we just increase the rate of detachment then instead of modeling a competitive effect we are actually speeding up the life cycle of the ticks which results in a cooperative effect. Modeling incomplete saturation due to premature detachment would require considering a population structured according to nutritional status which of course would be much more complicated and would contain many parameters that are difficult to estimate. Within the framework of the present model there seem to be only two ways to describe the observed competition. Either one assumes that the rate of attachment is a decreasing function of density of the on-host population, or one assumes that the mortality of the detached ticks is an increasing function of the density of the preceding on host stage. Of course one can incorporate both nonlinearities into the model. Both approaches do not exactly describe what happens in the field, but they seem sufficiently close to reality at this level of model complexity.

In the following we assume that similar competitive effects take place at every questing stage. Thus we are led to consider the following system

$$\begin{aligned}
\dot{x}_1 &= f x_{10} - p_1 x_1 - \mu_1 x_1 \\
\dot{x}_2 &= p_1 x_1 - h q_2(x_3) x_2 - \mu_2 x_2 \\
\dot{x}_3 &= h q_2(x_3) x_2 - p_3 x_3 - \mu_3 x_3 \\
\dot{x}_4 &= p_3 x_3 - p_4 x_4 - \mu_4(x_3) x_4 \\
\dot{x}_5 &= p_4 x_4 - h q_5(x_6) x_5 - \mu_5 x_5 \\
\dot{x}_6 &= h q_5(x_6) x_5 - p_6 x_6 - \mu_6 x_6 \\
\dot{x}_7 &= p_6 x_6 - p_7 x_7 - \mu_7(x_6) x_7 \\
\dot{x}_8 &= p_7 x_7 - h q_8(x_9) x_8 - \mu_8 x_8 \\
\dot{x}_9 &= h q_8(x_9) x_8 - p_9 x_9 - \mu_9 x_9 \\
\dot{x}_{10} &= p_9 x_9 - \mu_{10}(x_9) x_{10} \\
\dot{y} &= r - dy - c^T x y.
\end{aligned} \tag{4.77}$$

This system is of the general form

$$\begin{aligned}
\dot{x}_1 &= f x_n - (p_1 + hq_1)x_1 - \mu_1 x_1 \\
\dot{x}_2 &= (p_1 + hq_1)x_1 - (p_2 + hq_2)x_2 - \mu_2 x_2 \\
&\ldots\ldots \\
\dot{x}_j &= (p_{j-1} + hq_{j-1})x_{j-1} - (p_j + hq_j)x_j - \mu_j x_j \\
&\ldots\ldots \\
\dot{x}_{n-1} &= (p_{n-2} + hq_{n-2})x_{n-2} - (p_{n-1} + hq_{n-1})x_{n-1} - \mu_{n-1} x_{n-1} \\
\dot{x}_n &= (p_{n-1} + hq_{n-1})x_{n-1} - \mu_n x_n \\
\dot{y} &= r - dy - c^T xy.
\end{aligned} \tag{4.78}$$

where p_j and q_j depend on x_{j+1} for $j = 1, \ldots, n-1$, and μ_j depend on x_{j-1} for $j = 2, \ldots, n$. Thus the system has, apart from the last equation, a three-diagonal structure, the right hand side in the equation for x_j depends only on the three variables x_{j-1}, x_j, x_{j+1}.

4.5.1 General cyclic triangular systems

The first part of the system (4.78) has the general form

$$\begin{aligned}
\dot{x}_1 &= r_n(x_1)x_n - r_1(x_2)x_1 - \mu_1(x_n)x_1 \\
\dot{x}_2 &= r_1(x_2)x_1 - r_2(x_3)x_2 - \mu_2(x_1)x_2 \\
&\ldots \\
\dot{x}_j &= r_{j-1}(x_j)x_{j-1} - r_j(x_{j+1})x_j - \mu_j(x_{j-1})x_j \\
&\ldots \\
\dot{x}_{n-1} &= r_{n-2}(x_{n-1})x_{n-2} - r_{n-1}(x_n)x_{n-1} - \mu_{n-1}(x_{n-2})x_{n-1} \\
\dot{x}_n &= r_{n-1}(x_n)x_{n-1} - \mu_n(x_{n-1})x_n.
\end{aligned} \tag{4.79}$$

Note that when the transition rates are not density dependent then

$$r_j(x_{j+1}) = p_j + hq_j \quad j = 1, \ldots, n-1 \quad \text{and} \quad r_n(x_1) = f.$$

Now we look for stationary states of the system (4.79). At a stationary state the following equations hold,

$$
\begin{aligned}
r_n(x_1)x_n &= (r_1(x_2) + \mu_1(x_n))x_1 \\
r_1(x_2)x_1 &= (r_2(x_3) + \mu_2(x_1))x_2 \\
&\dots \\
r_{j-1}(x_j)x_{j-1} &= (r_j(x_{j+1}) + \mu_j(x_{j-1}))x_j \\
&\dots \\
r_{n-2}(x_{n-1})x_{n-2} &= (r_{n-1}(x_n) + \mu_{n-1}(x_{n-2}))x_{n-1} \\
r_{n-1}(x_n)x_{n-1} &= \mu_n(x_{n-1})x_n.
\end{aligned}
\tag{4.80}
$$

We consider two special cases corresponding to the two modeling approaches described above.

Case 1: Assume that the coefficients r_j do not depend on density, and the competion effect is described only by increased mortality after detachment.

Then in the jth equation we solve for the variable x_j. We obtain the following system

$$
\begin{aligned}
x_1 &= \frac{r_n x_n}{r_1 + \mu_1(x_n)} \\
x_2 &= \frac{r_1 x_1}{r_2 + \mu_2(x_1)} \\
&\dots \\
x_j &= \frac{r_{j-1} x_{j-1}}{r_j + \mu_j(x_{j-1})} \\
&\dots \\
x_{n-1} &= \frac{r_{n-2} x_{n-1}}{r_{n-1} + \mu_{n-1}(x_{n-2})} \\
x_n &= \frac{r_{n-1} x_{n-1}}{\mu_n(x_{n-1})}.
\end{aligned}
\tag{4.81}
$$

We can look at these equations as a cyclic iteration. Now we assume that the mortalities are linear functions of the form

$$\mu_j(x) = \mu_j^0 + \mu_j^1 x. \tag{4.82}$$

Then the equations assume the following form

$$
\begin{aligned}
x_1 &= F_1(x_n) = \frac{a_1 x_n}{c_1 x_n + d_1} = \frac{r_n x_n}{r_1 + \mu_1^0 + \mu_1^1 x_n} \\
x_2 &= F_2(x_1) = \frac{a_2 x_1}{c_2 x_1 + d_2} = \frac{r_1 x_1}{r_2 + \mu_2^0 + \mu_2^1 x_1} \\
&\dots \\
x_j &= F_j(x_{j-1}) = \frac{a_j x_{j-1}}{c_j x_{j-1} + d_j} = \frac{r_{j-1} x_{j-1}}{r_j + \mu_j^0 + \mu_j^1 x_{j-1}} \\
&\dots \\
x_{n-1} &= F_{n-1}(x_{n-2}) = \frac{a_{n-1} x_{n-2}}{c_{n-1} x_{n-2} + d_{n-1}} = \frac{r_{n-2} x_{n-2}}{r_{n-1} + \mu_{n-1}^0 + \mu_{n-1}^1 x_{n-2}} \\
x_n &= F_n(x_{n-1}) = \frac{a_n x_{n-1}}{c_n x_{n-1} + d_n} = \frac{r_{n-1} x_{n-1}}{\mu_n^0 + \mu_n^1 x_{n-1}}
\end{aligned}
\tag{4.83}
$$

These equations define a cyclic iteration. We can start with x_n, compute successively the x_j down to x_1 and again x_n. Thus we have the equation

$$x_n = F(x_n) \tag{4.84}$$

where

$$F = F_n \circ F_{n-1} \circ \cdots \circ F_2 \circ F_1 \tag{4.85}$$

Since all F_j are fractional linear functions and a product of fractional linear functions is again a fractional linear function, and furthermore $F(0) = 0$, we find that F can be represented as

$$F(x) = \frac{Ax}{Cx + D} \tag{4.86}$$

The coefficients can be found in the following manner. If

$$f_1 : x \to (a_1 x + b_1)/(c_1 x + d_1)$$

and

$$f_2 : x \to (a_2 x + b_2)/(c_2 x + d_2)$$

are two fractional linear functions then the function

$$f_3 = f_2 \circ f_1$$

has the form

$$f_3 : x \rightarrow (a_3x + b_3)/(c_3x + d_3)$$

with

$$\begin{pmatrix} a_3 & b_3 \\ c_3 & d_3 \end{pmatrix} = \begin{pmatrix} a_2a_1 + b_2c_1 & a_2b_1 + b_2d_1 \\ c_2a_1 + d_2c_1 & c_2b_1 + d_2d_1 \end{pmatrix}, \tag{4.87}$$

in other words, the coefficients multiply in the same way as 2 × 2 matrices. Thus the product $F_n \circ F_{n-1} \circ \ldots \circ F_1$ is a fractional linear function where the coefficients are given by the entries of the matrix product

$$\begin{pmatrix} a_n & b_n \\ c_n & d_n \end{pmatrix} \cdots \begin{pmatrix} a_2 & b_2 \\ c_2 & d_2 \end{pmatrix} \begin{pmatrix} a_1 & b_1 \\ c_1 & d_1 \end{pmatrix}. \tag{4.88}$$

In case these matrices are of triangular form, $b_j = 0$, the formulae get somewhat simpler because the diagonal elements of the product are simply

$$a_na_{n-1} \cdots a_2a_1 \quad \text{and} \quad d_nd_{n-1} \cdots d_2d_1 \tag{4.89}$$

and the left lower element has a form which we better give for a fixed length of the product, say $n = 6$,

$$\begin{aligned} &c_6a_5a_4a_3a_2a_1 + d_6c_5a_4a_3a_2a_1 + d_6d_5c_4a_3a_2a_1 \\ &+d_6d_5d_4c_3a_2a_1 + d_6d_5d_4d_3c_2a_1 + d_6d_5d_4d_3d_2c_1 \end{aligned} \tag{4.90}$$

In the general case we find

$$A = \prod_{j=1}^{n} a_j, \quad D = \prod_{j=1}^{n} d_j, \tag{4.91a}$$

$$C = \sum_{j=1}^{n} \left\{ \prod_{k=1}^{j-1} a_k \cdot c_j \cdot \prod_{k=j+1}^{n} d_k \right\} \tag{4.91b}$$

where to avoid ambiguity in the expression we define

$$\prod_{k=1}^{0} a_k = 1 \tag{4.91c}$$

and

$$\prod_{k=n+1}^{n} d_k = 1. \tag{4.91d}$$

Thus x_n must be obtained from the equation

$$x_n = \frac{Ax_n}{Cx_n + D} \tag{4.92}$$

This equation has the trivial solution $x_n = 0$, and possibly one nontrivial solution which satisfies

$$Cx_n = A - D. \tag{4.93}$$

Thus this (positive) solution exists if and only if

$$A > D \tag{4.94}$$

or

$$R_0 = \frac{A}{D} > 1 \tag{4.95}$$

where R_0 is the basic reproduction number. In terms of the original coefficients we have

$$R_0 = \prod_{j=1}^{n} \frac{a_j}{d_j} \tag{4.96}$$

or

$$R_0 = f \prod_{j=1}^{n-1} \frac{p_j + q_j h}{p_j + q_j h + \mu_j^0}. \tag{4.97}$$

Notice that R_0 is a nondecreasing function of the host density h.

If R_0, as defined by Eq.(4.97), has the property $R_0 > 1$ then the system (4.81) has a nontrivial solution. This solution can be obtained by first computing x_n from Eq.(4.93) and then successively, $x_1, \ldots, x_{n-1}$ from system (4.83)

Case 2: Here we assume that the questing parameters r_j depend on density, but that the mortalities are constant. In this case it is not possible to arrive at a first order recursion for the x_j but still a second order recursion can be derived. We find

$$
\begin{aligned}
x_n &= F_n(x_1, x_2) = \frac{r_1(x_2) + \mu_1}{r_n(x_1)} x_1 \\
x_1 &= F_1(x_2, x_3) = \frac{r_2(x_3) + \mu_2}{r_1(x_2)} x_2 \\
&\dots \\
x_j &= F(x_{j+1}, x_{j+2}) = \frac{r_{j+1}(x_{j+2}) + \mu_{j+1}}{r_j(x_{j+1})} x_{j+1} \\
&\dots \\
x_{n-2} &= F(x_{n-1}, x_n) = \frac{r_{n-1}(x_n) + \mu_{n-1}}{r_{n-2}(x_{n-1})} x_{n-1} \\
x_{n-1} &= F(x_n) = \frac{\mu_n}{r_{n-1}(x_n)} x_n
\end{aligned}
\tag{4.98}
$$

One can start from x_n, compute x_{n-1} from the last equation, and then continue in Fibonacci style down to x_1 and finally again to x_n. In this way we arrive at an equation

$$x_n = G(x_n) \tag{4.99}$$

where G is constructed by the iteration. This equation has again the trivial solution $x_n = 0$, and possibly also nontrivial solutions. Since the function F_j is increasing in the first argument and decreasing in the second, not much can be said about whether G is monotone. However we can find

$$R_0 = G'(0). \tag{4.100}$$

Forming partial derivatives does not lead anywhere. By direct expansion we find

$$x_j = \frac{r_{j+1}(0) + r'_{j+1}(0)x_{j+2} + \mu_{j+1}}{r_j(0) + r'_j(0)x_{j+1}} x_{j+1} \tag{4.101}$$

where r'_{j+1} is the first derivative of r_{j+1} with respect to x_{j+2}. Multiplying numerator and denominator of Eq.(4.101) by $r_j(0) - r'_j(0)x_{j+1}$ and deleting second order terms we find the first order recursion

$$x_j = \frac{r_{j+1}(0) + \mu_{j+1}}{r_j(0)} x_{j+1}, \quad j = 2, \dots, n-1 \tag{4.102}$$

hence the basic reproduction number is the inverse of the product of these numbers (since in equations (4.101), (4.102) the iteration is moving backwards). Thus

$$R_0 = f \prod_{j=1}^{n-1} \frac{r_j(0)}{r_{j+1}(0) + \mu_{j+1}}$$

Case 3: In the general case where both the μ_j and the r_j are nonconstant, one cannot solve the recursion for the equilibrium densities, but still, by linearization, one can get the basic reproduction number. Indeed, the Jacobian of the right hand side of the system (4.77) is a cyclic two-diagonal matrix.

4.5.2 Positive invariance

In the linear case we know that the solutions of the "tick only" system are unbounded unless the parameters are such that the population remains constant or is decaying. In the nonlinear case we have to pay attention to the qualitative behaviour, in particular we distinguish the cases where the system is dissipative. In order to establish dissipativeness we have to find a bounded set that attracts all orbits and which is positively invariant.

As a first step we show that the positive orthant R^n_+ is positively invariant with respect to the flow. We must show that at each boundary point of R^n_+ the vector field $f = (f_i)$ is pointing inward, that is for any $i = 1, \dots, n$

$$x \in R^n_+, \quad x_i = 0 \Rightarrow f_i(x) \geq 0. \tag{4.103}$$

From the system (4.79) we see immediately the implication assumes the form

$$x \in R^n_+, \quad x_i = 0 \quad \Rightarrow \dot{x}_i = r_{i-1}(0)x_{i-1} \geq 0 \tag{4.104}$$

with the subscript i taken cyclically. This is true because the coefficients p_i and q_i are positive.

Now we construct a positively invariant domain in the form of a generalized rectangle

$$U = \{x : 0 \leq x_i \leq m_i, \quad i = 1, \dots, n\} \tag{4.105}$$

where the $m_i > 0$ are constants to be chosen appropriately. Again we have to show that at any boundary point the vector field is pointing inward. We have already covered those boundary points where one of the x_i vanishes. We still have to treat those boundary points where one x_i assumes the value m_i. At such a point we have $x_i = m_i$ and $0 \le x_j \le m_j$ for $j \ne i$. The i-th equation reads

$$\dot{x}_i = r_{i-1}(x_i)x_{i-1} - r_i(x_{i+1})x_i - \mu_i(x_{i-1})x_i. \tag{4.106}$$

To get an upper bound on $\dot{x}_i$ we can dismiss the term containing r_i because it is nonpositive anyway. Since r_{i-1} is a nonincreasing function we can replace it by its maximum, which is $r_{i-1}(0)$. Since we look at a point where $x_i = m_i$ we can use this equality. Then we arrive at the bound

$$\dot{x}_i \le r_{i-1}(0)x - \mu_i(x)m_i \quad \text{for} \quad 0 \le x \le m_{i-1}. \tag{4.107}$$

Now we have to find a set of m_i that satisfy the following inequalities (We write r_j instead of $r_j(0)$).

$$\begin{aligned} r_n x_n &\le \mu_1(x_n)m_1, \quad 0 \le x_n \le m_n, \\ r_1 x_1 &\le \mu_2(x_1)m_2, \quad 0 \le x_1 \le m_1, \\ &\cdots\cdot \\ r_{i-1}x_{i-1} &\le \mu_i(x_{i-1})m_i, \quad 0 \le x_{i-1} \le m_{i-1}, \\ &\cdots\cdot \\ r_{n-1}x_{n-1} &\le \mu_n(x_{n-1})m_n, \quad 0 \le x_{n-1} \le m_{n-1}, \end{aligned} \tag{4.108}$$

We claim that we can satisfy these inequalities if we choose

$$m_1 = m_2 = \cdots m_n = m$$

where

$$m = \sup_i \sup_{0 \le y < \infty} \frac{r_i y}{\mu_{i+1}(y)} \tag{4.109}$$

where again the subscript i is taken cyclically, provided the supremum is finite. Indeed, in this case, for the ith component, we find

$$r_{i-1}x_{i-1} - \mu_i(x_{i-1})m_i = r_{i-1}x_{i-1} - \mu_i(x_{i-1})m \le 0. \tag{4.110}$$

Now we want to show that all trajectories in R^n_+ eventually end up in U. Suppose that $x \notin U$. Then $x_i > m$ for at least one i. Then at this point

$$\begin{aligned} \dot{x}_i &= r_{i-1}(x_i)x_{i-1} - r_i(x_{i+1})x_i - \mu_i(x_{i-1})x_i \\ &\leq r_{i-1}(0)x_{i-1} - \mu_i(x_{i-1})x_i \\ &< r_{i-1}(0)x_{i-1} - \mu_i(x_{i-1})m \\ &\leq 0 \end{aligned}$$

Thus whenever a component exceeds m then it strictly decreases.

Assume that the $\mu_i(x)$ increase at least linearly for $x \to \infty$. Then the quotients $\frac{r_i y}{\mu_{i+1}(y)}$ are bounded and m exists. Thus we have proved the following result.

Theorem 4.2:
If the mortalities are at least linearly increasing then the system (4.79) is dissipative with respect to the set

$$U = \{x : 0 \leq x_i \leq m, \quad i = 1, \ldots, n\}$$

where m is given by Eq.(4.109).

Next consider stationary points. These are obviously fixed points of the mapping T, where

$$T(x)_i = \frac{r_{i-1}(x_i)x_{i-1}}{r_i(x_{i+1}) + \mu_i(x_{i-1})} \tag{4.111}$$

again with i taken cyclically. By construction, $TU \subset U$. Thus, by the fixed point theorem of L.E.J.Brouwer, T has a fixed point in U. But trivially, 0 is a fixed point. Thus we do not get anything. Therefore consider the Jacobian $\tilde{J}$ of T at this trivial fixed point 0. This Jacobian is given by

$$\tilde{J} = \begin{pmatrix} 0 & & & 0 & d_1 \\ d_2 & & & & \\ & d_3 & & & \\ & & \ddots & & 0 \\ 0 & & & d_n & \end{pmatrix} \tag{4.112}$$

where

$$d_i = \frac{r_{i-1}(0)}{r_i(0) + \mu_i(0)} \tag{4.113}$$

Compare this matrix to the Jacobian of the right hand side of system (4.79) at the stationary point 0.

$$J = \begin{pmatrix} -r_1 - \mu_1 & & & r_n \\ r_1 & -r_2 - \mu_2 & & 0 \\ & & \ddots & \\ & & r_{n-1} & -\mu_n \end{pmatrix}.$$

From a general principle (see claim 4.1 below) it follows that the spectral radius of $\tilde{J}$ is greater than 1 if and only if the spectral bound of J is positive. Thus the spectral radius of $\tilde{J}$ is greater than 1 if and only if the trivial stationary point of the differntial equations system is unstable. Then the linearization of the mapping T at $x = 0$ has an eigenvalue greater than 1 with a positive eigenvector, that is an eigenvector pointing into the interior of the first orthant. Thus the point 0 (which is the vertex of R_+^n and a boundary point of U), is an ejective fixed point with respect to the set U (in general 0 will be a saddle point and have a stable manifold which however is not in U). By the F.Browder-Horn principle on ejective fixed points there is a second fixed point of the mapping T in U. This fixed point is a stationary point of the differential equation.
Usually the Browder-Horn principle is formulated only for infinite-dimensional sets (and is even false in finite dimensions). Here the result applies since 0 is a boundary point. However, we cannot claim that the nontrivial stationary point is stable. Indeed, at a *nontrivial* stationary point the Jacobian contains also a diagonal of negative elements above the main diagonal. Hence we cannot exclude cycling behavior.

4.5.3 Spectral radius and spectral bound

Let P be a Perron matrix and D a positive diagonal matrix. Then it is clear that $D^{-1}P$ is also a Perron matrix. It is also obvious that the matrix difference $P - D$ is an exponentially nonnegative matrix or what is known as a Metzler matrix (Metzler 1945).

Claim 4.1: $s(P - D) < 0 \iff \rho(D^{-1}P) < 1$ where $s(.)$ and $\rho(\cdot)$ denote the spectral bound and spectral radius of a matrix, respectively.

Proof: We show the equivalence for the case that P is irreducible. The general case is shown by approximation.

1) Assume $s(P - D) < 0$. Then there exists an eigenvector $\vec{x} > 0$ such that

$$\begin{aligned}(P - D)\vec{x} &= s\vec{x},\\ P\vec{x} - D\vec{x} &= s\vec{x},\\ P\vec{x} &= D\vec{x} + s\vec{x},\\ D^{-1}P\vec{x} &= \vec{x} + sD^{-1}\vec{x} < \vec{x}.\end{aligned}$$

The so called "quotient theorem" states that for a nonnegative matrix $A = (a_{jk})$ and any positive vector $\vec{x} = (x_j)$

$$\min_j \frac{(A\vec{x})_j}{x_j} \leq \rho(A) \leq \max_j \frac{(A\vec{x})_j}{x_j}.$$

Thus the quotient theorem gives $\rho(D^{-1}P) < 1$.

2) Now assume $\rho(D^{-1}P) < 1$. Then there exists $\vec{x} > 0$ such that

$$\begin{aligned}D^{-1}P\vec{x} &= \rho\vec{x},\\ (D^{-1}P - I)\vec{x} &= (\rho - 1)\vec{x},\\ (P - D)\vec{x} &= (\rho - 1)D\vec{x},\\ ((P - D) + \alpha I)\vec{x} &= \alpha x + (\rho - 1)D\vec{x} \quad \alpha \gg 0\end{aligned}$$

Thus $\rho(P - D + \alpha I) < \alpha, \forall \alpha \to \infty$ and hence $s(P - D) < 0$.

4.6 Simulations

A simulation model was developed to study the tick-host interaction systems developed in this work. The C programming language was used. The simulation model is divided into three versions of the model namely sim1, sim2 and sim3 with increasing number of features incorporated. Each of these is composed of three modules which are the header file where all inputs such as parameters, arrays etcetera are defined under a common pointer array which we call p. Then comes the graphics module where the graphic display is designed and finally the computation module which merges information from the header and graphics modules to carry out the actual calculations and produce the graphic representations.

Colour graphic display was used to distinguish between the different tick stages and the two host populations namely the domestic cattle and the wild animal host. The relative densities in the different tick stages were defined in an array $x[i], \quad i = 1, \ldots, 10$, the domestic host by a variable z and the wild animal host by the variable y as in the model set up. An extra output was designed to show the dynamics of the total tick population. The domestic host was set at a fixed value because, as mentioned in the modeling section, its dynamics are outside the current model specification.

The mathematical procedure used in the simulation is the Euler method for the differential equation $\dot{u} = F(u)$, that is $u(t_{i+1}) = hF(u(t_i)) + u(t_i)$, where the stepsize, h, is small and $t_{i+1} = h + t_i$. From the point of view of numerical analysis, this method is rather crude, but it is quite sufficient for the present purpose. It has the further advantage, that the Euler method, applied to the differential equation, is very close to a discrete time model. Such interpretation seems impossible for more sophisticated solution schemes such as the fourth order Runge-Kutta method. For more information on some of these procedures see the book by Braun (1975). The simulation program allows to choose suitable parameter inputs describing specific demographic conditions of the host and tick populations depending on the tick and host population. In general the simulations show the relative densities in the various tick stages as well as the host population in the progress of time.

Now we briefly outline what each sub-model does.

In sim1 the system (4.45) is simulated using the above method. A typical "run" is the following: Initially there is the host population and ticks are introduced at very low densities. The host population continues to stay or even to rise. Then, if the reproduction number is above one, the tick population will increase and the host population will go down. Eventually it starts to decline while the tick population keeps on rising but the rate of increase reduces and eventually the tick population attains a stable stage distribution and coexists together with the two host populations or eventually the tick population increases exponentially. Both cases described above can be observed. The important observation here was that there is a critical value of the host attachment rate below which the tick population starts to decline monotonically. In this computer experiment a value of $q_j = 0.07, \quad j = 2,5,8$ gives this kind of observation where the numbers 2, 5 and 8 denote the questing tick stages. Interestingly this value is of the same order of magnitude with that reported in Byrom and Gettinby (1992) of 0.04 in their ECFXPERT simulation model. Thus the conclusion here is that host availability during questing periods is paramount for tick existence. Finally in sim1 we observe that the stable tick stage distribution produces peaks a phenomena which is general for stage structured populations since when the rate of recruitment into a stage exceeds the transit rate from that stage individuals may pile up in that stage contrary to what we observe for a stable age distribution, a phenomenon which has also been explained in the book by Caswell (1989) page 105.

In sim2 the basic features of sim1 were maintained but for each stage the residence times were estimated by the reciprocal of the combined rate of leaving that stage that is through mortality and advancement. Then the stage frequencies were scaled by the corresponding residence time at each iteration step. Then to each stage (at a given time) the size of that stage is represented by the area in the histogram columns and the mean residence time is given by the width of that columns. We expected that by this rescaling of the heights of the histogram columns the histogram (for a growing or constant tick population) would be monotonically decreasing, similar to the age histogram of a growing or constant population, that we expected that the "piling up" in certain stages would disappear from the histogram when stage size would be spread over residence time. This expectation is mathematically not quite justified, because we use the mean residence time in the stage to define the width of the cohort. Nevertheless, experimentally it came out nicely. The observation was that in the stage frequency histograms, with different widths, the finally attained stable stage distribution was a strictly decreasing function of stage number. Again co-existence between the three population species was observed under suitable conditions. Both sim1 and sim2 do not include any competition effect for on host feeding ticks nor any effects carried forward to subsequent off host developing stages.

In sim3 the competition effect is simulated by expressing the mortality of an off host developping stage as a function of the previous on host density, that is $\mu_i = \mu_i^0 + \mu_i^1 x_{i-1}$. For the data set used, the observed stable stage distribution was similar to that in sim2 except that the total population size of ticks was relatively lower, in comparison to that in sim2.

Figure 5 in the next page shows the structure of the stable distribution without scaling down the stage frequencies at each model iteration step. We notice that in this case the stage frequencies in the stable distribution do not decrease monotonically like in the following case. The reason for this is of course due to the difference in residence times for the different stages. Figure 6 on the other hand shows the stable stage distribution but with stage frequencies scaled down by the corresponding stage residence times at each iteration step. We notice that the stable distribution in this case is similar to that of a population structured by age. We also note that in both cases we have more on host larvae followed by on host nymphs then on host adults the least. This result is in agreement with what is observed in the field. That given a host population in the field, there are more on host larvae, followed by on host nymphs then on host adults the least.

Figure 5: Model Simulation 1

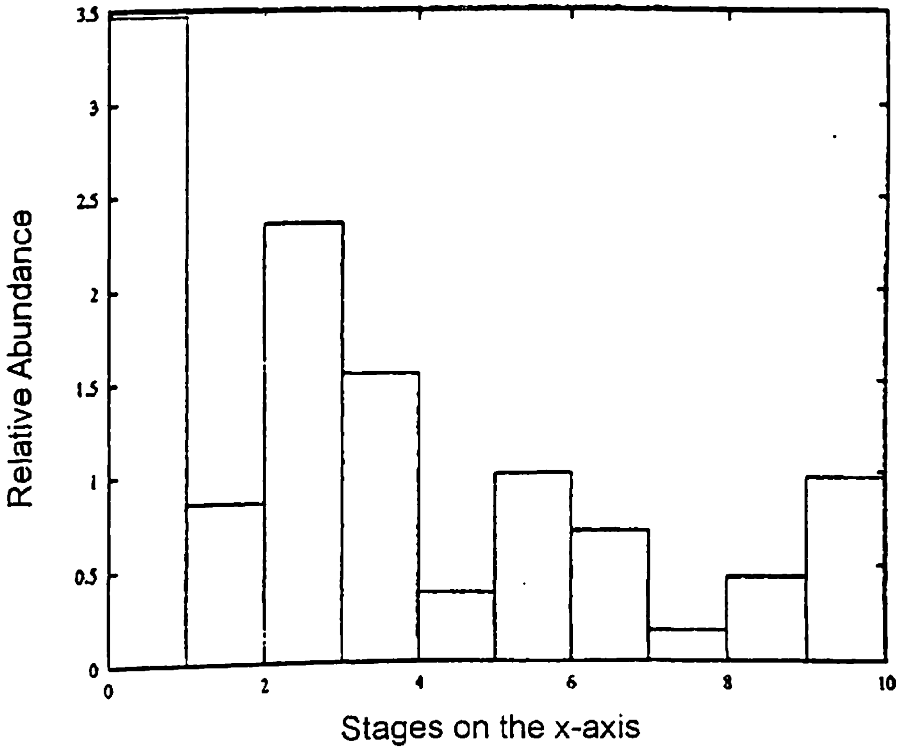
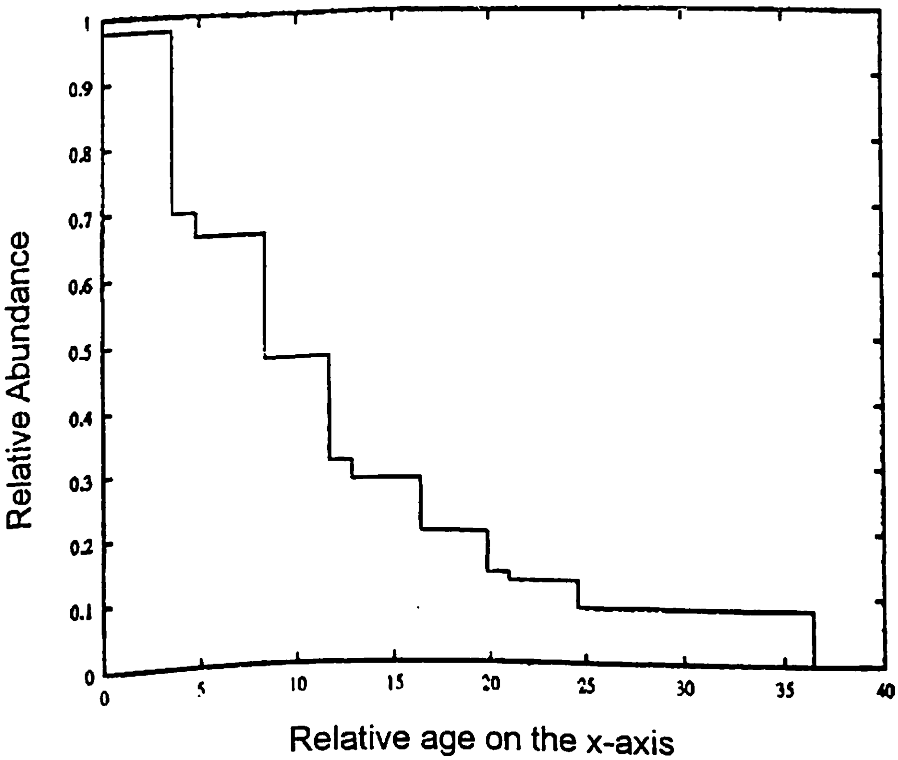


Figure 6: Model Simulation 2



CHAPTER V

SPATIAL DISTRIBUTION OF PARASITES

5.1 Introduction

In this chapter we consider the question of possible spatial frequency distributions of vector parasites in a habitat. The tick vector population will serve as a key example in the current study. Part of this question is the on-host distribution of vector parasites. An attempt is made to uncover the most proximate causes for observed phenomena such as inhomogeneity in the presence of homogeneous conditions or uniform distribution in spite of unevenly distributed oviposition sites.

Communal grazing is a common phenomena in most parts of eastern, central and southern Africa. Consider a typical communal grazing area which can be thought of as composed of identical units (observation plots) which are sufficiently small and very many. Take a typical grazing area as composed of n units (where n is large) each equally likely to be occupied by an individual parasite(tick). At the moment we do not differentiate between stages. Let N be the total number of parasites(ticks). Then $\mu = N/n$ is the average number of parasites(ticks) per unit area. Now the N parasites(ticks) are distributed. Observe a single space unit. Each individual parasite(tick) either occupies that unit or it doesn't. Thus we have a Bernoulli experiment. The parasite(tick) selects that particular area with probability $p = 1/n$. Then $\mu = Np$. The probability to find exactly k parasites(ticks) in the area considered, is

$$Prob\{k \text{ ticks in area}\} = \binom{N}{k} p^k (1-p)^{N-k} \quad k = 0, \ldots, N. \tag{5.1}$$

With the above assumptions the spatial distribution of parasites(ticks) follows a Bernoulli or binomial distribution.

Now we apply the following view. An ever larger area is taken into consideration, whereby the units (observation areas) stay constant in size. Thus the total number of parasites(ticks) is increasing, but the average number of parasites(ticks) per unit area remains the same. In mathematical terms, n is getting large, $p = 1/n$ is getting small, and N is also large in such a way that μ stays the same. Thus, with this most appropriate scaling of variables we arrive to the exact hypothesis for the transition from the binomial distribution to the Poisson distribution, that is,

$$Prob\{k \text{ ticks in area}\} = \binom{N}{k} p^k (1-p)^{N-k} \rightarrow \frac{\mu^k e^{-\mu}}{k!} \quad \text{as} \quad N \rightarrow \infty. \tag{5.2}$$

Of course in applications the probability of finding that the observation unit contains k parasites(ticks) is interpreted as the relative proportion of observation units containing k parasites(ticks). In other words, when the size of the observation area is selected in such a way that parasites(ticks) are sparse with respect to this size, then the spatial distribution of parasites(ticks) is described by the Poissson distribution with parameter μ, where μ is the average or expected number of parasites(ticks) per space area. We underline that this approach makes sense for sparsely distributed parasites(ticks). If μ in the Poisson distribution becomes large, we can as well use the normal distribution to approximate the original binomial distribution.

As we have said earlier any description of spatial distribution relies on a concept of observation unit. The Poisson distribution, being the limit of the binomial distribution for large N and large n, under the condition that N/n is constant, is by construction invariant to scaling. The binomial and the Poisson distribution both have been derived under the hypothesis, that each individual parasite(tick) can choose the unit area independent of the others, that is, the derivation is done excluding any a priori inhomegeneity such as staying near oviposition site or a posteriori inhomogeneity such as competition for space. In Poisson distribution the variance to mean ratio is 1. Although ticks are not insects (but nevertheless arthropods), most entomological studies indicate that the ratio of the sample variance and mean is usually not anywhere near one; the variance greatly exceeds the mean. Such observations are an indication that the frequency distribution itself is "contagious" and the observed tick pattern could be "clumped". The book by Pielou (1969,1977), pp.117 ff. provides detailed information on observed patterns and possible distributions. More realistic distributions are normally derived via two methods namely the method of generalized distributions and the method of compound distributions.

Case 1: Generalized distributions approach

Here we suppose individuals occur in clusters and these constitute the entities having a specified pattern and the number of individuals per cluster is random variate with its own probability distribution. One can derive the mean and variance say μ and σ^2 of the generalized distribution in terms of the means and variances of the cluster distribution that is distribution of clusters in space (μ_1 and σ_1^2) and disribution of individuals in each cluster (with mean μ_2 and variance σ_2^2). Let $G(z)$ denote the pgf of the cluster distribution and let $g(z)$ be that of the distribution of individuals. Then the generalized pgf for the number of individuals per unit area is

$$H(z) = G(g(z)). \tag{5.5}$$

Thus the mean and variance of the generalized distribution is

$$\mu = H'(1) \quad \text{and} \quad \sigma^2 = H''(1) + H'(1)(1 - H'(1)).$$

Now let p_i denote the probability that a unit contains i clusters $i = 0, 1, \ldots$ and π_j the probability a cluster contains j individuals $j = 1, 2, \ldots$ Then it follows by definition that

$$G(z) = \sum_i p_i z^i \tag{5.6}$$

and

$$g(z) = \sum_j \pi_j z^j. \tag{5.7}$$

Then combining these two formulae we get an expression for $H(z)$ as

$$H(z) = G(g(z)) = \sum_i p_i \left[\sum_j \pi_j z^j \right]^i.$$

Then we use this pgf to calculate the generalised mean and variance (μ and σ^2). By successive application of the chain rule we get

$$H'(1) = G'(g(1))g'(1) = \mu = \mu_1 \mu_2 \tag{5.8}$$

and from the relation

$$H''(1) = G''(g(1))(g'(1))^2 + G'(g(1)g''(1) = \sigma^2 - \mu + \mu^2 \tag{5.9}$$

we get

$$\sigma^2 = \mu_1\sigma_2^2 + \sigma_1^2\mu_2^2. \tag{5.10}$$

For example, if the number of clusters and individuals per cluster are both distributed as Poisson with parameters λ_1 and λ_2, respectively, then the mean and variance of number of ticks per grazing unit are

$$\mu = \lambda_1\lambda_2$$

and

$$\sigma = \lambda_1\lambda_2(1 + \lambda_2). \tag{5.11}$$

The resulting distribution here is known as a Poisson-Poisson distribution. The probability, p_k, that a randomly chosen grazing unit contains k individuals is given by the coefficient of z^k in the power series expansion of $H(z)$. As a second frequently used example of a generalized distribution, let the number of clusters per any grazing unit follow a Poisson distribution hence having pgf

$$G(z) = e^{\lambda(z-1)} \tag{5.12}$$

and assume that the number of individuals per cluster follows a logarithmic probability distribution with parameter α. This means that the probability $p(x)$ of a cluster to contain x individuals is proportional to α^x/x, for $x = 1, 2, \ldots$ (no cluster is empty). Then it follows from the normalization

$$\sum_{x=1}^{\infty} p(x) = 1$$

that

$$p(x) = \frac{-1}{\ln(1-\alpha)}\frac{\alpha^x}{x} \quad , x = 1, 2, \ldots \tag{5.13}$$

The pgf of the logarithmic disribution is

$$g(z) = \frac{\ln(1-\alpha z)}{\ln(1-\alpha)}. \tag{5.14}$$

Thus from these two probability laws it follows that the combined pgf $H(z)$ is then given by

$$H(z) = G(g(z)) = \exp\left\{\lambda\left[\frac{\ln(1-\alpha z)}{\ln(1-\alpha)} - 1\right]\right\}. \tag{5.15}$$

Now making the transformation $\lambda = k \ln \tilde{q}$, $\alpha = \tilde{p}/\tilde{q}$ with $\tilde{q} = 1 + \tilde{p}$, then substituting back and a bit of algebra gives

$$H(z) = (\tilde{q} - \tilde{p}z)^{-k}. \tag{5.16}$$

We notice that this $H(z)$ is the pgf of the negative binomial distribution. The mean of the combined or generalized distribution is given by

$$H'(1) = \mu = k\tilde{p} \tag{5.17}$$

while the variance σ^2 is given by

$$H''(1) + H'(1)(1 - H(1)) = \sigma^2 = k\tilde{p}(1 + \tilde{p}) = k\tilde{p}\tilde{q}. \tag{5.18}$$

Note that if we write the mean in the form $\mu = k\tilde{p}$ then the variance becomes

$$\sigma^2 = \mu + \mu^2/k. \tag{5.19}$$

Thus, the variance to mean proportion is larger than in the case of the Poisson distribution. Clearly the smaller the value of k, the greater the variance, but as $k \to \infty$, $\sigma \to \mu$, as for the Poisson distribution, the mean and the variance are equal, in fact it can be shown that

$$p_r \to \frac{\mu^r e^{-\mu}}{r!} \quad k \to \infty$$

where p_r gives the probability that a unit contains r individuals (for a proof see Pielou (1977)). The combined distribution derived above is also called the Poisson-logarithmic distribution where the first name indicates the distribution of the number of clusters and the second is the distribution of the number of individuals per cluster. What these distributions mean is this: if we are willing to accept that individuals (ticks in our case) exhibit a pattern of randomly dispersed clumps then the number of individuals per cluster may equally as well be a Poisson variate or a logarithmic variate.

Case 2: Compound distributions approach

Assume all individuals are independent (no clustering) of one another and that all units available are identical such that the pattern exhibited by individuals is uniform. Let λ denote the mean density, then the probability that any unit would contain k individuals is Poisson i.e.

$$Prob\{r \text{ ticks in area}\} = \frac{\lambda^r e^{-r}}{r!}. \tag{5.20}$$

The idea of compound distributions arises due to the fact that λ might itself be a random variable because some areas may provide more favourable environments than others. Assume λ has a gamma distribution with parameter $\alpha = k$ and $\beta = 1/\tilde{p}$, that is,

$$f(\lambda) = \frac{1}{\Gamma(k)}\left(\frac{1}{\tilde{p}}\right)^k \lambda^{k-1} e^{-\lambda(1/p)}, \quad \lambda \geq 0. \tag{5.21}$$

Then

$$p_r = \int_0^\infty \frac{\lambda^r e^{-\lambda}}{r!} f(\lambda) d\lambda. \tag{5.22}$$

On simplifying the right hand side by integrating out λ one arrives at the final expression given by

$$p_r = \frac{\Gamma(r+k)}{r!\Gamma(k)} \frac{\tilde{p}^r}{\tilde{q}^{k+r}} \quad r = 0, 1, \ldots \tag{5.23}$$

with $\tilde{q} = 1 + \tilde{p}$. Thus once again we arrive at the negative binomial distribution. In general there is a correspondence between every compound distribution and its generalized distribution counterpart and vice-versa. For a proof of this fact see Feller (1968). It is common experience to find that two or more theoretical distributions provide adequate fits to a set of observations since most of them resemble each other anyway. It is also important to note that since generalized and compound distributions are based on at least two assumptions, a single set of observations is quite often inadequate to confirm both assumptions, that is one on clusters and the other on ticks per cluster. Only if one of them were derived from an independent source of information could then the other be judged by fitting the generalized distribution. Thus the fitting of theoretical probability distributions is never by itself adequate to explain the pattern of natural populations; further analysis is definitely required.

5.2 On host distribution

In this section we focus on the on host distribution of ticks. Host species differ in their tick acquisition rates due to factors such as differences in exposure to ticks, heterogeneity due to age and behavioural or micro-habitat differences among hosts. It has been observed in various studies that host heterogeneity in susceptibilities results to:

i) On host parasite(vector) distribution that is aggregated or asymmetric in nature.

ii) Both mean number of parasites per host and the *variance to mean* ratio increase monotonically with age.

One important result due to the above observation is that we get density dependent parasite mortality and parasite induced-host mortality. According to Anderson and Gordon(1982) age-intensity relation and the relation between the variance to mean ratio to host age indicate the kind of density dependence present. To estimate age intensity relations host populations are typically classified according to age then the mean number of parasites calculated for each class. The problem is then to fit a mathematical relation to the data with host age as the explanatory variable. It is known that data from oldest age classes is scarce and it is mean parasite burdens associated with these age classes that determine if the age intensity relation is peaked. The most common applicable distribution used to describe skewed on host vector distribution is the negative binomial.

Thus the most general treatment or analysis of the above problem is

i) to allow parasite (tick) acquisition and mortality rates to be general functions of time, host age, exposure indices, rather than constant rates.

ii) define probability densities governing inherent differences among hosts which should be arbitrary rather than specific densities such as the Poisson distributuion.

The different forms of density dependence need to be distinguished. These include density-dependent parasite mortality, parasite induced host mortality and parasite induced changes in a host's susceptibility. As far as the tick population is concerned the first and the third forms of density dependence are the most important. This is because tick induced host mortality is an indirect relation since ticks only act as carriers of the actual disease parasites namely *Theileria parva* group of organisms. The negative binomial distribution has proven to be an excellent empirical descriptor of the on host tick distribution according to Anderson and May (1985). Now recall from section 5.1 that the mean μ and the variance σ^2 for a negative binomial distribution are related as

$$\sigma^2 = \mu(1 + \mu/k) \tag{5.24}$$

where k is the aggregation parameter. Thus the degree of agrregation decreases as k increases, that is as $k \to \infty$. Infact the distribution converges to the Poisson for large k. The problem normally is to seek maximum likelihood estimates for μ and k which in reality could depend on other explanatory variables such as host age. We will attempt to show how the maximum likelihood method can be used to estimate μ and k when they are functions of other factors. The ultimate aim is to address the question of heterogeneity in host susceptibility relaxing the assumption of homogeneity in susceptibility, hence on host distribution of vectors.

5.2.1 The model

Let $q_n(t,u)$ denote the probaility that a host of age u at time t carries n parasites or ticks in the present situation. Let $\lambda(t,u)\Delta u$ be the probability that a host of age u acquires an additional tick during the the time interval $(t, t+\Delta u)$ that is between ages u and $u + \Delta u$. Finally suppose that $n\mu(t,u)\Delta u$ is the probability that a single death occurs in the population of n tick parasites attaching a host aged u within the interval $(t, t + \Delta u)$. Thus the following balance equation holds:

$$\begin{aligned} q_n(t + \Delta u, u + \Delta u) = {} & \lambda(t,u)q_{n-1}(t,u)\Delta u + (n+1)q_{n+1}(t,u)\mu(t,u)\Delta u \\ & + q_n(t,u)[1 - \lambda(t,u)\Delta u - \mu(t,u)\Delta u]. \end{aligned} \tag{5.25}$$

Subtracting $q_n(t,u)$ from both sides and dividing both sides of the equation by Δu and letting $\Delta u \to 0$ yields

$$\begin{aligned} \frac{\partial q_n(t,u)}{\partial t} + \frac{\partial q_n(t,u)}{\partial u} = {} & \lambda(t,u)q_{n-1}(t,u) + (n+1)\mu(t,u)q_{n+1}(t,u) \\ & - \lambda(t,u)q_n(t,u) - n\mu(t,u)q_n(t,u). \end{aligned} \tag{5.26}$$

A solution of Eq.(5.26) is of the form

$$q_n(t,u) = \frac{e^{-\phi}\phi^n}{n!} \tag{5.27}$$

where,

$$\phi = \int_0^u \lambda(t-u+x,x)e^{-\int_x^u \mu(t-u+y,y)dy}dx. \tag{5.28}$$

This is a standard solution . Thus, the probability that there are n parasites on host of age u at time t is Poisson with mean ϕ. In the special case of constant μ and λ Eq.(5.28) becomes

$$\begin{aligned}\phi &= \int_0^u \lambda e^{-\int_x^u \mu dy}dx \\ &= \frac{\lambda}{\mu}(1-e^{-\mu u}).\end{aligned} \tag{5.29}$$

Now suppose

$$\lambda(t,u) = Z\,c(t,u) \tag{5.30}$$

where the non-negative random variable Z accounts for the difference among hosts in their susceptibilities to ticks. We may assume that each host is assigned a value Z at birth then it retains it throughout life. However this is different for different host individuals. The function $c(t,u)$ is a non-negative dependent on the host age and time. Now suppose $\theta\omega\Delta u$ is the probability that a host encounters a questing stage in the time interval $(t, t+\Delta u)$. These are host seeking tick stages which are namely the questing larvae, nymph and adult. However it is only the questing nymph and adult which can pass the disease organisms to the host when feeding. These can therefore be refered to as the infective stages. The variable θ denotes the number of the infective stages present in the host's grazing area. This number is affected by several factors therefore it is bound to be random in nature. The quantity $\omega\Delta u$ denotes the probability that the host encounters an infective stage where ω is is a measure of host preference by the questing stage. This quantity is also affected by several factors such as environmental factors, host age and type and many more therefore it can be taken as a random variable. Further let ε be the probability that the host is infected given an encounter. Then it follows that

$$\lambda(t,u) = \theta\omega\varepsilon \tag{5.31}$$

Next we give three possible relations between $Zc(t,u)$ and $\theta\omega\varepsilon$.

Case 1: $Z = \theta$ and $\varepsilon\omega = c(t,u)$

This case may arise if we suppose mean density and spatial distribution of the infective stages is constant in time, but the spatial distribution is patchy that is some host zones contain more infective stages than others which can be interpreted to mean that some areas are more tick prone than others. This set up brings about heterogeneity in susceptibilities to tick acquisition. It is assumed that ε and ω vary temporally with host age but do not vary among hosts of the same cohort.

Case 2: $Z = \omega$ and $\theta\varepsilon = c(t,u)$

Here we assume host behaviour varies such that ω is independent of age and time but differs among hosts. This could be due to between host variation in tick host preference. This time θ and ε vary temporally and with host age but do not vary among hosts of the same cohort.

Case 3: $Z = \varepsilon$ and $\omega\theta = c(t,u)$

This situation occurs if we assume that some hosts are able to resist tick attachment better than others and vice-versa, given an encounter, but ε is independent of age and time. The above characterisations do not represent an exhaustive list. They are among many that lead to the relation $\lambda(t,a) = Zc(t,u)$. With this representation Eq.(5.27) becomes

$$q_n(t,u) = \frac{e^{-zg(t,u)}[zg(t,u)]^n}{n!} \tag{5.32}$$

where,

$$g(t,u) = \int_0^u c(t-u+x,x)e^{-\int_x^u \mu(t-u+y,y)dy}dx \tag{5.33}$$

Thus the probability that a randomly chosen host of age u at time t will have n parasites is given by

$$\int_0^\infty f(z)q_n(t,u|Z=z)dz \tag{5.34}$$

where $f(z)$ is the probability density of Z. If Z is a discrete random variable, then the integral is replaced by a discrete sum. Let us assume that susceptibility to infection for different hosts is such that Z is a Poisson random variable. Let

$\pi(.)$ be the moment generating function of $f(z)$. Now the probability generating function of $q_n(t,u|Z=z)$ is given by

$$
\begin{aligned}
m(s) &= \sum_{n=0}^{\infty} s^n \frac{e^{-zg(t,u)}[zg(t,u)]^n}{n!} \\
&= e^{zg(t,u)(s-1)}
\end{aligned}
\tag{5.35}
$$

and so the probability generating function of Eq.(5.34) is given by

$$
\begin{aligned}
P(s,t,u) &= \sum_{n=0}^{\infty} s^n \int_0^{\infty} f(z) q_n(t,u|Z=z)dz \\
&= \int_0^{\infty} f(z) \sum_{n=0}^{\infty} s^n q_n(t,u|Z=z)dz \\
&= \int_0^{\infty} f(z) e^{zg(t,u)(s-1)}dz \\
&= \pi(g(t,u)(s-1))
\end{aligned}
\tag{5.36}
$$

where $\pi(.)$ is the moment generating function of $f(z)$. We thus obtain the mean, $\mu(t,u)$ and the variance $\sigma^2(t,u)$ of Eq.(5.34) directly from $\pi(g(t,u)(s-1))$ as

$$\mu(t,u) = \mu_z g(t,u) \tag{5.37a}$$

and

$$\sigma^2(t,u) = \mu_z g(t,u) + \sigma_z^2 g(t,u)^2 \tag{5.37b}$$

where μ_z and σ_z^2 are, respectively, the mean and variance of the variable Z. From Eq.(5.37a) and Eq.(5.37b), the *variance to mean ratio* as a function of age and time is given by

$$r_{\sigma^2:\mu}(t,u) = 1 + \frac{\sigma_z^2}{\mu_z} g(t,u) \tag{5.38}$$

Note that parasite(tick) distributions are always aggregated if the host population is heterogeneous with respect to susceptibility to parasites. The ***variance to mean ratio*** is a measure of the degree of aggregation which is a linear increasing function of the mean number of parasites per host. This is seen from Eq.(5.38) assuming σ_z^2 and μ_z are fixed. Infact an indication that the on host parasite is aggegated is when $r_{\sigma^2:\mu} > 1$. In general Eq.(5.37a), Eq.(5.37b) and Eq.(5.38) are not valid for systems where density-dependent parasite mortality or parasite induced mortality are present. The *variance to mean ratio* often decreases as $\mu(t,u)$ increases and the ratio may as well be less than one. The same would also be true if host susceptibility were a function of its parasite burden. This means that the relation between $r_{\sigma^2:\mu}(t,u)$ and $\mu(t,u)$ is in general not monotone. Thus if $r_{\sigma^2:\mu}(t,u)$ is not a linearly increasing function of $\mu(t,u)$ then it is an evidence of density dependence. However the converse is not necessarily true since a linear relation might be expected in some systems with density dependent parasite mortality that might alter the probability of further acquisition of ticks. The result in Eq.(5.37a), Eq.(5.37b) and Eq.(5.38) is dependent on the inherent assumption that the probability density $f(z)$ does not depend on host age and time. The density $f(z)$ would be a function of host age, for example, if hosts become immunologically or behaviourally less heterogeneous as they age. The negative binomial distribution is empiriclly suitable in many studies because its *variance to mean ratio* is of the form

$$r_{\sigma^2:\mu} = 1 + \frac{\mu(t,u)}{k}. \tag{5.39}$$

It follows that the result in Eq.(5.38) is related to the negative binomial distribution as follows

$$\begin{aligned} r_{\sigma^2:\mu}(t,u) &= 1 + \left(\frac{\sigma_z^2}{\mu_z}\right) g(t,u) \\ &= 1 + \left(\frac{\sigma_z^2}{\mu_z}\right) \frac{\mu(t,u)}{\mu_z} \\ &= 1 + \left(\frac{\sigma_z^2}{\mu_z^2}\right) \mu(t,u). \end{aligned} \tag{5.40a}$$

since $\mu(t,u) = \mu_z g(t,u)$. Thus the result in Eq.(5.38) resembles the negative binomial case provided that the parameter

$$k = \frac{\mu_z^2}{\sigma_z^2} \tag{5.40b}$$

is constant. One could obtain evidence of density dependence from negative binomially distributed field data by checking whether k varies significantly from cohort to cohort.

Adjei, Barnes and Lester (1986) gave a method of estimating parasite-induced host mortality that is based on truncated negative binomial distribution. Now suppose that the age-intensity relation in Eq.(5.37a) and Eq.(5.38) is estimated using data from a longitudinal study in which one cohort is repeatedly sampled through time. A peak in the age intensity relation from such a study could be caused by

i) parasite invasion rate that decreases with time say due to seasonal decrease in abundance of questing stages.

ii) vector parasite mortality rates that increase over time

One interesting case apart from the two above is the following. Suppose that parasite invasion and mortality rates vary temporally but are unaffected by host age. Further suppose a cross-sectional study is done where several host cohorts are sampled at a single point in time. Then the invasion and mortality rates become $\lambda(t)$ and $\mu(t)$ and age-intensity relation in Eq.(5.37a) becomes

$$\mu(u) = \mu_z \int_0^u \lambda(t-u+x)e^{-\int_x^u \mu(t-u+y)dy}dx \tag{5.41}$$

with t constant because the study is cross sectional. On making the change of variables $x' = x - u$ and $y' = y - u$ then Eq.(5.41) becomes

$$\mu(u) = \mu_z \int_{-u}^0 \lambda(t+x')e^{-\int_{x'}^0 \mu(t+y')dy'}dx' \tag{5.42}$$

Thus using the Leibnitz rule it follows that

$$\frac{d\mu}{du} = \mu_z \lambda(t-u)e^{-\int_{-u}^0 \mu(t+y')dy'} \tag{5.43a}$$

Now since $\lambda(t-u)$ and $\mu(t+y')$ are both nonnegative it follows that

$$\frac{d\mu}{du} \geq 0. \tag{5.43b}$$

This tells us that the mean number of parasites is a non-decreasing function of age. Note that this is true because of the assumption of a temporally varying system where the epidemiological parameters are independent of age and the study is cross sectional.

5.2.2 Parameter estimation by the MLE method

Suppose a sample of N hosts is collected and let x_i be the the number of parasites on or in the i-th host and let $\vec{\Theta}_i = (\vec{\theta}_i, \vec{\varphi}_i)$ be a vector of a series of measured attributes of the i-th host excluding x_i. In the context of parasite populations $\vec{\Theta}_i$ would include the age and/or time of collection of the i-th host but other time and host-specific variables such as habitat descriptors or host size or reproduction conditions are also possible. Under the assumption of asymmetrical vector parasite distribution on host we may asssume the probability that a host with vector of attributes $\vec{\Theta}_i$ has a given number of parasites is given by the negative binomial distribution with mean $\mu(\vec{\theta}_i)$ and over- dispersion parameter $r(\vec{\varphi}_i)$; $i = 1, \ldots, N$. We know that in general the negative binomial distribution with parameters p and r is given by

$$f(x, p, r) = \begin{cases} \binom{r+x-1}{x} p^r q^x & , \quad x = 0, 1, 2, \ldots \\ 0 & , \quad \text{elsewhere} \end{cases} \tag{5.44}$$

where $q = 1 - p$. Now we know that

$$E(X) = \mu = \frac{rq}{p} = \frac{r(1-p)}{p} \tag{5.45a}$$

which means that one can solve for p in terms of r and μ. Particularly in terms of the above parameter specification p can be written as a function of $\vec{\theta}_i$ and $\vec{\varphi}_i$ as

$$p(\vec{\theta}_i) = \frac{r(\vec{\varphi}_i)}{r(\vec{\varphi}_i) + \mu(\vec{\theta}_i)} \tag{5.45b}$$

Thus,

$$f(X = x_i, r(\vec{\varphi}_i), \mu(\vec{\theta}_i)) = \begin{cases} \binom{r(\vec{\varphi}_i)+x_i-1}{x_i} \left(\frac{r(\vec{\varphi}_i)}{r(\vec{\varphi}_i)+\mu(\vec{\theta}_i)}\right)^{r(\vec{\varphi}_i)} \left(\frac{\mu(\vec{\theta}_i)}{r(\vec{\varphi}_i)+\mu(\vec{\theta}_i)}\right)^{x_i} \\ 0 \quad \text{elsewhere} \end{cases} \tag{5.46}$$

Since the parameters of the negative binomial here are functions of the host-specific variables, the goal is to estimate the parameters $\mu(\vec{\theta}_i)$ and $r(\vec{\varphi}_i)$. Let the k parameters of the $\mu(\vec{\theta}_i)$ function be θ_u; $u = 1, \ldots, k$ and let the s parameters of the $r(\vec{\varphi}_i)$ function be φ_v; $v = 1, \ldots, s$. Values of the θ_u and φ_v are those that maximize the log- likelihood function for the data $(x_i, \vec{\theta}_i, \vec{\varphi}_i)$; $i = 1, \ldots, N$. Infact the log-likelihood function can be derived from Eq.(5.46) and is given by

$$L(x_i, r(\vec{\varphi}_i), \mu(\vec{\theta}_i)) = \sum_{i=1}^{N} \Big[r(\vec{\varphi}_i) \log r(\vec{\varphi}_i) - r(\vec{\varphi}_i) \log(r(\vec{\varphi}_i) + \mu(\vec{\theta}))$$

$$+ x_i \log \mu(\vec{\theta}_i) - x_i \log(\mu(\vec{\theta}_i) + r(\vec{\varphi}_i)) + \sum_{j=1}^{x_i} \Big(\log(r(\vec{\varphi}_i) + x_i - j) \Big) - \log(x_i!) \Big]. \tag{5.47}$$

The estimates for θ_u; $u = 1, \ldots, k$ and φ_v; $v = 1, \ldots, s$ are the MLE estimates which are roots of $k + s$ simultaneous equations given below:

$$\frac{\partial L}{\partial \theta_u} = \sum_{i=1}^{N} \frac{\partial \mu(\vec{\theta}_i)}{\partial \theta_u} \left[\frac{x_i}{\mu(\vec{\theta}_i)} - \frac{r(\vec{\varphi}) + x_i}{\mu(\vec{\theta}_i) + r(\vec{\varphi}_i)} \right] = 0, \quad u = 1, \ldots, k \tag{5.48a}$$

and

$$\frac{\partial L}{\partial \varphi_v} = \sum_{i=1}^{N} \frac{\partial r(\vec{\varphi}_i)}{\partial \varphi_v} \Big[1 + \log r(\vec{\varphi}_i) - \log(\mu(\vec{\theta}_i) + r(\vec{\varphi}_i)) - \frac{r(\vec{\varphi}_i) + x_i}{\mu(\vec{\theta}) + r(\vec{\varphi}_i)} + \sum_{j=1}^{x_i} \frac{1}{(r(\vec{\varphi}_i) + x_i - j)} \Big], \quad v = 1, \ldots, s \tag{5.48b}$$

These estimates are denoted by $\hat{\theta}_u$ and $\hat{\varphi}_v$ where $u = 1; \ldots, k$ and $v = 1, \ldots, s$. This procedure is important in host-vector or host-parasite systems where there is empirical evidence that the on host vector or parasite distribution is asymmetric. After estimating the parameter vectors $\vec{\varphi}_i$ and $\vec{\theta}_i$ these can then be used to estimate the parameters of the negative binomial distribution.

5.3 Density dependent and host heterogeneity on susceptibility

In this section we assume a general on host parasite distribution rather than assuming a specific distribution. The general assumption is to take the variance of the parasite distribution as a function of the mean on host parasite load. Adler and Kretzschmar (1992) observe that for a given set of system parameters, dispersion decreases as the mean on host parasite load increases and the system stabilizes. To generalise the model they proposed a model that allows the mean and variance to act independently as a better abstraction of the dynamics of the system.

The key issue was the relationship between density dependence and the on host parasite or vector distribution. In such kind of systems there are several parameters of interest among them (i) attachment rates or tick acquisition rates (ii) host renewal rates by birth and immigration (iii) host death (iv) parasite reproduction and (v) parasite mortality. For example host renewal is bound to be reduced for a heavily infested host population. These die more rapidly than do lightly infested hosts. Thus the effect of density dependence to these parameters is important. However including the effect of density dependence to all these parameters can prove complex. Thus the most reasonable thing to do is to study single quantities that reflect density dependence and are biologically meaningful. One of such quantities is the *effective reproductive rate* of parasites and hosts. In most of the previous studies, focus has been on the widely observed pattern of aggregated distributions of parasites, as opposed to a completely random distribution such as the Poisson. One reasonable distribution for aggregated on host parasite or vector distributions is the negative binomial. Reasons for observed aggregated parasite distributions include host heterogeneity in susceptibility due to several factors such as age (Anderson and May 1985). Distributions studied include (i) the regular positive binomial (ii) the negative binomial with fixed overdispersion parameter (iii) the random or Poisson ditributions. The results by Anderson and May (1978) showed that the equilibrium point is unstable in the first case, stable in the second and neutrally stable in the last. This suggests that aggregated distributions enhance stability. Adler and Kretzschmar (1992) suggest an improvement to this by taking dispersion as a dynamic variable. A problem of interest has been the analysis of the relationship between density dependence at the individual level as opposed to the entire host population. This is very important in the design of control strategies. This requires the understanding of the complexities of parasite-host interraction and their respective population dynamics. This is because justification for chemotherapeutic intervention against parasite or ticks must be made with sound quantitative arguments.

5.3.1 The general model

The model to be developed is dynamic in nature. It incorporates the host birth and death, parasite death, reproduction and transmission. We ignore the structuring of the host population, assuming that attached or on host parasites/ticks die (or their survival to the next stage is greatly curtailed) when their hosts die. It follows that their is need to classify hosts according to their parasite burden, an approach which has been extended to include host age-structuring by Hadeler

(1982) and Kretzschmar (1989a,b).

Let h_{i_k} denote the number of hosts per unit area carrying i_k parasites. Here a unit area is equivalent to a grazing area and k denotes parasite type. We thus define the following model variables:

i_k: the number of on host type k parasites.

t: the time variable

h_{i_k}: *the number of hosts with type k parasites*

H: the total number of hosts

Y: the total number of parasites

x: the mean number of parasites per host

π: the *variance to mean ratio* of the distribution of parasites on host.

Next we also list the parameters of interest. We note that these parameters can easily be made density dependent if need be. We introduce the following parameters

b_{i_k}: rate at which hosts with i_k parasites die.

a_{i_k}: rate at which hosts with i_k parasites reproduce.

s_{i_k}: relative susceptibility of hosts with i_k parasites.

μ_{i_k}: per capita parasite death rate in hosts with i_k parasites.

λ_{i_k}: per capita parasite egg production rate in hosts with i_k parasites.

and

ϕ_{i_k}: rate at which hosts with i_k parasites acquire new parasite.

We make the assumption that newborn hosts are parasite free that is are in class h_0 by definition. The system of equations describing how hosts change state is described by the following set of equations

$$\dot{h}_0 = -(b_0 + \phi_0)h_0 + \mu_1 h_1 + \sum_{i=0}^{\infty} a_{i_k} h_{i_k} \qquad (5.49a)$$

and

$$\begin{aligned}\dot{h}_{i_k} = &-(b_{i_k} + \phi_{i_k} + i_k\mu_{i_k})h_{i_k} \\ &+ (i_k + 1)\mu_{i_k+1}h_{i+1} + \phi_{i_k-1}h_{i_k-1}, \quad i_k = 1, 2, \cdots \end{aligned} \qquad (5.49b)$$

where $\dot{h}_{i_k}$ denotes the derivative h_{i_k} with respect to time. The system of differential equations describes the time evolution of parasite population and host population starting from some given initial distribution of parasites on the host.

Next we define the aggregated variables which are given by

$$H_k = \sum_{i_k=0}^{\infty} h_{i_k}, \quad Y_k = \sum_{i_k=0}^{\infty} i_k h_{i_k}, \quad E_k = \sum_{i_k=0}^{\infty} i_k \lambda_{i_k} h_{i_k} \tag{5.50}$$

where

H_k is the total density of hosts carrying parasites type k

Y_k is the total number of type k parasites harboured by total host community in a typical grazing area say; and

E_k is the total number of eggs per unit area per unit time by fecund type k parasites. We can then express ϕ_{i_k} defined earlier on as

$$\phi_{i_k} = s_{i_k} E_k g(H) \tag{5.51}$$

That is, the infection rate is assumed to depend linearly on the number of eggs produced. The function $g(H)$ gives the probability that a single host picks a single egg and is expressed as a function of total host density. Adler and Kretzschmar (1992) assume $g(H)$ is a decreasing function of H. This means that as H increases the chance that a host picks an off host egg diminishes because of the simple reason that there are more host individuals exposed to infection. To generalise the model for vector parasites models we define $g(H)$ as the probability that a single off host questing individual is picked by a single host expressed as a function of host density, H. This means that $g(H)$ is necessarily an increasing function of H. Thus in general if the on host parasite type is k then Eq.(5.51) is more generally written as

$$\phi_{i_k} = s_{i_k} E_{k-1} g(h) \tag{5.52}$$

where E_{k-1} now denotes the off host questing individuals prior to stage k and $\lambda_{i_{k-1}}$ becomes the moulting rate to stage $k-1$. The quantity $H_k g(H_k)$ gives the probability that an individual in a grazing area attaches and it should be an increasing function of H_k since the probability of locating a host should increase with host density. Thus

$$\frac{d}{dH_k} H_k g(H_k) > 0 \tag{5.53}$$

We can define further aggregated variables as

$$H_{b_k} = \sum_{i_k=0}^{\infty} b_{i_k} h_{i_k}, \quad H_{a_k} = \sum_{i_k=0}^{\infty} a_{i_k} h_{i_k}, \quad H_{s_k} = \sum_{i_k=0}^{\infty} s_{i_k} h_{i_k} \tag{5.54}$$

and

$$Y_{b_k} = \sum_{i_k=0}^{\infty} i_k b_{i_k} h_{i_k}, \quad Y_{\mu_k} = \sum_{i_k=0}^{\infty} i_k \mu_{i_k} h_{i_k} \tag{5.55}$$

where

H_{b_k}: denotes total number of hosts dying per unit time due to type k parasites;

H_{a_k}: denotes total number of hosts born per unit time in the presence of type k parasites;

H_{s_k}: denotes the total susceptible host density per unit time for a type k parasite;

Y_{b_k}: denotes the total number of type k parasites dying per unit time due to host death;

Y_{μ_k}: denotes the total number of type k parasites dying per unit time due to natural mortality. It follows that

$$\dot{H}_k = -H_{b_k} + H_{a_k} \tag{5.56}$$

and

$$\dot{Y}_k = -Y_{b_k} - Y_{\mu_k} + H_{s_k} g(H_k) E_k \tag{5.57}$$

where the notation $\dot{H}_k$ and $\dot{Y}_k$ denote the derivative of the variables H_k and Y_k with respect to time. As a special case following Anderson and May (1978) we assume no density dependence effects and set

$$\mu_{i_k} = \mu, \quad \lambda_{i_k} = \lambda, \quad s_{i_k} = s, \quad a_{i_k} = a \quad \forall i_k \tag{5.58}$$

Thus we have

$$H_{a_k} = aH_k, \quad H_{s_k} = sH_k, \quad E_k = \lambda Y_k, \quad P_{\mu_k} = \mu Y_k \tag{5.59}$$

Case I

Assume host mortality increase linearly with parasite burden such that

$$b_{i_k} = b + \alpha i_k \qquad (5.60)$$

We note here that in the case of tick-host interractions we can assume that hosts exit a typical grazing area due to natural mortality b and also by avoiding an over infested area at rate α. Substituting the constant parameter values and b_{i_k} into the expressions for $\dot{H}_k$ and $\dot{Y}_k$ we get

$$\begin{aligned} \dot{H}_k &= -\sum_{i_k=0}^{\infty}(b+\alpha i_k)h_{i_k} + \sum_{i_k=0}^{\infty} a h_{i_k} \\ &= (a-b)H_k - \alpha Y_k \end{aligned} \qquad (5.61a)$$

and

$$\begin{aligned} \dot{Y}_k &= -\sum_{i_k=0}^{\infty} i_k(b+\alpha i_k)h_{i_k} - \mu Y_k + H_{s_k} g(H_k)\lambda Y_k \\ &= -bY_k - \alpha\sum_{i_k}^{\infty} i_k^2 h_{i_k} - \mu Y_k + H_{s_k} g(H_k)\lambda Y_k \\ &= -(b+\mu)Y_k + sH_k g(H_k)\lambda Y_k - \alpha\sum_{i_k=0}^{\infty} i_k^2 h_{i_k}. \end{aligned} \qquad (5.61b)$$

The only term that is not a function of Y_k and H_k is the last term. Now the quantity

$$q_{i_k} = h_{i_k}/H_k \qquad (5.62a)$$

can be looked as the probability that a host is carrying i_k type k parasites. If the assumption of aggregated on host parasite distribution holds and i_k is discrete then we can assume it follows the negative binomial distribution with an over-dispersion parameter or clumping parameter r. Let the on host mean parasite load be m_k and its variance σ^2. We next wish to reformulate the entire host-parasite interraction system in terms of the *variance to mean ratio* π_k. Notice that the mean number of type k parasites per host is thus given by

$$m_k = \sum_{i_k=0}^{\infty} i_k h_{i_k}/H_k = Y_k/H_k \qquad (5.62b)$$

By definition the *variance to mean ratio* is given by

$$\pi_k = \sigma_k^2/m_k \quad \Rightarrow m_k\pi_k = \sigma_k^2 \tag{5.63a}$$

but σ_k^2 can be expressed as

$$\sigma_k^2 = \sum_{i_k=0}^{\infty} i_k^2 q_{i_k} - m_k^2 \tag{5.63b}$$

thus

$$\sum_{i_k=0}^{\infty} i_k^2 q_{i_k} = m_k\pi_k + m_k^2 = m_k(\pi_k + m_k). \tag{5.63c}$$

We now make the following change of variables

$$Y_k = m_k h_k \quad \text{and} \quad \sum_{i_k=0}^{\infty} i_k^2 q_{i_k} = m_k(\pi_k + m_k) \tag{5.64}$$

in equations (5.61a) and (5.61b) to obtain

$$\begin{aligned} \dot{H}_k &= (a-b)H_k - \alpha m_k H_k \\ &= (a - b - \alpha m_k)H_k. \end{aligned} \tag{5.65a}$$

Now $\dot{Y}_k$ can be expressed as

$$\dot{Y}_k = \dot{m}_k H_k + m_k \dot{H}_k \tag{5.65b}$$

hence (5.61b) becomes

$$\begin{aligned} \dot{m}_k H_k + m_k \dot{H}_k &= -(b+\mu)m_k H_k + s\lambda H_k g(H_k) m_k H_k - \alpha H_k \sum_{i_k=0}^{\infty} i_k^2 q_{i_k} \\ &= -(b+\mu)m_k H_k + s\lambda H_k g(H_k) m_k H_k \\ &\quad - \alpha H_k(m_k(\pi_k + m_k)). \end{aligned} \tag{5.65c}$$

Using Eq.(5.65a) in Eq.(5.65c) we get

$$\begin{aligned} \dot{m}_k H_k = -(b+\mu)m_k H_k &+ s\lambda H_k g(H_k) m_k H_k \\ &- \alpha H_k(m_k(\pi_k + m_k) - m_k H_k(a - b - \alpha m_k) \end{aligned} \tag{5.65d}$$

then cancelling out terms in the entire equation followed by a reorganisation of the equation we get

$$\dot{m}_k = m_k(s\lambda H_k g(H_k) - a - \mu - \alpha\pi_k) \tag{5.66}$$

Setting $\dot{H}_k = 0$ and $\dot{m}_k = 0$ in Eq.(5.65a) and Eq.(5.66) respectively we get the equilibrium state $(\bar{m}_k, \bar{H}_k)$ which satisfies

$$\bar{m}_k = (a - b)/\alpha \tag{5.67a}$$

and

$$s\lambda \bar{H}_k g(\bar{H}_k) = a + \mu + \alpha\pi(\bar{m}_k) \tag{5.67b}$$

It follows that $\bar{m}_k$ is positive as long as $a > b$ and a positive solution for $\bar{H}_k$ as long as the product of host susceptibility with tick fecundity , $s\lambda$, is sufficiently large since $\bar{H}_k g(\bar{H}_k)$ is an increasing function of H_k.

Now the Jacobian at the equilibrium state $(\bar{m}_K, \bar{H}_k)$ is given by

$$J = \begin{pmatrix} 0 & -\alpha\bar{H}_k \\ \lambda s \bar{m}_k \frac{d}{H_k} H_k g(H_k)|_{H_k=\bar{H}_k} & -\alpha\bar{m}_k\pi'(\bar{m}_k) \end{pmatrix} \tag{5.67c}$$

where $\pi'(m_k)$ is the derivative of π with respect to m_k. Of course here we assume that m_k is varying. In general the stability of the 2-dimensional system is determined by

i) the determinant of J

ii) the trace of J

Now since

$$\frac{d}{H_k} H_k g(H_k) > 0$$

it follows that the determinant is given by

$$|J| = \alpha\lambda s\bar{m}_k\bar{H}_k \frac{d}{H_k}(H_k g(H_k))|_{H_k=\bar{H}_k} \tag{5.67d}$$

is positive. The general known result about such systems is that the equilibrium is stable if the trace is negative and in this particular case stability is achieved if

$$\alpha\bar{m}_k\pi'(\bar{m}_k) > 0 \tag{5.68}$$

and unstable if the inequality is reversed. Stability when the trace is zero is not determined by the linearized system.

Since $m_k > 0$ Eq.(5.68) indicates that the equilibrium will be stable if the *variance to mean ratio* π_k is an increasing function of the mean parasite load m_k and unstable if the opposite holds. This is in line with the work by Hassel and Pacala (1990) on host-parasitoid models where hosts experience a range of risks. It is shown here that for a wide range of variability -generating mechanisms the *system stabilizes if the* coefficient of variation of the degree of risk is less than 1. Work by Perry and Taylor (1986) showed that *variability in the clumping* parameter r can modify the stability of the equilibrium. This means that model parameters can systematically depend on the mean rather than being fixed values.

There is strong empirical evidence that most on host parasite distributions are asymmetric the negatve binomial way, meaning that most host individuals will carry intermediate tick loads while few animals will carry heavy tick loads. Thus if one assumes the negative binomial distribution for the on host parasite distribution then from Eq.(5.19)

$$\pi(m_k) = 1 + \frac{m_k}{r} \tag{5.69a}$$

where m_k is the mean of the underlying on host parasite distribution. This is a linearly increasing function and thus leads to a stable equilibrium by Eq.(5.68). A Poisson distribution on the other hand has a constant *variance to mean ratio* π_k producing a zero derivative of π_k with respect to m_k and thus implying a neutral stability. In the case of the positive binomial distribution one gets

$$\pi_k(m_k) = m_k - m_k c \tag{5.69b}$$

where c is a fixed parameter. In this case $\pi_k(m_k)$ is a decreasing function of m_k (since $\pi'_k = -c$) and thus from Eq.(5.68) we get an unstable equilibrium.

Case II

Now we introduce density dependence by making the parasite death rate a linearly increasing function of the on host parasite burden. This assumption breaks down the simplicity of the above results. That is, assume that

$$\mu_{i_k} = \mu + \gamma i_k \tag{5.70a}$$

Then

$$\begin{aligned} Y_{\mu_k} &= \sum_{i_k=0}^{\infty} i_k(\mu + \gamma i_k)h_{i_k} \\ &= \mu Y_k + \gamma \sum_{i_k=0}^{\infty} i_k^2 h_{i_k} \end{aligned} \tag{5.70b}$$

then substituting this into the expression of $\dot{Y}_k$ in Eq.(5.57) we get,

$$\begin{aligned} \dot{Y}_k &= -\sum_{i_k=0}^{\infty} i_k b_{i_k} h_{i_k} - \mu Y_k - \gamma \sum_{i_k=0}^{\infty} i_k^2 h_{i_k} + H_{s_k} g(H_k) E_k \\ &= -\sum_{i_k=0}^{\infty} i_k(b + \alpha i_k)h_{i_k} - \mu Y_k - \gamma \sum_{i_k=0}^{\infty} i_k^2 h_{i_k} + H_{s_k} g(H_k) \sum_{i_k=0}^{\infty} i_k \lambda h_{i_k} \\ &= -\sum_{i_k=0}^{\infty} i_k(b + \alpha i_k)h_{i_k} - \mu Y_k - \gamma \sum_{i_k=0}^{\infty} i_k^2 h_{i_k} + H_{s_k} g(H_k) \lambda Y_k \\ &= -b \sum_{i_k} i_k h_{i_k} - \alpha \sum_{i_k=0}^{\infty} i_k^2 h_{i_k} - \mu Y_k - \gamma \sum_{i_k=0}^{\infty} i_k^2 h_{i_k} + H_{s_k} g(H_k) \lambda Y_k \\ &= -bY_k - \alpha H_k \sum_{i_k=0}^{\infty} i_k^2 q_{i_k} - \mu Y_k - \gamma H_k \sum_{i_k=0}^{\infty} i_k^2 q_{i_k} + H_{s_k} g(H_k) \lambda Y_k \\ &= -(b + \mu)Y_k - (\alpha + \gamma)H_k \sum_{i_k=0}^{\infty} i_k^2 q_{i_k} + H_{s_k} g(H_k) \lambda Y_k \end{aligned}$$

Then using Eq.(5.63c) we get

$$\dot{Y}_k = -(b + \mu) - (\alpha + \gamma)H_k m_k(\pi_k + m_k) + \lambda H_{s_k} g(H_k) Y_k. \tag{5.71}$$

Now recall that

$$m_k = Y_k / H_k \Rightarrow \dot{Y}_k = \dot{m}_k H_k + m_k \dot{H}_k$$

Therefore

$$\dot{m}_k H_k + m_k \dot{H}_k = -(b + \mu)Y_k - (\alpha + \gamma)H_k m_k(\pi_k + m_k) + \lambda H_{s_k} g(H_k) m_k H_k$$

Now using the expression for $\dot{H}_k$ in Eq.(5.65a) and using the fact that

$$Y_k = m_k H_k$$

we obtain

$$\begin{aligned}\dot{m}_k H_k = & -(b+\mu) m_k H_k - (\alpha+\gamma) H_k m_k(\pi_k + m_k) \\ & + \lambda H_{s_k} g(H_k) m_k H_k - m_k(H_k(a - b - \alpha m_k))\end{aligned}$$

Cancelling out like terms and simplifying we get

$$\dot{m}_k = m_k(s\lambda H_k g(H_k) - a - \mu - \alpha\pi_k - \gamma\pi_k - \gamma m_k) \tag{5.72}$$

and

$$\dot{H}_k = H_k(a - b - \alpha m_k)$$

Next we present the Jacobian of the system above at the equilibrium state $(\bar{H}_k, \bar{m}_k)$:

$$J = \begin{pmatrix} 0 & -\alpha\bar{H}_k \\ \lambda s\bar{m}_k \frac{d}{dH_k} H_k g(H_k)|_{H_k=\bar{H}_k} & (-(\alpha+\gamma)\pi'_k(m_k) - \gamma)\bar{m}_k \end{pmatrix} \tag{5.72}$$

The determinant of the system is unchanged from that obtained in the earlier system and it is positive. The trace at equilibrium is given by

$$(-((\alpha+\gamma)\pi'_k(m_k) + \gamma))m_k$$

Thus the equilibrium is stable if

$$\pi'_k(\bar{m}_k) > -\gamma/(\gamma+\alpha) \tag{5.73}$$

and unstable if the inequality is reversed. Thus as before the equilibrium is stable if $\pi'_k(m_k) > 0$, and is necessarily stable if $\pi'_k(m_k) > 1$. However if $-1 < \pi'_k(m_k) < 0$ the equilibrium may be stabilized by sufficiently large γ. This means that a decreasing *variance to mean ratio* ($\pi'_k(m_k) < 0$ but > -1) may be sufficient to stabilize the system in the presence of sufficiently high density dependent parasite mortality. An extension to this approach would be to consider a 3.dimensional system tracking the dynamics of H_k, m_k and say $\pi_k(m_k)$ which may accurately describe the dynamics of the infinite system. That is, although the equilibrium distribution might remain constrained to a fixed family throughout the dynamics the idea is to allow more than one parameters describing that distribution to vary. For example in the case of the negative binomial one can allow the clumping parameter to vary along with say the mean. This approach is left out as a future research area.

5.4 The reproduction ratio and density dependence

In this section we investigate the effect of density dependence to quantities that explain population dynamics. An example of such density dependent variables is the reproduction ratio, R_0. The aim is to understand the population dynamics of harmful populations such as ticks or parasites in general. This is because parasites are important causes of morbidity and mortality in host communities and are thus important causes of production losses in animals of economic importance. The models aid in the design of control strategies of both the parasite populations and the diseases they cause. One of the methods used is the use of chemicals or chemotherapy. The problem here is about the most optimal control strategy to reduce cost and effort. Thus the justification to use them has to be supported by sound quantitative arguments.

The on host distribuion of parasites is central to this approach. An overdispersed ditribution means that most individuals are lightly infested or infected and few harbour heavy parasite loads. Consequently a heavily infected fraction of hosts attract most of the medical or veterinary attraction. Another aim is to focus on stages in the parasite life cycle that are the target of chemotherapy.

The critical issue in the control of parasite populations is that the populations involved fluctuate with time. Both hosts and parasites are continually being removed and replaced by death and emigration and by birth and immigration respectively. This is regardless of whether the population is constant or not. Now when the population is constant the average number of female parasites attaining maturity produced by a female parasite during her life time is 1, that is it replaces itself in the next generation. However a more realistic reproduction ratio is that which takes account of density dependence. Thus let $f(M)$ denote the average density effects where M is the average parasite burden per host. Then we can write

$$R_e = f(M)R_0. \tag{5.74a}$$

such that when there is no density dependence.

$$f(M) = 1 \tag{5.74b}$$

where R_0 is the basic reproduction ratio. The quantity R_e is called the effective reproduction ratio such that when $R_e > 1$ the population is increasing and when $R_e < 1$ then the population is declining. The quantity R_e is always less than the basic reproduction ratio R_0 and it is defined as the average number of female parasites produced by one female in a completely susceptible host population. Note that difference between R_e and R_0 is density dependence and or crowding effects.

Density dependence functions in complex ways and actually affects the rate of recovery of parasite population following intervention regimes. Now at equilibrium

$$R_e = 1 \quad \text{and} \quad f(M) = 1/R_0 \tag{5.74c}$$

In actual fact those female parasites in very lightly infected hosts may have R_e very close to R_0 while it will be considerably less than R_0 in heavily infested hosts. The most common approach in the formulation of models to capture density dependence is to assume some separate relationship for on host parasite individuals. One can then average over the whole parasite population using some distribution for parasites.

The situation is complex in the sense that the distribution of parasites is itself a dynamic entity and is thus a function of the population dynamics of the parasites, pattern of transmission within a community, and the perturbation as a result of a control intervention. Thus the rate of infection of hosts is dependent on the distribution of parasites and the density dependence exerted as a function of the distribution which in turn determines the rate of infection of hosts. Consider the rate of change of the mean parasite load per host given by

$$\dot{M} = \frac{dM}{dt} \tag{5.74d}$$

This value is negative when the population is declining, positive during parasite growth and zero at equilibrium and is measured in numbers of parasites per unit time. Thus we can write

$$\begin{aligned} \dot{M} &= \mu M(R_0 f(M) - 1) \\ &= \mu M(R_e - 1) \end{aligned} \tag{5.74e}$$

wher μ is the parasite mortality. The equation is in this form because the population is being removed at a rate μ through mortality and when a parasite dies it replaces itself by a factor R_e. Eq.(5.74e) emphasizes that the death rate of adult parasite, μ, has an overall effect on the rate of recovery of a parasite population from a perturbation due to intervention measures. Paradoxically the equation says that the larger the death rate (i.e the shorter the life expectancy of parasites) the faster the rate of recovery. Such a concept is useful in deciding the frequencies of chemotherapeutic intervention required to control the population. We mention here that host heterogeneity to susceptibility is bound to exist. One source of such a heterogeneity is age related factors. For example if intensity of infection is higher in some groups than in others, then groups with higher average burdens generally provide best targets for treatment. Acquired resistance to infection and disease are important components of this pattern and the determination of the effect of chemotherapy. Density dependence also governs the probability of mating and hence R_e as follows. Let $g(M)$ denote the proportion of female parasites that is mated as a function of the mean parasite burden. The effective reproduction ratio is given by

$$R_e = f(M)g(M)R_0 \tag{5.74f}$$

This equation shows that as the mean parasite burden increases following chemotherapy the probability of mating increase but the effect of density dependence increases as well. Thus the effective reproduction ratio is a peaked function of the mean parasite burden. The theory of chemotherapy application for control of parasite populations revolves around attempts to include a dynamic distribution of parasites in population models (Hadeler and Dietz 1983). For vector parasite populations such as ticks reduction in the population through dipping say will reduce the rate of infectious agents that they carry. The relationship between the density of vectors and the equilibrium prevalence of the transmitted infection is non-linear, where a significant reduction in transmitted infection is achieved only at very low densities of the vector. For chemotherapy against parasite vectors to alter the pattern of transmission of the carried infection significantly, it ought to be intensive and may be beyond the levels required to reduce morbidity and mortality due vector parasites.

5.4.1 Contagious and Truncated distributions

Let $f_1(.),\dots,f_n(.),\dots$ be a sequence of density functions which may or may not depend on parameters. Let $p_1, p_2,\dots,p_n,\dots$ be a sequence of parameters satisfying $p_i \geq 0$ and $\sum_{i=0}^{\infty} p_i = 1$, then

$$f(x) = \sum_{i=0}^{\infty} p_i f_i(x)$$

is a density function called a contagious distribution or a mixture of distributions. The concept of mixing is naturally extended in the following manner,.

Let $\{f(x;\theta), \theta \in \Omega\}$ be a family of density functions parametrized or indexed by $\theta \in \Omega$, where Ω is the parameter space; and let $g(\theta)$ be a probability density function which is zero for all $\theta \notin \Omega$. Then

$$f(x) = \int_{\Omega} f(x;\theta) g(\theta) d\theta \tag{5.75a}$$

is again a density function called a contagious distribution or a mixture. Thus parametric families of densities can be obtained from existing families by the technique of mixing. Truncation could also be employed to generate new families of discrete densities. It can as well be used to form families of continuous distributions.

In general if X is a random variable with density $f(x)$ and corresponding cumulative distribution $F(x)$, then the density of X truncated at a and on the right of b is given by

$$\frac{f(x)}{F(b) - F(a)} \qquad a < x < b \tag{5.75b}$$

5.4.2 The model

In order to model parasite distribution, relaxing the assumption of any particular theoretical distribution, a method need be devised of incorporating host heterogeneity. Each host has some susceptibility to type k parasite. This susceptibility may be time dependent or independent. For now we assume the latter. The susceptibility index measures a host's relative susceptibility to parasite establishment. It could be perceived as having its basis in exposure differences or acquired immune resistance due to experience to tick challenge.

Let h_i denote the susceptibility factor for host i, and $\lambda(t)$ denote the mean attachment rate for parasites in a host community. Then $\lambda(t)h_i$ will give the mean establishment rate for host i. The parasite burden for host i denoted by M_i is described by an immigration death process, that is

$$\dot{M}_i = \lambda(t)h_i - \mu M_i \tag{5.75c}$$

The general solution to such a system is the Poisson distribution (Cox and Miller(1965) pg. 168) of parasites both between hosts having same susceptibility factor and within the same host at different times. From case 2 of section 5.1, it follows that if susceptibility factors are gamma distributed the distribution of ticks follows the negative binomial distribution. This approach has been used previously by Dietz(1982), Hadeler and Dietz(1983) and Anderson and May(1985). Let us assume that the variable h for host susceptibility has mean one and its distribution is skewed. The variable h is continuous. For example the gamma distribution with mean unity and parameter k fits well to such a description. That is

$$g(h,k) = \frac{k^k h^{k-1} e^{-kh}}{\Gamma(k)}, \quad h > 0 \tag{5.75d}$$

Obviously the variance for the distribution above is given by

$$var(h) = \frac{1}{k}$$

The same argument of heterogeneity generation mechanisms based on an individual apply equally to groups of hosts each with same susceptibility. The host population can be divided into a number of parasite types or categories according to suscetibility indexed by $j = 1, 2, \ldots$ each having a rate of susceptibility relative to the whole population equal to h_j and proportional representation in the community given by w_j. The types or classes are simply theoretical constructs to enable us deal with the dimension of susceptibility in a discrete rather than in a continuous manner without focussing on individual hosts specifically. Thus in order to calculate h_j and w_j the continuos variable h is divided into discrete intervals with upper limit for each interval given by H_j that is class j is $\{h : \quad H_{j-1} < h < H_j\}$. The weighted average value of h within each interval and the integral of $g(h, k)$ over the interval are h_j and w_j respectively. Let

$$P(x, k) = \frac{k^k}{\Gamma(k)} \int_0^x \tau^{k-1} e^{-\tau} d\tau \qquad (5.76a)$$

then for host j spanning the h dimension from H_{j-1} to H_j $(H_0 = 0)$

$$\begin{aligned} w_j &= \frac{k^k}{\Gamma(k)} \int_{kH_{j-1}}^{kH_j} \tau^{k-1} e^{-\tau} d\tau \\ &= P(kH_j; k) - P(kH_{j-1}; k) \end{aligned} \qquad (5.76b)$$

Since w_j is the proportional representation of class j in the entire community, it follows that the mean of h in the interval (kH_{j-1}, kH_j) is given by

$$\begin{aligned} h_j &= \frac{k^{k+1}}{\Gamma(k)} \int_{kH_{j-1}}^{kH_j} \frac{h^k e^{-kh} dh}{w_j} \\ &= \frac{p(kH_j, k+1) - p(kH_{j-1}, k+1)}{p(kH_j, k) - p(kH_{j-1}, k)} \end{aligned} \qquad (5.76c)$$

Now let the probability that a host of type j has n parasites be denoted by p_{n_j}. Definitely the distribution is discrete because we cannot have a fractional number of parasites on a host. The most reasonable distribution to choose is the Poisson with mean w_j. However the distribution of parasites over the entire host community is according to empirical evidence asymmetric where majority of host individuals carry intermediate parasite loads while only a few carry heavy parasite loads. Thus the distribution of parasites over the whole community is found by mixing the distributions of the individual host types which in this case is most reasonably given by a gamma mixture of Poissons such that

$$p_n = \sum_{j=1} p_{n_j} w_j \qquad (5.76d)$$

where the p_n is now the probability that a host has n parasites. The distribution is negative binomial because we had seen in section 5.1 that a gamma mixture of Poissons is negative binomial. Using Eq.(5.76d) one may calculate the variance and prevalence of parasite burdens. These may then be compared with expected values from the negative binomial distribution .

Now before we study the effect of host heterogeneity on susceptibility on density dependence we consider the homogeneous case first where there is no assumption on differential susceptibility. Consider a situation where the mean parasite burden y in a host community is governed by the equation

$$\frac{dy}{dt} = \mu R_0 f(y) - \mu y \tag{5.77a}$$

where μ is the per capita death rate of parasites and R_0 is the basic reproduction ratio. The function $f(y)$ represents the density-dependence effects caused by parasite crowding. Note that under no density effects

$$f(y) = y \tag{5.77b}$$

The simplest assumption on density dependence is to assume the exponential distribution with parameter γ such that

$$f(y) = y \sum_{n=0} p_n e^{-\gamma n} \tag{5.77c}$$

Thus given a distribution for p_n, it may then be possible to simplify the expression for $f(y)$ explicitly. We consider three cases one by one.

<u>Case 1</u>

Assume the distribution of parasites on host is negative binomial with overdispersion parametr k then

$$p_n(k,p) = \binom{k+n-1}{n} p^k q^n$$

and since the mean parasite burden is the dynamic variable y then

$$E(n) = \frac{kq}{p} = y \quad \text{and} \quad \text{var}(n) = \frac{kq}{p^2}$$

therefore

$$
\begin{aligned}
f(y) &= y\sum_{n=0}\binom{k+n-1}{n}p^k q^n e^{-\gamma n}\\
&= y\sum_{n=0}\binom{k+n-1}{n}p^k(qe^{-\gamma n})^n\\
&= y\left(\frac{p}{1-qe^{-\gamma}}\right)^k\\
&= y\left(\frac{1}{\frac{1}{p}-\frac{q}{p}e^{-\gamma}}\right)^k\\
&= y\left(\frac{1}{1+\frac{y}{k}-\frac{y}{k}e^{-\gamma}}\right)^k
\end{aligned}
$$

Thus we have

$$f(y) = y\left[1+\frac{y}{k}(1-e^{-\gamma})\right]^{-k} \tag{5.77d}$$

Case 2

Assume p_n is Poisson with mean rate λ. Then

$$p_n(\lambda) = \begin{cases} \frac{e^{-\lambda}\lambda^n}{n!} & n = 0, 1, \ldots \\ 0 & \text{elsewhere} \end{cases}$$

and since we know the on host mean parasite load is y then

$$E(y) = \lambda = y \quad \text{and} \quad \text{var}(n) = \lambda = y$$

thus

$$
\begin{aligned}
f(y) &= y\sum_{n=0}\frac{e^{-y}y^n}{n!}e^{-\gamma n}\\
&= y\sum_{n=0}\frac{e^{-y}(ye^{-\gamma})^n}{n!}\\
&= ye^{-y}\sum_{n=0}\frac{(ye^{-\gamma})^n}{n!}\\
&= ye^{-y}e^{ye^{-\gamma}}
\end{aligned}
$$

That is

$$f(y) = ye^{-y(1-e^{-\gamma})} \tag{5.78a}$$

Case 3

Assume that a host can only carry upto a maximum parasite load say N. Then p_n the probability that a host carries $n < N$ parasites will be given by

$$p_n(n, p, N) = \binom{N}{n} p^n q^{N-n}, \quad n = 0, 1, 2, \ldots, N$$

and

$$\begin{aligned} f(y) &= y \sum_{n=0}^{N} \binom{N}{n} p^n q^{N-n} e^{-\gamma n} \\ &= y \sum_{n=0}^{N} \binom{N}{n} (pe^{-\gamma})^n q^{N-n} \\ &= y(q + pe^{-\gamma})^N. \end{aligned}$$

Now since the mean parasite load is y then it follows that

$$E(n) = Np = y \Rightarrow p = \frac{N}{y}.$$

Thus

$$\begin{aligned} f(y) &= y\Big(1 - p + pe^{-\gamma}\Big)^N \\ &= y\Big(1 - p(1 - e^{-\gamma})\Big)^N \\ &= y\Big(1 - \frac{N}{y}(1 - e^{-\gamma})\Big)^N \end{aligned}$$

That is

$$f(y) = y\Big(1 - \frac{N}{y}(1 - e^{-\gamma})\Big)^N \tag{5.78b}$$

In order to solve Eq.(5.77a) we need to know the distribution of parameters at different times say before and after treatment and during reinfection. Generally the distributions may not follow any particular simple distribution.

To calculate the effect of density dependence we assume the distribution of parasites within each host type j is Poisson. Thus the effect of density dependence for host type j is $f(y_j, \gamma)$ where $y_j = h_j y$. As before h_j is the susceptibility factor for host type j and y is the mean parasite burden in the community. Recall also that w_j is the proportional representation of class j in the entire community.

Thus from the assumption of completely random acquisition of parasites by hosts and summing Eq.(5.78a) over all possible classes we get

$$f(y,k,\gamma) = \sum_{j=1}^{s} w_j y_j e^{-y_j(1-e^{-\gamma})}$$

$$= \sum_{j=1}^{s} w_j h_j y e^{-h_j y(1-e^{-\gamma})}$$

That is

$$f(y,k,\gamma) = y\sum_{j=1}^{s} w_j h_j e^{-h_j y(1-e^{-\gamma})} \qquad (5.78c)$$

where the dependence of $f(y,k,\gamma)$ on k takes care of the different host types.

Now consider Eq.(5.77a). Setting the left hand side of this equation equal to zero we see that there are two equilibrium points namely

$$\bar{y} = 0 \iff f(0) = 0 \qquad (5.78d)$$

with no parasites and another one with a parasite population given by

$$\bar{y} = R_0 f(\bar{y}). \qquad (5.78e)$$

Now Eq.(5.78e) can also be written as

$$f(\bar{y},\gamma) = \frac{\bar{y}}{R_0}$$

or from Eq.(5.78c)

$$\sum_{j=1}^{s} w_j h_j e^{-h_j \bar{y}(1-e^{-\gamma})} - \frac{1}{R_0} = 0 \qquad (5.78f)$$

which is an important condition because it may be used to numerically solve for γ for a given mean parasite burden and basic reproductive ratio by varying the value of γ until Eq.(5.78f) is satisfied. The first point of $\bar{y} = 0$ is stable for $R_0 < 1$, but if $R_0 > 1$ then the parasite population attains the second equilibrium point which is stable for $R_0 > 1$ and unstable for $R_0 < 1$. We next discuss three cases of importance in the study of parasite populations and their control.

Case 1: Estimating the host population with a critical parasite burden

Here we hypothesize that there is a critical parasite load n_c above which the host reaches a critical phase or dies. Given the distribution of parasites across the host population it is possible to define the proportion of the host population with the critical burden or more. If we let $D(t)$ denote this proportion at time t then

$$D(t) = \sum_{i=n_c}^{N} p_i(t) \tag{5.79a}$$

where N is the maximum parasite load possible and $p_i(t)$ the proportion of the host population carrying i parasites at time t. Note that solution of Eq.(5.77a) gives an overall mean parasite burden $y(t)$ with respect to time. From Eq.(5.78c) we notice that the weights w_j and h_j are probability values derived from the gamma distribution. It follows that the mean parasite burden $y(t)$ which is time dependent is derived from a gamma mixture of Poissons. Therefore the final variable we obtain is from section 5.1 an approximately distributed variable.

Case 2: Modelling the effect of treatment on population dynamics

Consider an intervention stategy such as the use of acaricides for the case of ticks. Then at any particular time it is possible to divide the parasite population into two cohorts according to those that have survived the last round of acaricidal application and those that have freshly infested hosts after the last treatment. Let $v(t)$ denote the burden of surving parasites and $x(t)$ the mean number of parasites that have established since treatment. Thus the total parasite load is

$$y(t) = v(t) + x(t) \tag{5.79b}$$

Now it is assumed that both categories of cohorts die at a common rate μ but the first category replaces itself with a factor R_0 per individual therefore

$$\begin{aligned} \frac{dy}{dt} &= \frac{dv}{dt} + \frac{dx}{dt} \\ &= -\mu v + \mu R_0 f(y,k,\gamma) - \mu x \\ &= \mu R_0 f(y,k,\gamma) - \mu(v+x) \\ &= \mu R_0 f(y,k,\gamma) - \mu y. \end{aligned} \tag{5.79c}$$

The non-trivial equilibrium state (one with parasites) is given by

$$\tilde{r} = 0 \quad \text{and} \quad \tilde{y} = \tilde{x} \tag{5.79d}$$

with a corresponding distribution of parasites.

Case 3: Modelling the effect of treatment on the distribution of parasites

The distribution of parasites following an intervention strategy or policy will be a mixture of the existing distribution in those individuals not treated, and the induced distribution in those that received treatment. Let us define:

α : as the drug efficacy (proportion of parasite individuals killed by the drug)

p_{n_j}: as the pre-treatment parasite distribution in host type j

and

s_{n_j}: as the corresponding post-treatment distribution

The effect of a drug with efficacy parameter α and a population load of r parasites per host is to produce a binomial distribution with

$$B(n, r, \alpha) = \binom{r}{n} \alpha^{r-n}(1-\alpha)^{n}, \quad n = 0, \ldots, r \tag{5.80a}$$

which is the probability of having $r-n$ parasites killed by the drug or n parasites surviving the treatment out of the r initial parasites. We ignore any density dependent effects on drug efficacy. Let θ denote the proportion of hosts treated then

$$s_{n_j} = (1-\theta)p_{n_j} + \theta \sum_{r=n}^{N} B(n; r, \alpha)p_{r_j} \tag{5.80b}$$

where the first term gives the probability of finding n parasites on untreated hosts and the second gives the probability of finding n parasites surviving treatment on treated hosts. Thus the summation in the second term runs over all possible pre-treatment parasite loads that could contribute to a post-treatment parasite burden of n parasites. Now let us assume that the surviving parasite population suffers mortality at a constant rate μ. Then after time t the initial population will have declined by a factor $e^{-\mu t}$. Now we re-define $s_{n_j}(t)$ as the probability that a host of type j has n surviving parasites at time t after the previous treatment such that $s_{n_j}(0)$; $n = 0, \dots, N$ gives the distribution of surviving parasites immediately after treatment.

The distribution of these parasites is given as the sum of terms from a series of binomial distributions one for each initial condition, thus

$$s_{n_j} = \sum_{r=n}^{N} s_{r_j}(0) B(n; r, e^{-\mu t}) \tag{5.80c}$$

Now let p_{n_j} denote the distribution of all parasites whether those surviving treatment or those arising as a result of reinfection within each host type. Then

$$p_{n_j}(t) = \sum_{r=0}^{n} q_{r_j}(t) s_{(n-r)_j}(t), \quad n = 0, \dots, N-1 \tag{5.80d}$$

and

$$P_{N_j} = 1 - \sum_{n=0}^{N-1} p_{n_j}(t) \tag{5.80e}$$

Eq.(5.80d) and Eq.(5.80e) is just a convolution of the surviving parasite distribution, s_{n_j}, and the reinfection parasite distribution q_{n_j}. Assuming parasite acquisition by hosts to be a Poisson process then the q_{n_j} are Poisson for each j with mean $h_j x(t)$, where $x(t)$ is given by the establishment-death equation (5.79c). The distribution across all the host type is the weighted average from each host type as in Eq.(5.76d). Then total density dependence effect over all host types and for different number of on host parasites per host type is

$$f(w; k, \gamma) = \sum_{j} w_j y_j \sum_{n=0}^{N} p_{n_j}(t) e^{-\gamma n} \tag{5.81}$$

Now define the following three benefit measures

$B_y(x)$: reduction of mean parasite burden over solution year x

$B_p(x)$: reduction of prevalence of infection over time interval $(x-1, x)$

$B_D(x)$: reduction of prevalence of disease over the time interval $(x-1, x)$

These are calculated as

$$B_y(x) = y^* - \int_{x-1}^{x} y(t)dt$$

$$B_p(x) = (1 - p_0^*) - \int_{x-1}^{x} (1 - p_0(t))dt$$

$$B_D(x) = D^* - \int_{x-1}^{x} D(t)dt$$

where x is the year of the model solution. These benefits are generally the differences between the equilibrium values and those of the model solution with treatment.

5.5 Towards a stochastic dynamical model

In this section we attempt to develop a stochastic time dependent model for a general multi-stage vector population that is a population whose life cycle is a sequence of distinct developmental life stages. Then some analytical aspects of the model will follow. The three host tick *R. appendiculatus* is our typical example. The mathematical tool which will set the foundation for the model is the idea of probability generating functions for a multivariate observation. We follow closely the ideas in the model by Hadeler (1982) which was further studied by Hadeler and Dietz (1983, 1984). The model was then generalized by Kretzschmar (1989a,b) where she studies a multi-stage disease parasite on a host as a birth death process model with reference to schistosomiasis. These models are hybrid models in the sense that a birth and death process with catastrophes for the on host parasite population is coupled to a deterministic age structured model for the host population. In the present context the age structure does not play any role. We just keep the stochastic part of that model. In the present biological situation the multistage tick population lives freely in a typical grazing area with some individuals on the vegetation and some on a host for a blood meal. Individuals move from one stage to the next through survival and development while some ultimately exit the area through death. We also allow for immigration into the area through other agents such as the domestic and wild animal hosts. We number the stages by $1, \ldots, n$ and let i denote the state or stage variable. Thus without any ambiguity i_k can count the number of individuals in stage k. Define the functions

$$p(t, i_1, \ldots, i_k). \tag{5.82}$$

Either $p(t, i_1, \ldots, i_n)$ with $\sum_i p(t, i_1, \ldots, i_n) = 1$ is the probability that a randomly selected patch contains i_k, $k = 1, \ldots, n$ individuals where k denotes the stage or $p(t, i_1, \ldots, i_n)$ with $\sum_i p(t, i_1, \ldots, i_n) > 0$ is the number of patches with this distribution of individuals. Next define the probability generating function for the state vector at time t as follows

$$u(t,z_1,\ldots,z_n) = \sum_{\mathbf{i}} z_1^{i_1}\cdots z_n^{i_n} p(t,i_1,\ldots,i_n) \tag{5.83}$$

where

$$\mathbf{z} = (z_1,\ldots,z_n)^T \tag{5.84}$$

is a vector of dummy variables to aid in carrying the discrete distribution into a differentiable function. Now introduce the notation

$$\mathbf{z}^{\mathbf{i}} = \prod_{k=1}^{n} z_i^{i_k}. \tag{5.85}$$

then we can compactly write the expression for u as

$$u(t,\mathbf{z}) = \sum_{\mathbf{i}} z^{\mathbf{i}} p(t,\mathbf{i}). \tag{5.86}$$

We can find the derivative of u with respect to z_l, say as follows

$$\frac{\partial u(t,\mathbf{z})}{\partial z_l} = \sum_{\mathbf{i}} i_l z_1^{i_1}\cdots z_l^{i_l-1}\cdots z_n^{i_n} p(t,\mathbf{i}).$$

In vector notation we have

$$u_{\mathbf{z}}(t,\mathbf{z}) = \frac{\partial u(t,\mathbf{z})}{\partial \mathbf{z}} = \begin{pmatrix} \sum_{\mathbf{i}} i_1 \mathbf{z}^{\mathbf{i}-\mathbf{e}_1} p(t,\mathbf{i}) \\ \vdots \\ \sum_{\mathbf{i}} i_n \mathbf{z}^{\mathbf{i}-\mathbf{e}_n} p(t,\mathbf{i}) \end{pmatrix} \tag{5.87}$$

where

$$\mathbf{e}_k = (0,\ldots,0,1,0,\ldots,0)^T \tag{5.88}$$

is the k-th coordinate vector. Define

$$\mathbf{e} = (1,\ldots,1). \tag{5.89}$$

The right hand side of (5.87) evaluated at $\mathbf{z} = \mathbf{1}$ gives the expectation of the vector-valued random variable $\mathbf{X}$,

$$E(\mathbf{X}) = u_{\mathbf{z}}(t,\mathbf{1}). \tag{5.90}$$

Now we wish to derive a system of partial differential equations for the probabilities $p(t, i_1, \dots, i_n)$ but before doing so we define the following parameters:

$b_{jk} \geq 0$: denotes the rate at which individuals of stage j give birth to those of stage k, $j, k = 1, \dots, n$.

$\mu_j > 0$: denotes the mortality rate for individuals in stage j

$\varphi_j \geq 0$: denote the immigration rate into stage j

$\tau_{jk} \geq 0$: denotes the transition rate from stage j to stage k

With these parameters we further define the matrices and vectors below

$$
\begin{aligned}
[y] &= diag(y_1, \dots, y_n) \quad \forall y \in R^n \\
B &= (b_{jk}), \quad j, k = 1, \dots, n \\
T &= (\tau_{jk}), \quad j, k = 1, \dots, n \\
[Te] &= diag\left(\sum_{k=1}^{n} \tau_{jk}\right) \quad j = 1, \dots, n \\
Z &= diag(z_1, \dots, z_n) \\
M &= diag(\mu_1, \dots, \mu_n) \\
\phi &= (\varphi_1, \dots, \varphi_n)^T
\end{aligned}
$$

Then an explicit expression for the partial derivative of $u(t, \mathbf{z})$ with respect to t is given by

$$\frac{\partial u(t,\mathbf{z})}{\partial t} = \phi^T(\mathbf{z}-\mathbf{e})u(t,\mathbf{z}) + ((B(\mathbf{z}-\mathbf{e}))^T Z + (M(\mathbf{e}-\mathbf{z}))^T + (T\,\mathbf{z} - [T\,e]\,\mathbf{z})^T)\frac{\partial u(t,z)}{\partial z}. \tag{5.91}$$

Thus if we define the coefficient function $(g(\mathbf{z}))$ as a row vector with each component being a second order polynomial in the variables z_i

$$g(\mathbf{z}) = -(Z\,B(\mathbf{z}-\mathbf{e}) + M(\mathbf{e}-\mathbf{z}) + (T\,\mathbf{z} - [T\,e]\,\mathbf{z}))^T \tag{5.92}$$

then the differential equation assumes the compact form

$$\frac{\partial u(t,\mathbf{z})}{\partial t} + g(\mathbf{z})\frac{\partial u}{\partial \mathbf{z}} - \phi^T(\mathbf{z}-\mathbf{e})u(t,\mathbf{z}) = 0$$

The initial condition of our system describes the state of the population at $t = 0$,

$$u(0,\mathbf{z}) = u_0(\mathbf{z})$$

where we assume that

$$\left.\frac{\partial u_0(z)}{\partial z}\right|_{z=1} < \infty$$

This amounts to assuming that the total number of space units observed is finite. The implication of this value to the extinction probabilities of the population is important. Compared to the equations in Kretzschmar (1989) equation (4.5) the terms containing partial derivatives with respect to the age of the host a do not occur in the current system. This is because currently we are considering the dynamics of the parasite population only. Here the host is considered as part of the patch.

Example for a multi-stage vector population

For a better understanding of the model derived above we consider the life cycle of *R. appendiculatus*. As earlier we divide the life cycle into $N = 10$ distinct stages and only the adult stage is capable of reproducing while other stages are completely characterized by their death and transition rates $(\mu_j, q_{j\,j+1})$, respectively. We include immigration where we assume that immigration takes place mainly in the on host stage by migrating host animals. The immigration rate $\varphi_j \geq 0 \quad j = 1, \dots, n$ but strictly positive for on host stages. Thus in general we have

$$B = \begin{pmatrix} 0 & 0 & \cdots & 0 \\ 0 & 0 & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ b_{n,1} & 0 & \cdots & 0 \end{pmatrix}$$

which we call the birth matrix,

$$T = \begin{pmatrix} 0 & q_1 & 0 & \cdots & 0 \\ 0 & 0 & q_2 & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & q_{n-1} \\ 0 & 0 & 0 & \cdots & 0 \end{pmatrix}$$

where $q_i = q_{i,i+1} > 0$ for $i = 1, \dots, n-1$ and the last row is zero because the adult stage cannot transit to any other stage except ultimate death. Next we have

$$[T\,e] = \begin{pmatrix} q_1 & 0 & \cdots & 0 & 0 \\ 0 & q_2 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & q_{n-1} & 0 \\ 0 & 0 & \cdots & 0 & 0 \end{pmatrix}.$$

Then we finally have

$$\phi = (\hat{\gamma}_1, \ldots, \hat{\gamma}_n) \quad \hat{\gamma}_j > 0 \quad j = 3, 6, 9.$$

where 3, 6 and 9 denote the on host stages. Then for the mortalities we have

$$M = diag(\mu_1, \ldots, \mu_n).$$

In this chapter we have studied population dynamic models where the host population is structured according to the number of parasites it harbours. The models were first developed to study the dynamics of endo-parasites such as heliminths in cattle and human host populatioms as in Hadeler and Dietz(1983). It is our conviction that the same approach is also possible for vector populations such the brown ear tick *Rhipicephalus appendiculatus* in our case. The classification of the host population according to vector parasite load is important particularly when considering the use of such a model in the design of control strategies. The last section is very convenient in the study of multistage vector populations such as the brown ear tick where the stages in the life cycle can now be considered as the 'types'. Thus there is need to extend further research in this area.

CHAPTER VI
AN APPLICATION

6.1 Introduction

In this chapter we shall demonstrate an application of the theories developed in the preceding chapters to the brown ear tick *R. appendiculatus*. More specifically we apply the generalised matrix model developed and analysed in chapter III and its continuous time counterpart in chapter IV. The life cycle of the tick has been discussed in detail in sub-section 1.3.2 of chapter I and represented diagramatically in figure 1 in page 28. In this chapter we study the dynamics of the population with an aim of inferring on some aspects of control measures in relation to susceptibility of cattle to ticks, the suitability of the environment (climate and vegetation) for tick survival and other factors both biotic and abiotic in nature. Alternate hosts are also an important factor . The biotic factors include factors related to the biology of the tick population such as survival, mortality or fertility rates specific to the population. The abiotic factors include climatic and environmental factors such as seasonality, vegetation type, geographical location and so on. The main source of data and information is that reported in Short *et al*(1989a,b) where an extensive study on development rates, fecundity and survival of development stages of the ticks *R. appendiculatus*, *Boophilus decoloratus* and *B. microplus* was carried out under field conditions in Zimbabwe. The second paper reports on the survival and behaviour of unfed stages of the same species of ticks again under field conditions in Zimbabwe.

The current work focuses on the life cycle of the brown ear tick, a three host tick. In the model the population is categorized into 10 stages in a similar manner as in Byrom and Gettinby (1992). The diagramatic representation of the life cycle is in figure 1 page 28. The main stages in the life cycle of the tick are the egg, larvae, nymph and adult. However to be able to study the life cycle much better by the matrix approach the larval, nymphal and adult stages are further classified according to whether questing, on host or developing. Thus in total there are 10 stages in the system. A further complication in the system formulation is that each of these main stages and substages have variable stage duration or sojourn time. These durations vary due to several factors for example the season of the year, vegetation type, and so on. In the current model the year is partitioned into rainy, cool and hot seasons, each with duration and time span according to how they were reported in Short *et al*(1989a,b).

The region where the study was conducted could broadly be classified into two vegetation types. These are mainly the short grass vegetation type which is associated with communal grazing areas and the long grass vegetation type which is associated with commercial grazing areas. The model therefore studies the tick dynamics in relation to these vegetation ecotypes and the aim is to attempt and bring out the differences between these two farming systems in terms of the model outputs. One such output is a measure of the overall population growth calculated as the dominant eigenvalue of a particular matrix to be presented in the next section.

6.2 The Model

The life cycle is subdivided into ten classes or compartments namely the egg (1), questing larvae (2), host larvae (3), developing larvae (4), questing nymph (5), host nymph (6), developing nymph (7), questing adult(8), host adult (9) and developing/ovipositing adult (10). From published data particularly that by Branagan (1973a,b) and Short *et al*(1989a,b) it is known that each of these stages have a variable sojourn time which can be denoted by T_i, $i = 1, \ldots, n$, where n is ten in the current application. The variation in T_i is due to several factors both biotic and abiotic in nature. Some of these factors just to mention a few include moisture, temperature, vegetation type, geographical location and so on.
The times T_i are also different for different stages.

The current model is based on Zimbabwe data as reported in Short *et al*(1989a,b). The longest stage durations were observed during the cool seasons for both types of vegetation. Now from the life cycle of ***R. appendiculatus***, the shortest stage duration in its entire life cycle is about 5 days which is the on host feeding stage. Thus using this fact a five day interval is adopted as the model time step. This implies that every actual time duration is expressed as a multiple of 5 days. Each stage is subdived into t_i age classes such that ($5t_i = T_i$).

Thus the progression in the life cycle can be looked at as composed of within and between stage dynamics. This means that an individual in stage i say, has to advance in age until it reaches the maximum age class t_i in that stage after which it transits to the first age class of the next stage depending on whether conditions are favourable for such an event or not. This transition is conditional on survival of the tick individual. Since there was no exact information concerning the stage duration for ticks in the questing stage the model allocates one age class (5 day duration) to this stage for all the three stages namely the larvae, nymph and adult. This means that by the end of a time step such an individual may either attach to a passing host or remain questing if it survives. Thus for each season and vegetation type stage durations are calculated for each of the ten life cycle stages. The climate in Zimbabwe is highly seasonal starting with the rainy, cool and hot seasons respectively. Thus based on data by Short*et al*(1989a,b) the stage durations for the long grass(short grass) vegetation type are given in table 3 below:

Table 3: Stage durations in long grass

STAGE	COOL	HOT	RAIN
1	13	8	10
2	1	1	1
3	1	1	1
4	12	3	4
5	1	1	1
6	1	1	1
7	17	6	7
8	1	1	1
9	1	1	1
10	10	2	1
TOTAL	58	25	28

The corresponding stage durations in the short grass vegetation type for the three seasons are given in table 4 below

Table 4: Stage durations in short grass

STAGE	RAINY	COOL	HOT
1	7	13	7
2	1	1	1
3	1	1	1
4	3	5	2
5	1	1	1
6	1	1	1
7	5	8	4
8	1	1	1
9	1	1	1
10	2	4	2
TOTAL	23	36	19

The next task is to parametrize a population projection matrix which is season and vegetation specific. This means that in all, six matrices are required one for each of the seasons namely rainy, cool and hot respectively in each of the two vegetative ecotypes. The three season specific projection matrices are denoted by A_1, A_2 and A_3 where the subscripts 1, 2 and 3 refer to the rainy, cool and hot seasons respectively.

As earlier stated in the model every time duration is in multiples of five day intervals. Thus a year of 365 days is equivalent to 73 model time steps of 5 days each. The data by Short *et al*(1989a,b) implies that the year can progressively be partitioned into 27 time steps of rain, 22 times steps of cool season, 15 time steps of hot season and finally 9 timesteps of the late rainy season. Now since the matrices A_1, A_2 and A_3 are the season specific matrices in a five day time step or interval, it follows that the population projection matrix corresponding to the full one year period is given by

$$A = A_1^9 \, A_3^{15} \, A_2^{22} \, A_1^{27} \tag{6.1}$$

In simple terms this matrix product means that if the population structure at the beginning of the year is given by the vector $\vec{y}_{t_0}$ then after one year (equivalent to

73 model time steps) the population structure will be given by

$$\vec{y}_{t_0+73} = A_1^{9}\, A_3^{15}\, A_2^{22}\, A_1^{27}\, \vec{y}_{t_0}. \tag{6.2}$$

However this is just one of several cases that may occur depending on the initial time in the model. For example if the initial population vector is considered from the start of the cool season, then Eq.(6.2) becomes

$$\vec{y}_{t_0+73} = A_1^{36}\, A_3^{15}\, A_2^{22}\, \vec{y}_{t_0}. \tag{6.3}$$

while if the initial population vector is considered from the start of the hot season then the equation becomes

$$\vec{y}_{t_0+73} = A_2^{22}\, A_1^{36}\, A_3^{15}\, \vec{y}_{t_0}. \tag{6.4a}$$

These cases are not exhaustive but any particular case can be derived in a similar manner as above. All the possible cases for the one year population projection matrices are given by the matrix valued indicator variable S_j where,

$$S_j = \begin{cases} A_1^{9+j}\, A_3^{15}\, A_2^{22}\, A_1^{27-j} & 0 < j < 27 \\ A_2^{j-27}\, A_1^{36}\, A_3^{15}\, A_2^{49-j} & 27 < j < 49 \\ A_3^{j-49}\, A_2^{22}\, A_1^{36}\, A_3^{64-j} & 49 < j < 64 \\ A_1^{j-64}\, A_3^{15}\, A_2^{22}\, A_1^{100-j} & 64 < j < 73 \end{cases} \tag{6.4b}$$

The variable S_j denotes the season variable that is S_j could be R_j^1, C_j, H_j or R_j^2 depending on the season of the year. The notations R_j^1 and R_j^2 denote the first and second rainy periods which occur at the beginning and towards the end of the year respectively. The rainy season is referred to in terms of these two variables just for the purpose of time reference only otherwise the assumption is that the effect of the rainy season to tick population dynamics is the same for the two rainy periods. The variables C_j and H_j denote the cool and hot seasons respectively. Thus the system is generally cyclic in nature. Note that the superscripts always have to add up to 73, the number of time steps equivalent to one year of 365 days. In general there are four cases to discuss depending on the initial time with respect to the season of the year when the model is initiated. Next the four cases are analysed one by one.

Case I

Let us define

$$A_{r_1} = A_1^{9} A_3^{15} A_2^{22} A_1^{27}. \qquad (6.5a)$$

This matrix determines the dynamics of a tick population with initial time at the beginning of the first rainy season, early in the year. Further assume that the maximum eigenvalue of this matrix is λ_{r_1} with its corresponding right eigenvector given by $\vec{v}_{r_1}$. By definition

$$A_{r_1} = \lambda_{r_1} \vec{v}_{r_1}. \qquad (6.5b)$$

Now in general the dynamics of a system whose initial time is anywhere during the first rainy season is determined by the following matrix product

$$R_j^1 = A_1^{9+j} A_3^{15} A_2^{22} A_1^{27-j} \quad 0 < j < 27. \qquad (6.6)$$

Lemma 6.1: λ_{r_1} is an eigenvalue of the matrix R_j^1 for $0 < j < 27$.

This is clear from the following

$$R_j^1 A_1^j \vec{v}_{r_1} = (A_1^{9+j} A_3^{15} A_2^{22} A_1^{27-j}) A_1^j \vec{v}_{r_1}$$

but from the definition of A_{r_1} this expression reduces to

$$R_j^1 (A_1^j \vec{v}_{r_1}) = A_1^j (A_{r_1} \vec{v}_{r_1}) = \lambda_{r_1} (A_1^j \vec{v}_{r_1})$$

which is more compactly expressed as

$$R_j^1 \vec{u}_1 = \lambda_{r_1} \vec{u}_1 \quad 0 < j < 27 \qquad (6.7)$$

where

$$\vec{u}_1 = A_1^j \vec{v}_{r_1} \quad 0 < j < 27.$$

Thus the conclusion is that λ_{r_1} is also an eigenvalue of R_j^1 for $0 < j < 27$ (i.e for a population initially in the early rainy season).

Case II

Now consider the growth of a population whose initial time is from the begining of the cool season. It was stated in Eq.(6.3) that the dynamics of such a population are governed by the matrix product

$$A_c = A_1^{36}\, A_3^{15}\, A_2^{22}. \tag{6.8a}$$

Now let the maximum eigenvalue of A_c be λ_c with the corresponding right eigenvector given by $\vec{v}_c$. Generally the dynamics of a population originating at any point in the cool season is given by

$$C_j = A_2^{j-27}\, A_1^{36}\, A_3^{15}\, A_2^{49-j}, \quad 27 < j < 49. \tag{6.8b}$$

Lemma 6.2 λ_c is an eigenvalue of the matrix C_j for $27 < j < 49$.

Since λ_c is an eigenvalue of A_c then it satisfies the equation.

$$A_c\, \vec{v}_c = \lambda_c\, \vec{v}_c. \tag{6.9}$$

Now post multiplying matrix C_j with the vector $A_2^{j-27}\vec{v}_c$ then using Eq.(6.8a) and Eq.(6.9) gives

$$\begin{aligned} C_j\,(A_2^{j-27}\,\vec{v}_c) &= A_2^{j-27}\, A_1^{36}\, A_3^{15}\, A_2^{49-j}\,(A_2^{j-27}\,\vec{v}_c) \\ &= A_2^{j-27}\,(A_1^{36}\, A_3^{15}\, A_2^{22})\,\vec{v}_c \\ &= A_2^{j-27}\,(A_c\,\vec{v}_c) \\ &= A_2^{j-27}\,(\lambda_c\,\vec{v}_c) \\ &= \lambda_c\,(A_2^{j-27}\,\vec{v}_c) \end{aligned}$$

and letting

$$\vec{u}_2 = A_2^{j-27}\,\vec{v}_c, \quad 27 < j < 49$$

it follows that

$$C_j\,\vec{u}_2 = \lambda_c\,\vec{u}_2, \quad 27 < j < 49 \tag{6.10}$$

and the result follows.

Proof:

Let $\vec{w}_{r_1}^T$, $\vec{w}_c^T$, $\vec{w}_h^T$ and $\vec{w}_{r_2}^T$ be the left eignvectors corresponding to the maximum eigenvalues λ_{r_1}, λ_c, λ_h and λ_{r_2} for the matrices A_{r_1}, A_c, A_h and A_{r_2} respectively. Then by definition the following is true

$$\begin{aligned} \vec{w}_{r_1}^T\, A_{r_1} &= \lambda_{r_1}\, \vec{w}_{r_1}^T \\ \vec{w}_c^T\, A_c &= \lambda_c\, \vec{w}_c^T \\ \vec{w}_h^T\, A_h &= \lambda_h\, \vec{w}_h^T \\ \vec{w}_{r_2}^T\, A_{r_2} &= \lambda_{r_2}\, \vec{w}_{r_2}^T \end{aligned} \tag{6.20b}$$

Now consider the matrix R_j^1 corresponding to the early rainy season that is

$$R_j^1 = A_1^{9+j}\, A_3^{15}\, A_2^{22}\, A_1^{27-j}$$

then

$$\begin{aligned} (\vec{w}_c^T\, A_1^{27-j})\, R_j^1 &= (\vec{w}_c^T\, A_1^{27-j})\, A_1^{9+j}\, A_3^{15}\, A_2^{22}\, A_1^{27-j} \\ &= \vec{w}_c^T(\, A_1^{36}\, A_3^{15}\, A_2^{22})\, A_1^{27-j} \\ &= \vec{w}_c^T\, A_c\, A_1^{27-j} \\ &= (\lambda_c\, \vec{w}_c^T)\, A_1^{27-j} \\ &= \lambda_c\, (\vec{w}_c^T\, A_1^{27-j}) \end{aligned}$$

that is if we define $\vec{v}_1^T = \vec{w}_c^T\, A_1^{27-j}$ then

$$\vec{v}_1^T\, R_j^1 = \lambda_c\, \vec{v}_1^T \tag{6.21}$$

implying that λ_c is also an eigenvalue of R_j^1. Now consider the matrix C_j which is given by

$$C_j = A_2^{j-27}\, A_1^{36}\, A_3^{15}\, A_2^{49-j}$$

then it follows that,

$$\begin{aligned} (\vec{w}_h^T\, A_2^{49-j})\, C_j &= (\vec{w}_h^T\, A_2^{49-j})\, A_2^{j-27}\, A_1^{36}\, A_3^{15}\, A_2^{49-j} \\ &= \vec{w}_h^T\, (A_2^{22}\, A_1^{36}\, A_3^{15})\, A_2^{49-j} \\ &= (\vec{w}_h^T\, A_h)\, A_2^{49-j} \\ &= (\lambda_h\, \vec{w}_h^T)\, A_2^{49-j} \\ &= \lambda_h\, (\vec{w}_h^T\, A_2^{49-j}) \end{aligned}$$

and letting $\vec{v}_2^T = \vec{w}_h^T A_2^{49-j}$ then

$$\vec{v}_2^T C_j = \lambda_h \vec{v}_2^T \tag{6.22}$$

implying that λ_h is an eigenvalue of C_j. Next consider the matrix H_j given by

$$H_j = A_3^{j-49} A_2^{22} A_1^{36} A_3^{64-j}.$$

Then

$$\begin{aligned}
(\vec{w}_{r_2}^T A_3^{64-j}) H_j &= (\vec{w}_{r_2}^T A_3^{64-j}) A_3^{j-49} A_2^{22} A_1^{36} A_3^{64-j} \\
&= \vec{w}_{r_2}^T (A_3^{15} A_2^{22} A_1^{36}) A_3^{64-j} \\
&= (\vec{w}_{r_2}^T A_{r_2}) A_3^{64-j} \\
&= (\lambda_{r_2} \vec{w}_{r_2}^T) A_3^{64-j} \\
&= \lambda_{r_2} (\vec{w}_{r_2}^T A_3^{64-j})
\end{aligned}$$

Thus letting

$$\vec{v}_3^T = \vec{w}_{r_2}^T A_3^{64-j}$$

we have

$$\vec{v}_3^T H_j = \lambda_{r_2} \vec{v}_3^T \tag{6.23}$$

which implies that λ_{r_2} is an eigenvalue of H_j. Finally consider the matrix R_j^2 given by

$$R_j^2 = A_1^{j-64} A_3^{15} A_2^{22} A_1^{100-j}.$$

Then

$$\begin{aligned}
(\vec{w}_c^T A_1^{100-j}) R_j^2 &= (\vec{w}_c^T A_1^{100-j}) A_1^{j-64} A_3^{15} A_2^{22} A_1^{100-j} \\
&= \vec{w}_c^T (A_1^{36} A_3^{15} A_2^{22}) A_1^{100-j} \\
&= (\vec{w}_c^T A_c) A_1^{100-j} \\
&= (\lambda_c \vec{w}_c^T) A_1^{100-j} \\
&= \lambda_c (\vec{w}_c^T A_1^{100-j}),
\end{aligned}$$

and letting

$$\vec{v}_4^T = \vec{w}_c^T A_1^{100-j}$$

we obtain

$$\vec{v}_4^T R_j^2 = \lambda_c \vec{v}_4^T \tag{6.24a}$$

which implies that λ_c is an eigenvalue of R_j^2.

Now in general if a matrix B can be represented in the form QR the product of two square matrices of the same order, such that RQ is equal to A then the eigenvalues (roots) of A are the same as those of B. This is the QR factorization principle which is covered well in Horn and Johnson (1985).

Using this result, Eq.(6.21) and lemma 6.1 it follows that the eigenvalues of A_c are same as those of R_j^1 which in turn has same eigenvalues as matrix A_{r_1} therefore

$$\lambda_c = \lambda_{r_1} \tag{6.24b}$$

But using the result, Eq.(6.24a) and lemma 6.4 it follows that the eigenvalues of A_c are the same as R_j^2 which in turn has same eigenvalues as matrix A_{r_2} therefore

$$\lambda_c = \lambda_{r_2} \tag{6.24c}$$

and from Eq.(6.24b) above

$$\lambda_c = \lambda_{r_2} = \lambda_{r_1}. \tag{6.24d}$$

Similarly from Eq.(6.22) and lemma 6.2 it follows that the eigenvalues of A_h are the same as those of C_j which in turn has same eigenvalues as those of A_c, therefore

$$\lambda_h = \lambda_c. \tag{6.25a}$$

Finally from Eq.(6.23) and Lemma 6.3 the eigenvalues of A_{r_2} are the same as those of H_j which in turn has the same eigenvalues as those of A_h therefore

$$\lambda_h = \lambda_{r_2} = \lambda_c. \tag{6.25b}$$

Now combining (6.24d) and (6.25b) gives

$$\lambda_c = \lambda_{r_1} = \lambda_{r_2} = \lambda_h = \lambda_{max} \tag{6.25c}$$

Thus a quasi-steady state will be reached when the tick numbers will increase each successive year by a factor given by the dominant eigenvalue λ_{max}. For each time step j of the year the quasi-steady state distribution will be given by the corresponding eigenvector of S_j associated with the dominant eigenvalue λ_{max} where

S_j was defined in Eq.(6.4b). The above analysis is similar to that by Gettinby and McClean (1979) where they present a matrix formulation of the life cycle of liver fluke in Britain and Ireland. This demonstrates the potentiality of such models in the study of vector and parasite populations in general.

It is important to note that the situation above is a long term effect but on the short term there might be population fluctuations about an equilibrium state. The matrix system is studied for the two vegetation types and the results compared.

From the work in chapter IV for continuous time matrix models and that from chapter III for discrete matrix models it is shown for both cases that the maximum eigenvalue of either systems is a function of the matrix elements. This means that the matrix model can be used to study the sensitivity of the maximum eigenvalue to different matrix elements. In the current model the effect of several life cycle parameters of the brown ear tick to this value is studied since the matrix elements are themselves a function of the life cycle parameters of the population in question. Now one of the difficulties encountered in such models for practical systems like the one just described is the availability of data to be able to estimate the elements of the entire population projection matrix. The following is a brief discussion of how the matrix input elements for the system being studied are derived. As earlier mentioned the source of data is from published information and personal communications. The main problem in applying matrix population models is in relating the transition probabilities in the classical Leslie matrix model and those from experimental cumulative distributions. This area has been addressed in chapter III section 3.6.

6.3 Matrix parametrization

The aim in this section is to briefly describe how the matrices A_1, A_2 and A_3 are parametrized. Of course this exercise involves several assumptions. As earlier stated each stage of development say i, (i=1,...,10) is further subdivided into t_i age classes of five day interval each. For example $i = 4$ for the cool season in long grass vegetation type denotes the developing larvae stage and from table 3, $t_4 = 12$ meaning that this particular stage was divided into 12 age classes. Consider an individual in age class j in stage i. After one model time step this individual may *do the following:*

(i) transit to the next age class within the same stage that is age class $j + 1$

(ii) transit to the first age class of the next stage if it is in the last age class of the current stage or

(iii) die if it does not survive

Since the life cycle of this particular tick is composed of a sequence of questing, on host and developing stages one particular stage will be considered for each case then the other stages can be handled similarly.

The egg stage:

According to Short *et al*(1989a,b) the average stage duration in this stage is $D_1 = 65$ days. This is equivalent to thirteen five day age classes. It was reported that during the cool season about 38.5% of the eggs hatch to larvae over this period. Now let us assume a common five day survival probability s_1 for all the age classes. Then given E_0 eggs initially $.385E_0$ are expected to hatch into larvae after D_1 days which is equivalent to 13 time steps. Thus letting s_1 denote the within egg stage survival then

$$s_1^{13} = 0.385 \tag{6.26a}$$

gives $\hat{s}_1 = 0.929$. This value gives an estimate of the the probability that an egg currently in age class j will transit to the next age class in the next time step. This also means that once an egg attains the maximum age then the probability is 0.929 that it will hatch to become a larvae. Thus 0.929 is also an estimate of the transition probability to the next stage in this case the questing larvae stage. This precisely means that given E_{t_1} eggs are in the last age class at time t then $s_1 E_{t_1}$ will hatch to larvae by time $t + 1$.

The questing stage:

Information on questing ticks was reported in terms of 50% survival times that is the time until 50% of the initial cohort of questing ticks of a particular questing stage has been lost through mortality. Now take the case of the questing larvae during the cool season in the long grass vegetation type. The 50% survival time for questing larvae in this season is reported as 91 days which is equivalent to 18 model time steps of five days each. Now letting the within stage survival probability be s_2 then it follows that

$$s_2^{18} = 0.5 \tag{6.26b}$$

which implies that $\hat{s}_2 = 0.962$. This means that given $N_q(t)$ questing ticks at the beginning of a time step $0.962\,N_q(t)$ are expected to survive upto the end of the time period and $0.038\,N_q(t)$ to exit the system through mortality. Since this is a questing stage the surviving ticks have two alternatives either to survive and remain questing or attach onto a passing host. In general let the daily attachment probability be p then the conditional probability that it attaches within a period of D days is given by

$$p_a = 1 - (1 - p)^D. \tag{6.27}$$

In general there are three important events that can take place for a questing tick in the next time step given it was present at the beginning of the time step. These are

(i) attach onto a passing host
(ii) remain questing
(iii) die due to unfavourable conditions.

These events have been illustrated diagramatically in Figure 2 on page 28. The unconditional probability that it attaches within D days is

$$p_{att} = s_2(1 - (1 - p)^D). \tag{6.28}$$

The probability that it survives and remains questing is then given by

$$s_2(1 - p_a) = s_2(1 - p)^D = s_2 - p_{att} \tag{6.29}$$

and the probability of dying within a time step is given by

$$q = 1 - s_2 \tag{6.30a}$$

Note that the sum of these three probabilities is one as required. Thus given there were $N_q(t)$ questing ticks at the beginning of a time step then at the end of the time step that is by time t+1 these individuals are accounted for in the following balance equation

$$N_q(t) = N_q(t)\,p_{att} + N_q(t)\,(s_2 - p_{att}) + N_q(t)\,(1 - s_2) \tag{6.30b}$$

where the three terms on the right hand side denote individuals who attach, remain questing and die respectively. The total questing ticks at time $t+1$ are then given by

$$N_q(t+1) = N_q(t)\,(s_2 - p_{att}) + R_q(t+1) \tag{6.30c}$$

where $R_q(t+1)$ denotes recruitment term into the questing state from the previous developing stage in the life cycle of the tick. The term takes specific forms for a particular developing stage. For example if we consider eggs moulting into questing larvae then

$$R_q(t+1) = s_1\,E_{t_1} \tag{6.30d}$$

where E_{t_1} denotes the number of eggs in the maximum age class about to moult. Now assuming a reported value of $p = 0.04$ a value $p_a = .185$ is calculated as the initial input value for the model. This value is the same for all the three questing stages namely the questing larvae, nymph and adult. It is not possible to use different values for the three different questing stages because this kind of information is lacking. The above kind of analysis is carried out for all the questing stages in all the seasons and vegetation types. A phenomena of importance in the study of tick dynamics is diapause. What this means in simple terms is that an adult tick undergoes a state of dormancy when climatic conditions are not favourable for questing. This means that in Eq.(6.30b) p_{att} is zero such that

$$N_d(t) = N_d(t)\,s_8 + N_d\,(1 - s_d) \tag{6.30e}$$

and

$$N_d(t+1) = N_d(t)\,s_8 + R_d(t+1) \tag{6.30f}$$

where $N_d(t)$ denotes diapausing adults at time t and s_8 their survival probability in a unit time step. Questing adults or diapausing adults fall in the eighth stage according to the current model formulation of the tick's life cycle hence the notation s_8. Again $R_d(t+1)$ denotes the recruitment term into the diapausing state. Precisely these will be nymphs moulting into adults when conditions are not favourable for active questing.

Developing stage:

As an example of how the matrix elements were derived from the data from Short *et al*(1989a,b) consider the developing larvae in long grass vegetation in the cool season. In general after a tick has fed to repletion it detaches from the host and drops onto the ground where it will undergo a process of development before moulting into the next instar of development. The stage duration under these conditions is reported as $D_4 = 60$ days which is equal to 12 five day age classes. It was further reported that the percentage of larvae that moulted was 80.5%. Let the within stage survival probability be s_4. Then since there are 12 age classes before an individual moults it follows that

$$s_4^{12} = 0.805, \tag{6.31a}$$

which implies that $\hat{s}_4 = .982$. This value means that at the end of one time step 0.982 of the individuals initially in age class j will transit to the next age class $(j+1, \quad j = 1, \dots, 12)$ after one time step. In a more precise manner this means that if $N_j^4(t)$ denotes individuals in age class j of stage 4 at time t then the number in age class $j+1$ at time $t+1$ is given by

$$N_{j+1}^4(t+1) = s_4 N_j^4(t), \tag{6.31b}$$

and generally

$$N_{j+1}^i(t+1) = s_i N_j^i(t), \quad j = 1, \dots, t_i \quad i = 1, \dots, 10. \tag{6.31c}$$

In this case $N_j^i(t)$ denotes the number of individuals in age class j of stage i at time t and s_i the stage specific survival probability in a unit model time step. It is further assumed that individuals transitting(moulting) into the next stage do so only after attaining the maximum age class. Thus individuals initially in the last age class of stage i at the beginning of a time step will by the end of that time step transit to the 1-st age class of the next stage. This process can therefore be represented as

$$N_1^{i+1}(t+1) = s_i N_{t_i}^{i}(t), \quad i = 1, \ldots, 9. \tag{6.31d}$$

This equation describes the between stage recruitment process in the system. The subscript t_i denotes the last age class in stage i. This value depends on the stage duration because the longer the duration the more the number of age classes. Thus t_i is different for different stages. The values s_i are estimated for all seasons and vegetation types in order to parametrize the matrices A_1, A_2 and A_3 which have already been defined. All the questing and developing stages were handled in exactly the same way.

Fecundity:

Based on survival probabilities to ovipositioning and assuming a sex ratio of 1 : 1 total fecundity F by an adult female tick is adjusted to f in order to estimate the number of eggs which are female and will actually be realised to await hatching. Precisely f is obtained from F by the formula

$$f = 0.5\,(s_{10})^{t_{10}}\,F \tag{6.32}$$

where t_{10} is the number of age classes in the pre-ovipositioning female adult stage. The quantity $(s_{10})^{t_{10}}$ gives the probability that an adult female initially in age class 1 will survive to oviposit at the end of the last age class.

The parametrization process is done for the entire life cycle for each of the vegetation types namely the long grass and short grass respectively. This is almost enough to parametrize the season specific population projection matrices but since there is no information on the feeding probabilities the assumption that a tick attaching will successfully feed almost surely is used. Thus an initial probability of one is assigned to this event. This assumption is unrealistic and was later modified. The longest life cycle duration is 58 model time steps occurring in the the cool season and in the long grass vegetation type. Since the corresponding life cycle stage durations in the hot and rainy seasons are less than 58 time steps imaginary pseudostages are created also in order to achieve compartibility in the matrix products. These are just imaginary stages therefore transition probabilites into these stages were set to zero. No diapause effects are included at the initial stage of model simulations.

The model is then simulated to give future population structures given by the sequence $\{\vec{y}_t; \quad t \geq 0\}$ where t is expressed in multiples of the model time step. Of course one has to specify the initial population structure say $\vec{y}_0$ but as was shown in the analysis the long time population structure is independent of $\vec{y}_0$. The tick model for simulation purposes is developed using the SPLUS computer software for applied statistics as described by Venables and Ripley (1994). As explained above the population growth is determined by the dominant eigenvalue of the matrix A and the initial model simulation is that with the model parameters as calculated from the paper by Short *et al*(1989a,b). Under these initial inputs the dominant eigenvalue of the matrix A is far much greater than one consequently indicating a population increase. This suggested some aspects in the model which were not realisic. Based on the data by Fivaz *et al* (1990) it is obvious that the value of one as the probability of successful feeding is not realistic. This is because animals vary according to the degree of resistance to ticks due to several factors among them age and/or breed of the animal. Previous exposure to tick challenge is also an important factor as far as host resistance to ticks is concerned. Therefore a value of one as the probability of successful feeding, implies that the host population is 100% susceptible to ticks which is not realistic. In otherwords it means that every time a tick attaches then it feeds to repletion contrary to what is observed in practice. Success of feeding probabilities are therefore set to 0.11 for the larvae, 0.16 for the adult and 0.49 for the nymph according to the information reported in Fivaz (1990). A further assumption we make is that an adult tick is only actively questing during the rainy season thus we set the probability of attaching to zero in the cool and the hot seasons respectively. Although with these modifications the tick growth index (λ_{max}) that is the maximum eigen value of A_{r_1} was greatly reduced, the value is still geater than 1 namely $\lambda_{max} = 2.35$. This value is equivalent to an intrinsic growth rate of

$$r = \log_e \lambda_{max} = 0.856 > 0 \tag{6.33}$$

meaning the value similarly indicates a population increase. Thus an extensive sensitivity analysis to study the effect of some of the matrix inputs on the growth index λ_{max} seems most appropriate. The findings of such an analysis are outlined in the following section.

6.4 Sensitivity analysis

The input parameters in the model are those derived from the information reported in Short *et al*(1989a,b) and Fivaz *et al*(1990). Starting with these inputs a sensitivity analysis is carried on the model by gradually varying attachment probabilities, probabilities of successfull feeding and the mortalities of questing tick stages separately. The results from these kind of simulations are then presented in figures 7 through 15. The results will briefly be discussed and their implications to tick control strategies pointed out

As earlier stated a daily attachment probability of 0.04 as reported in Byrom and Gettinby (1992) gives a five day attachment probability of 0.185. This is therefore one of the initial input parameters for the model. At these initial inputs the growth index calculated as the maximum eigenvalue of the matrix A_{r_1} denoted by λ_{max} is found to be 2.35. Thus the population increases. Next the behaviour of λ_{max} for different values of attachment probabilities p_{att} is investigated by simulating the tick model for different values of attachment probabilities. Figure 7 shows the case for long grass vegetation type. It can be seen that in general lambda (λ_{max}) is an increasing function of the attachment probabilities. The implications here is that control measures aimed at reducing attachment probabilites can be adopted as a means of lowering the growth of tick populations. This result therefore supports methods such as pasture spelling, lowering stocking rates or moving out the cattle hosts during seasons when the tick population is expected to be questing. All these methods are aimed at lowering the chances to attach for a questing tick. This has the effect of retarding the general population growth rate. The same kind of analysis is done for short grass vegetation type and the results are depicted in Figure 12. An interesting feature seen in these two figures is that the growth index lambda (λ_{max}) increases with attachment probability values upto a maximum then it starts to decline. This scenario is more evident in the short grass vegetation type. In this type of vegetation the growth index hardly exceeds the value of one which is the value where the population neither increases nor decreases. It is clear from the graphs that there is a big difference between the two vegetation types as far as the growth of the tick population is concerned. It can be seen from the two graphs that for the same value of attachment probability, the growth rate is higher in long grass than in short grass. Thus on average the growth index for the tick population is higher in the long than in short grass vegetation type. This shows that even control strategies should not be uniform for the two types of vegetation. As mentioned in Norval*et al* (1992) tick abundance on cattle in the absence of control is determined by the susceptibility of cattle to ticks, the suitability of the environment(climate and vegetation) for tick survival and other factors such as the presence of alternate hosts.

The second computer experiment involves the effect of varying the successful feeding probabilities. From the model formulation this is done by varying the probability of transiting from the on host state to the off host developing stage. The results of this type of simulation are shown in Figure 8 for the long grass vegetation type. The corresponding results for short grass vegetation type are depicted in Figure 13. The figures indicate that the growth index λ_{max} is a monotonically increasing function of this probability as expected. Still in short grass vegetation the competence of the nymph stage in feeding is considered separately from the larvae and adult stages by varying the success of feeding by the nymph but fixing the values for the adult and the larvae. The result is shown in Figure 14 and the graph shows the same trend as for the larvae and adult. Note that in the graphs the probabilities are referred to as detachment probabilities. What is observed here is that for both vegetation types the growth index lambda(λ_{max}) is a monotonically inreasing function of the probabilities of successful feeding. It is noted however that for the same value of successful feeding probability the growth index or factor is higher in long grass than in short grass vegetation type. Now from the tick-host interaction system it is known that the probabilities of successful feeding for an on host tick is highly dependent on the degree of resistance to ticks by the host. The higher the resistance to ticks say due to previous exposure to ticks the lower the chances of successful feeding for an on host tick. Other factors also come to play for example Fivaz *et al*(1990) reports on average that the nymph seem to be more competent in feeding than the larvae and adult. From the analysis in chapter IV there are also density dependent effects which can affect the overall successful feeding probabilities. In general the graphs indicate that for highly resistant herds the growth of *Rhipicephalus appendiculatus* can greatly be reduced. Thus the use of resistant breeds can be considered as an alternative future option to the tick problem which has become of great economic importance. Theoretically what the graphs indicate is that other factors constant detachment probabilities can be lowered to a point beyond which the tick population will decline monotonically towards zero. This will happen when the probabilities are such that $\lambda_{max} < 1$. It is obvious that this is not true in reality because of the many factors that come into play. Some of the factors are advantageous to the tick population growth while some have a negative impact. The tick control problem therefore requires an integrated approach where several control measures are applied in the most optimal way not forgetting there are costs to be incurred in the whole execise in general.

Some control strategies are aimed at causing an increased mortality to the questing tick stages. These include for example burning of the pasture which results to killing the questing ticks. However this practise should be carried out with caution because if it is not properly done it can cause a serious environmental degradation. This prompted the study of the overrall effect of mortality of questing ticks to the population growth index λ_{max}. Figure 9 shows the effect of questing larval mortality on λ_{max} in the long grass vegetation type. Initial model input parameters are calculated from the data by Short *et al*(1989a,b) and this gives us an initial value of larval questing mortality of 0.056. The assumptions are that on surviving one time step a questing tick may attach or remain questing with probability $1 - p_a$ where p_a is the probability of attaching. This probability is conditional on surviving therefore a function of questing tick mortality. This initial value of 0.056 of questing larvae mortality gave a value of growth index of 2.35 which indicates a population increase. Thereafter the model is simulated for different values of questing larvae mortality and the results are depicted in Figure

9. Clearly the growth index is a decreasing function of questing larval mortality. The whole process is repeated for questing nymph and adult ticks and the results are shown in Figures 10 and 11. Again as with the questing larvae mortality the growth index is a decreasing function of questing nymph and adult mortalities. Thus control measures aimed at increasing the mortalities of any of the questing tick stages should be appropriate. It is noted however that when the mortalites of the adult and larval stages are set to one the model gives a growth index of almost zero while it is not the case for questing nymph mortality. This observation tends to indicate that the growth index is more sensitive to larval and adult mortality than nymph mortality. The process is repeated for the short grass vegetation type and the observation is that for questing tick mortalities in the range between zero and one the growth indices are always less than one. This tends to suggest *that for a tick population to persist* in short grass vegetation type there must be several factors acting in its favour and their overall effect must outweigh that from the negative factors. Recall that short grass vegetation type is associated with communal grazing areas, where high stocking rates are common. This could be one of the contributing factors to the maintenance of the tick population in this type of vegetation and land use. A further simulation experiment which is carried out in short grass vegetation type is that of the survival of diapausing adult ticks. The growth index is an increasing function of the survial probabilities of diapausing adult ticks. However it is noticed that for the tick population to grow, high values of the survival probabilities for diapausing ticks are necessary as can be seen from Figure 15.

Figure 7: Attachment probabilities on lambda

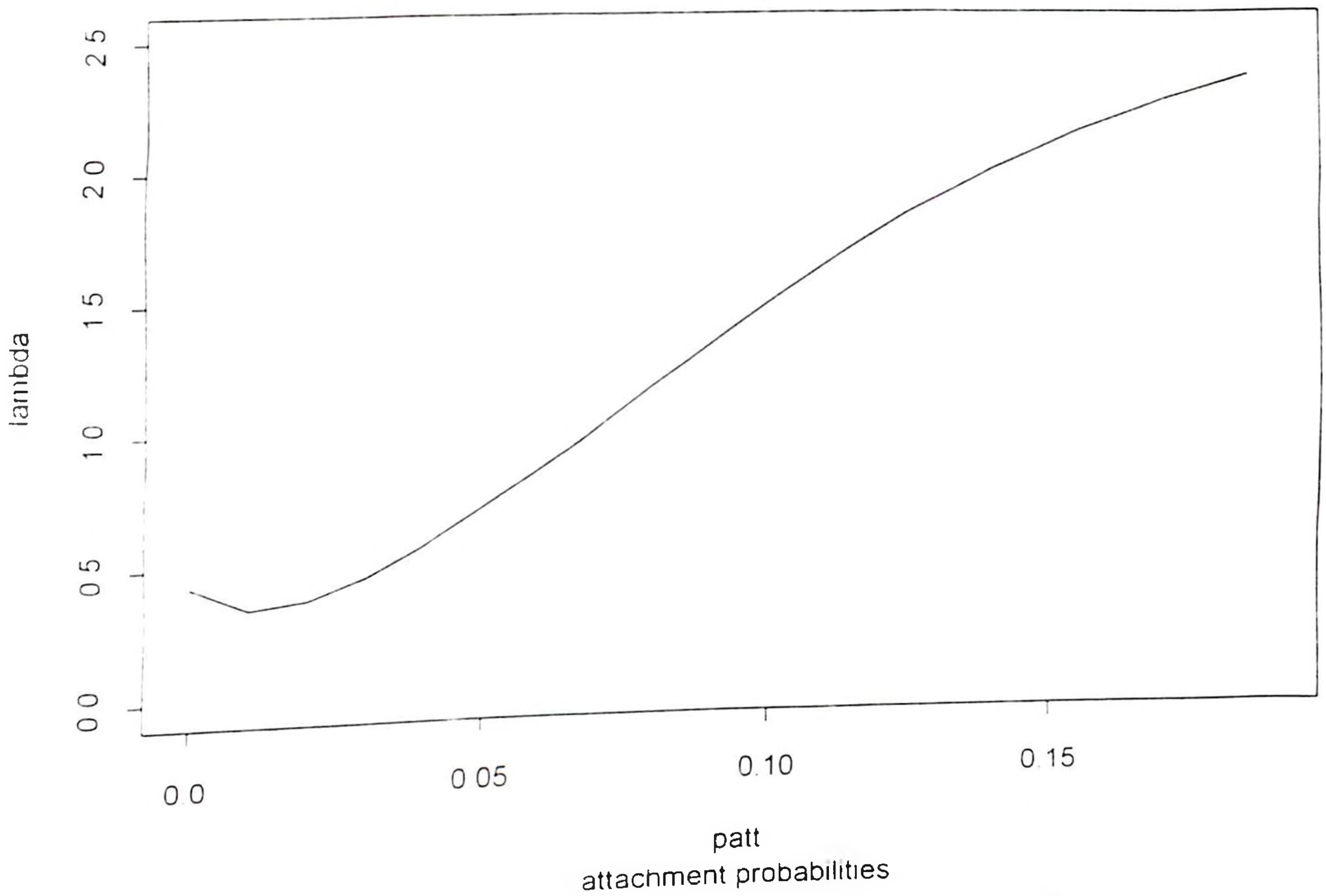


Figure 8: Detachment probabilities on lambda

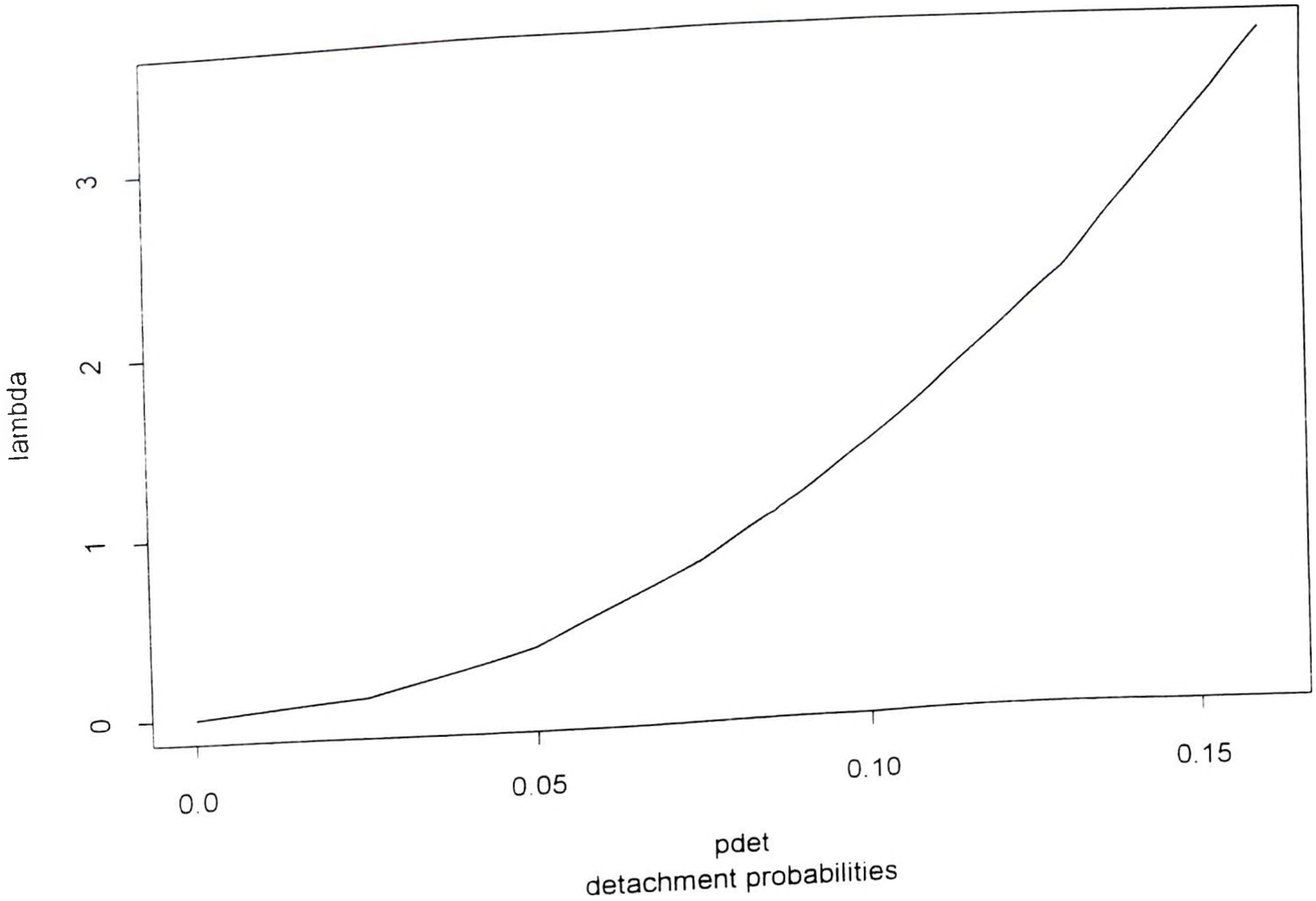


Figure 9: Larval mortality, rainy season

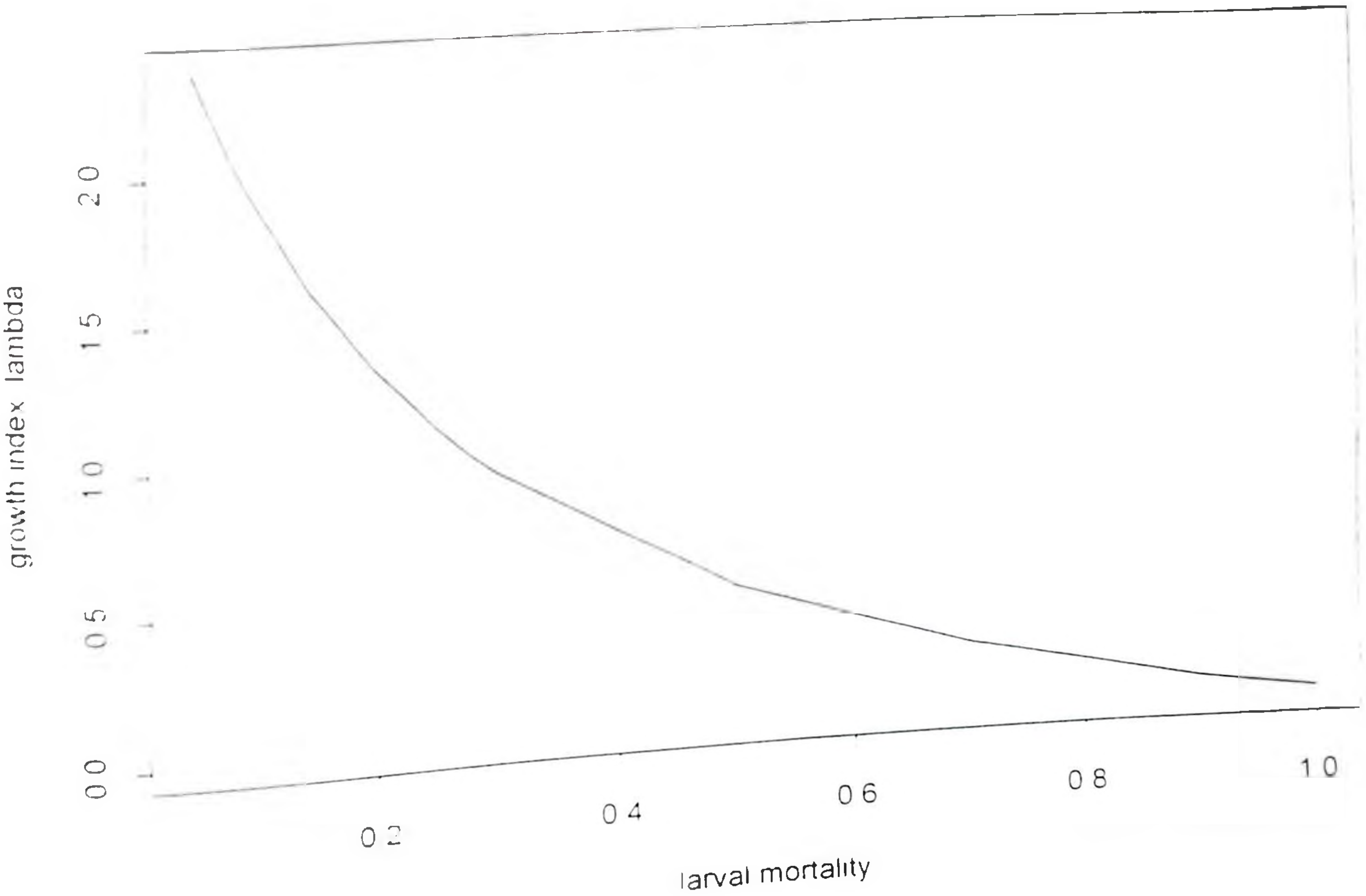


Figure 10: Nymphal mortality, rainy season

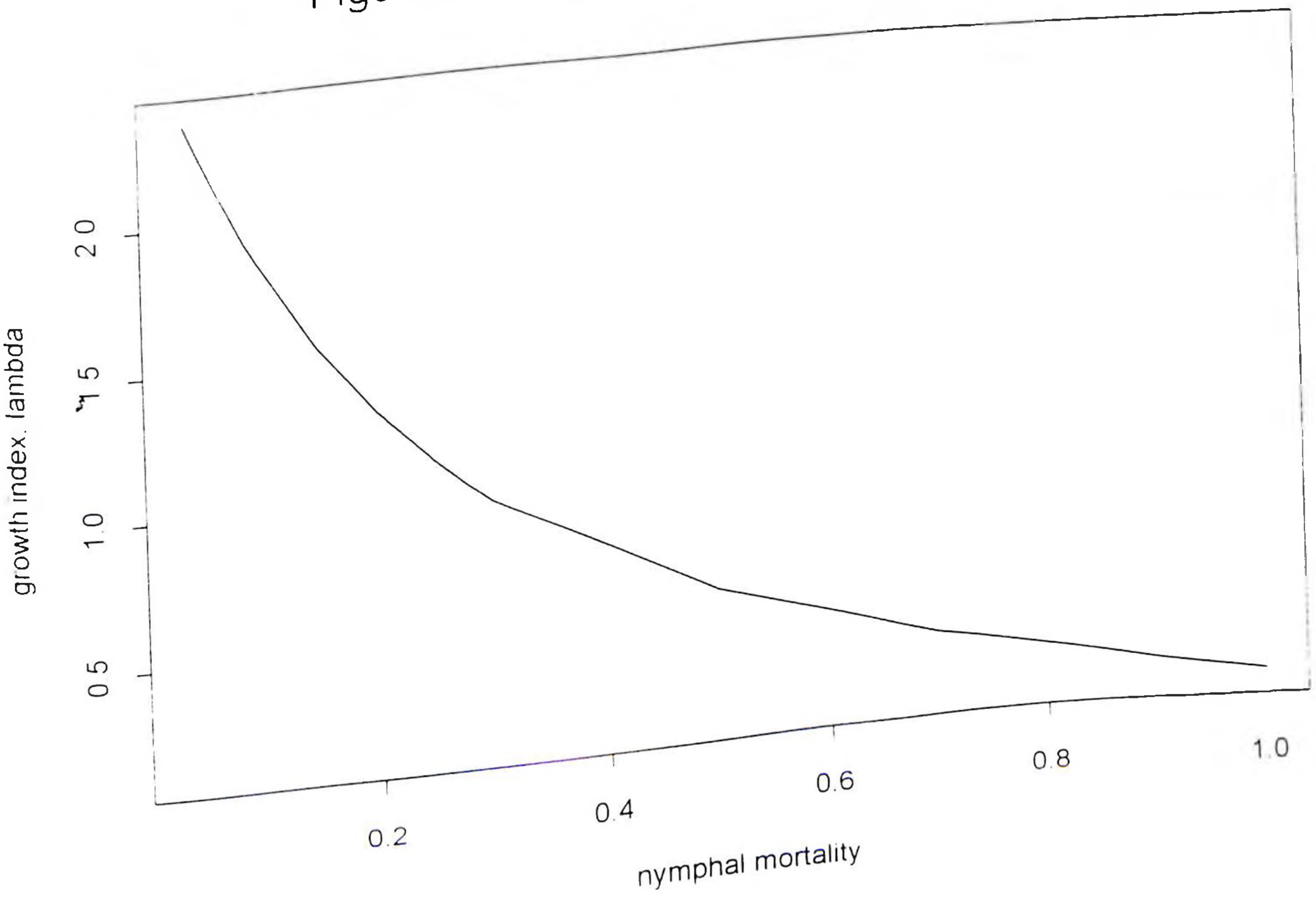


Figure 11: Adult mortality, rainy season

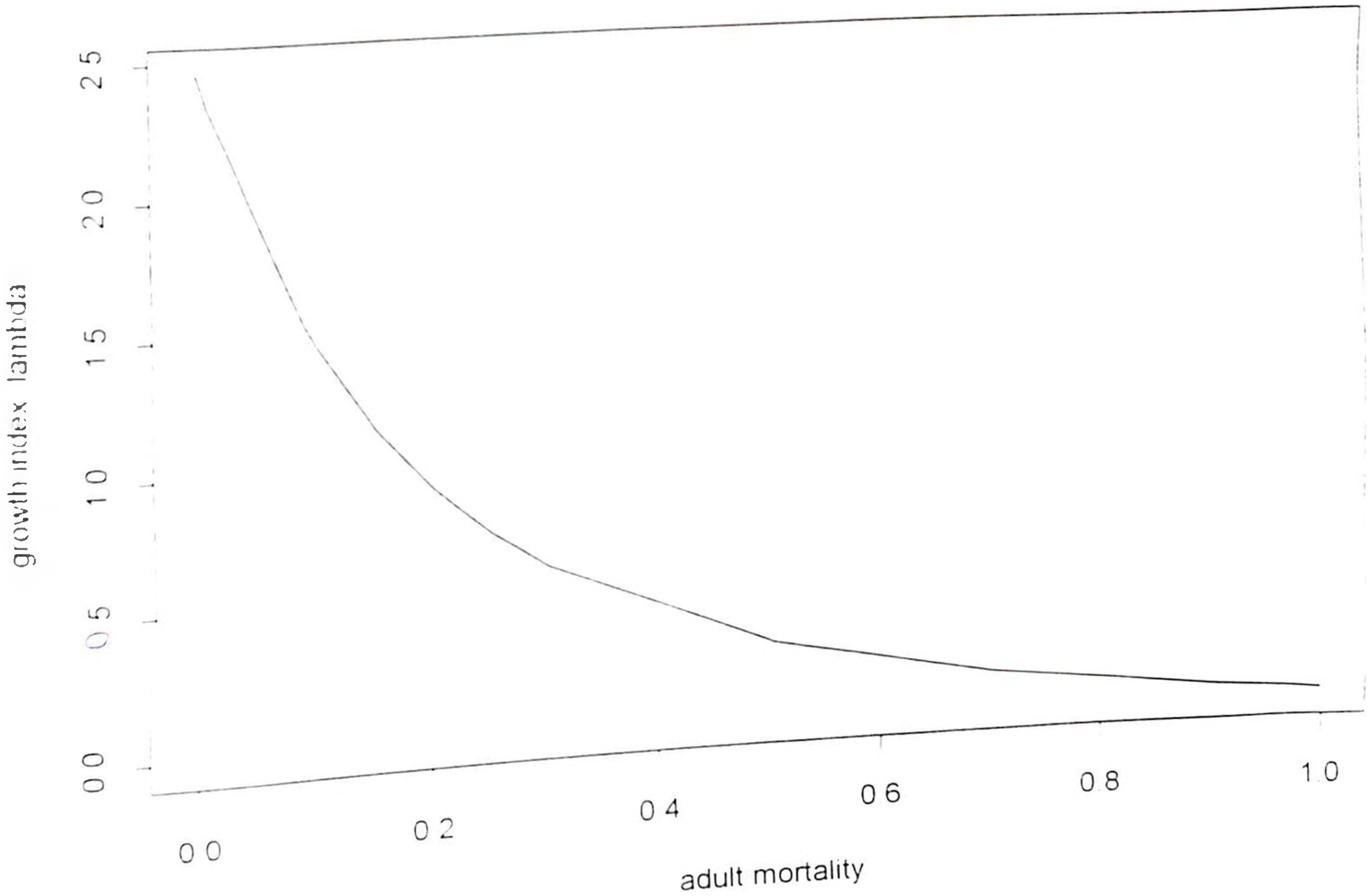


Figure 12:Attachment probabilites on Lambda; Short Grass

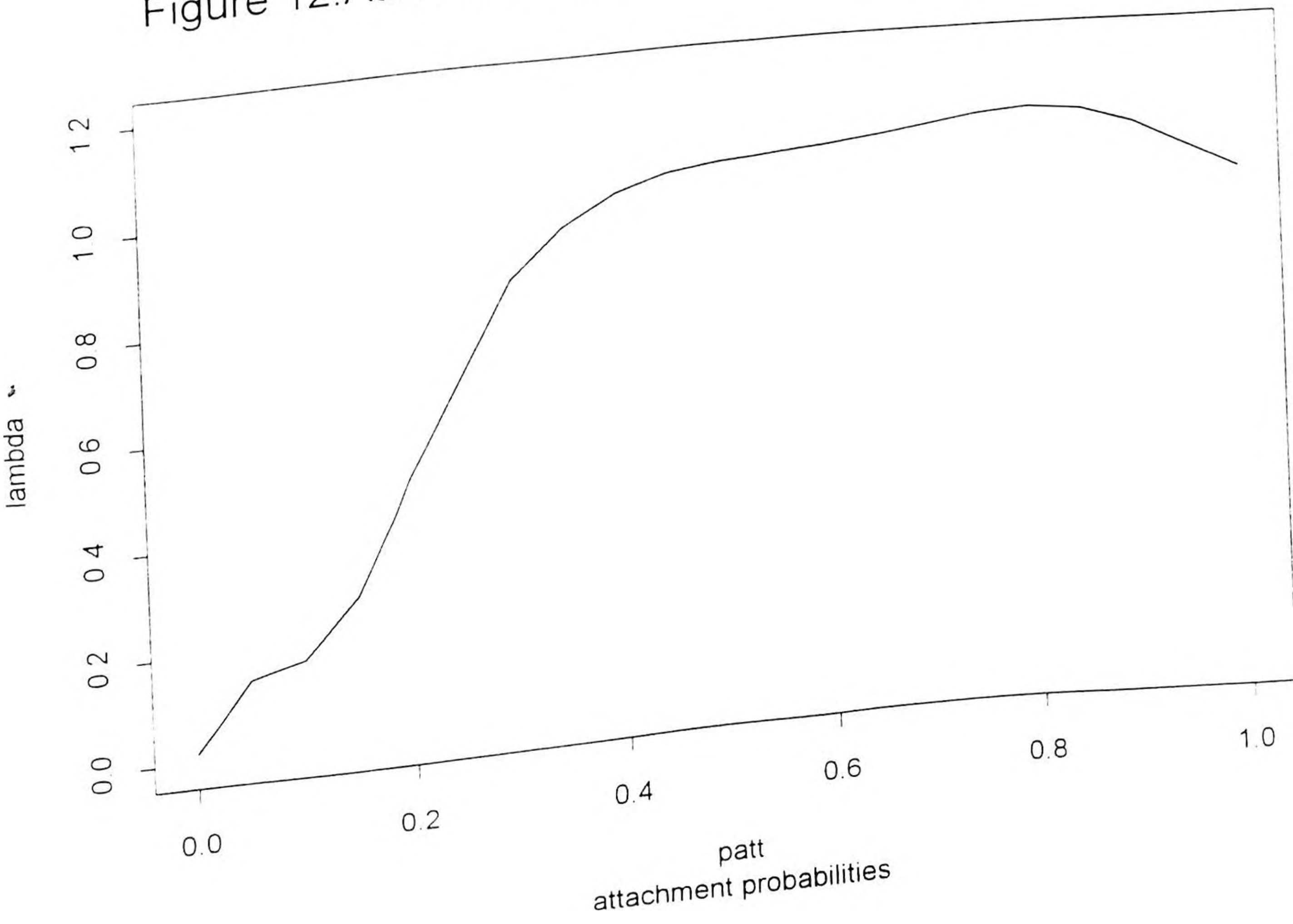


Figure 13: Detachment Probabilities on Lambda; Short Grass

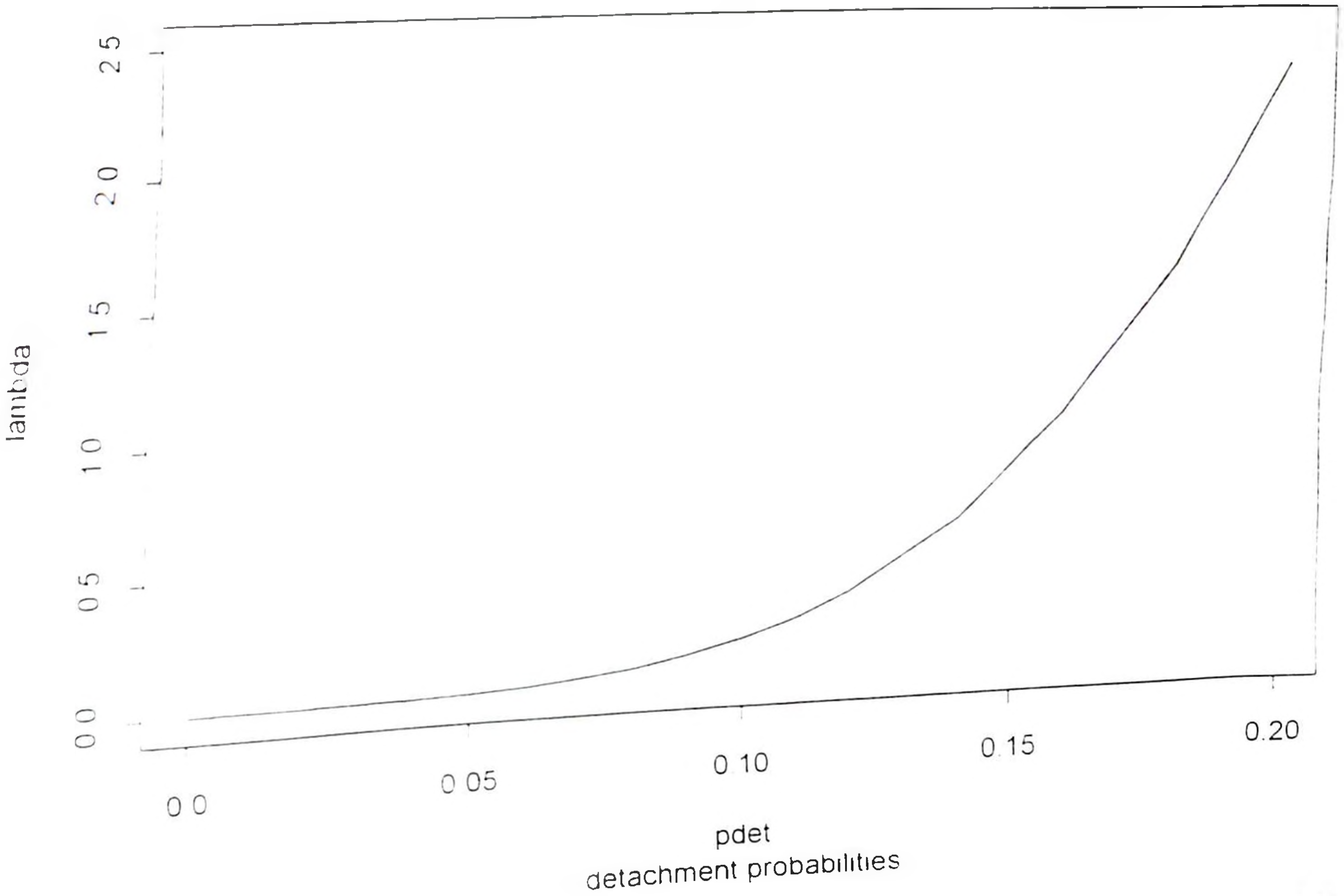


Figure 14: Nymphal Detachment Probabilities on Lambda; Short Gras

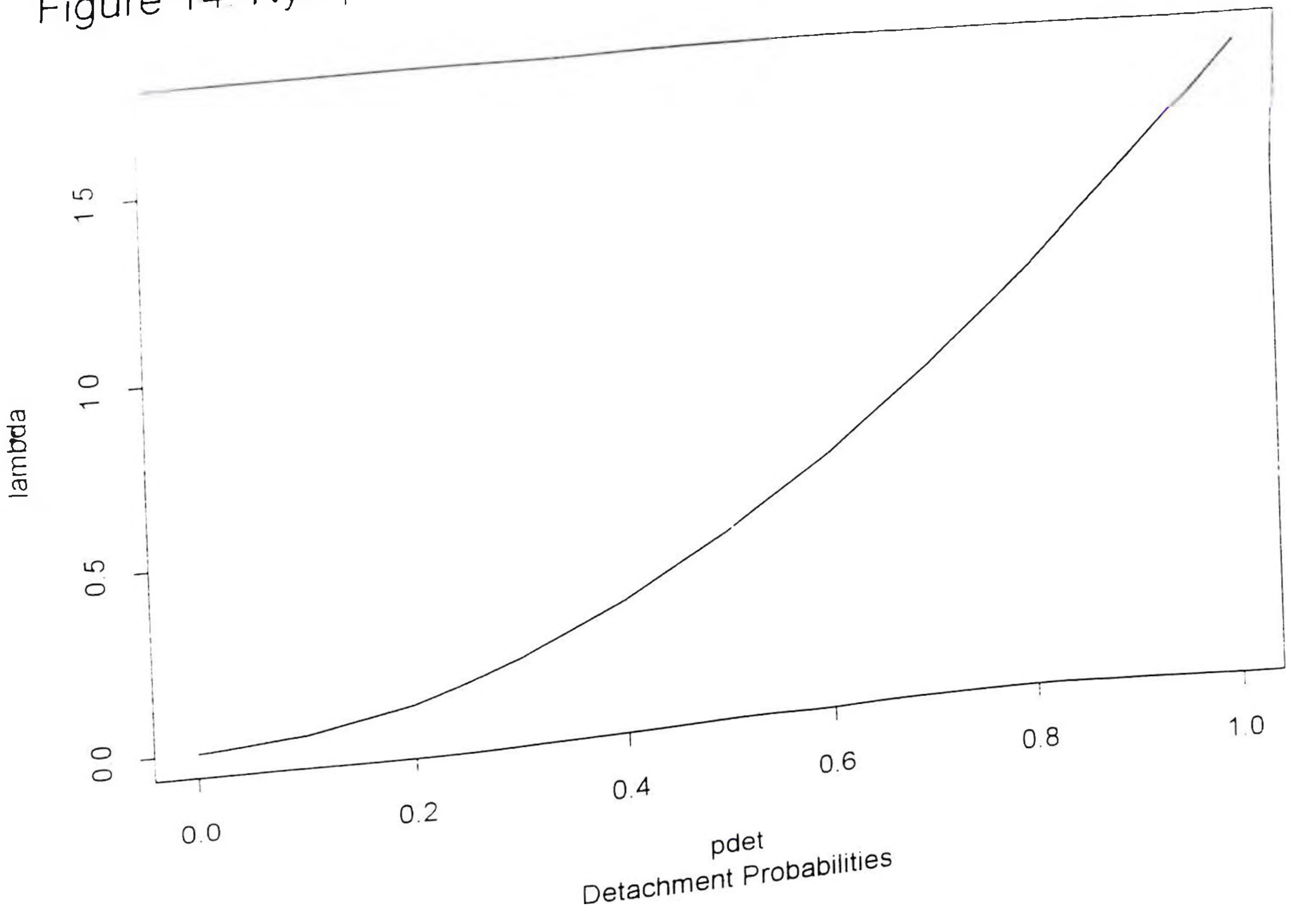
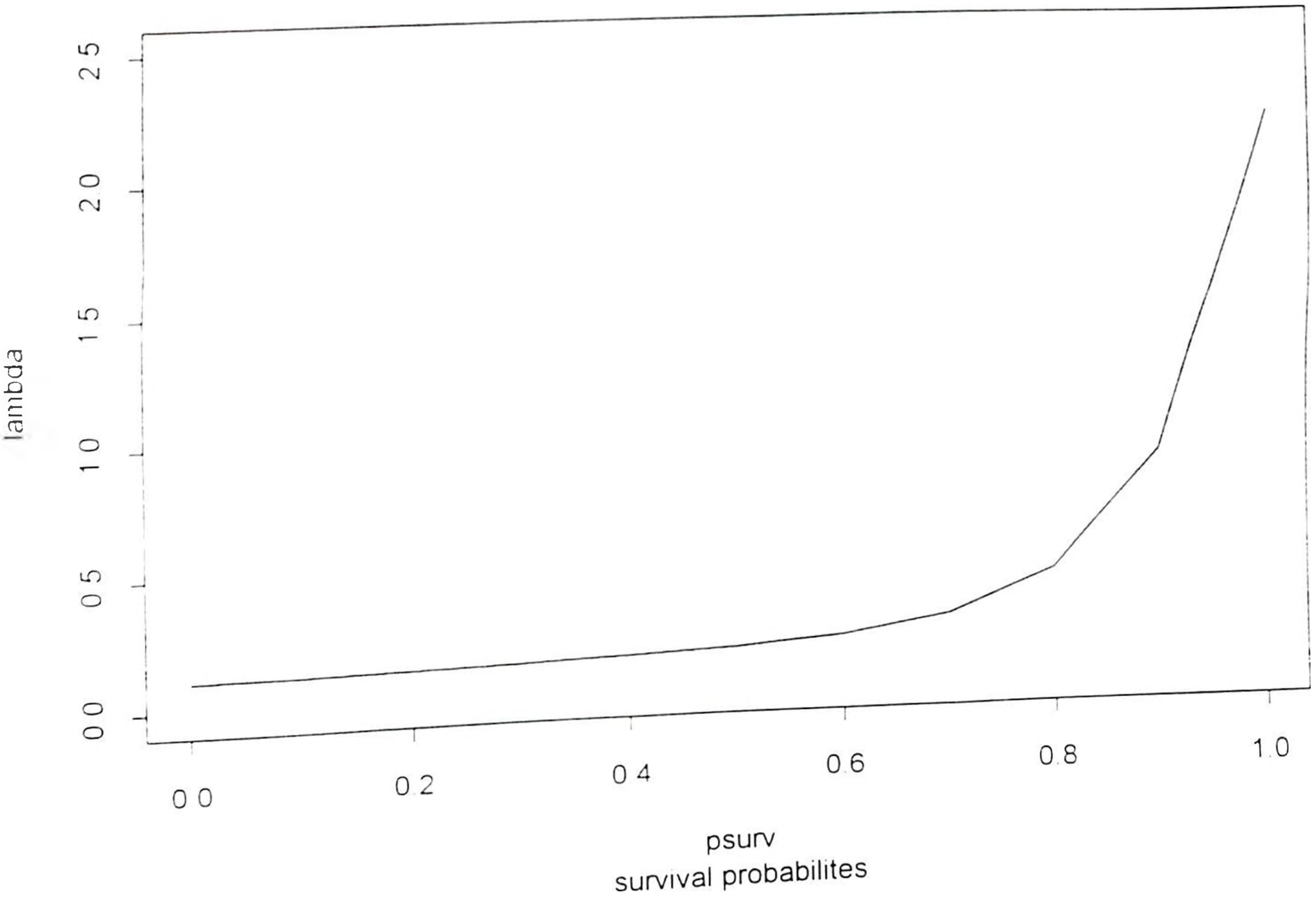


Figure 15: Diapausing Adult Survival on Lambda; Short Grass



CHAPTER VII

CONCLUDING REMARKS

This thesis is concerned with the development of mathematical models for stage structured populations. In particular the study has dealt mostly with matrix and compartmental population models. These approaches are both suitable when dealing with structured population models.

Matrix population models have been a subject of theoretical and practical study for many years, particularly the time homogeneous matrix models. Starting from the time homogeneous age structured model a more general stage structured population model applicable to a general n stage classified population is constructed. Conditions relating the transition probabilities in the classical population projection matrix to those experimentally derived are given for such kind of populations.

It is shown that the age structured matrix model is actually a special case of the generalised n stage structured model. The latter model is flexible in that one can study the within and between stage population dynamics. In this way the question of residence times in a stage can be taken care of because individuals have to age within a stage before transitting into the next stage.

In time dependent population trajectories, the projection matrix at time t, may not necessarily be equal to that at time $t + 1$. Time dependence in such models is brought about by several interacting factors acting on the population vital rates. These factors are themselves time dependent. These include factors such as seasonality, vegetation type and so on. A practical time dependent matrix model is constructed for the brown ear tick(*R. appendiculatus*), the causal vector for East Coast fever (ECF). In this model the effect of seasonality and vegetation type is incorporated hence making the model time dependent. The model has a big potential in assessing the effectivity of various control strategies in relation to various environmental factors. It can be extended to include the effect of more environmental factors on the population parameters. A similar approach can be applied to other vector population species.

The study also dealt with continuous time compartmental models for stage structured populations, taking the brown ear tick (*R. appendiculatus*) taken as a special case. The model is associated with a continuous time evolution operator similar to the population projection matrix for the discrete case. It has been shown that the sign of the spectral bound, positive or negative, associated with this operator determines whether the population will grow or decline respectively. Formulae showing the dependence of the spectral bound on the population vital parameters are obtained through the use of the implicit function theorem. The reproduction number $R(h)$ on a host density h is derived. The model is useful in the explanation of the interactions between the tick and its host population. It is shown that the tick population will persist only when the host population density exceeds a certain threshold value h_0. Stability analysis indicates that the uninfected stationary state is stable if the spectral bound is less than zero a condition corresponding to $R(h) < 1$. It is argued that the infected stationary state is necessarily stable otherwise secondary bifurcations of the infected state would be expected.

The study also deals in depth with the aspect of density dependence on host attachment rates and mortality rates for the tick population. An alternative derivation of the basic reproduction number $R(h)$ via the general cyclic triangular systems apart from the direct expansion method is given. The study distinguishes between the linear and non-linear cases as follows.

In the linear case it is clear that the solution of the "tick only" system is unbounded unless the parameters are such that the population remains constant or is decaying. In the nonlinear case attention is focussed on the qualitative behaviour of the system, distinguishing the case where the system is dissipative. In order to establish dissipativeness a bounded set is found that attracts all orbits and which is positively invariant.

The study finally deals with a class of vector-host interraction models where the host population is classified according to the number of parasites it carries. Such models are useful in the sense that for most vector diseases, the severity of the disease to the host depends on how heavy is the parasite load. The null hypothesis that on host vector distribution is asymmetric and is negative binomial is investigated in depth.

The results of the study are useful in the understanding of vector population dynamics in general. It brings out clearly the connection between discrete and continuous population models. The generalised matrix model for stage structured populations is more flexible and can be adopted for other vector populations apart from *R. appendiculatus*. Incorporating time dependence in matrix models by including various environmental factors is a more realistic approach. This implies that monitoring and control of biological populations can in general be carried out with more reliability, especially with the advent of more powerful computers and software. The results of the study provide useful information towards the understanding of complex vector- host interaction systems.

It is hoped that the interpretations of the findings will contribute significantly to the study of general vector population dynamics and more specifically towards the development of vector control methods. In conclusion we list some problems which require further investigation:

(a) Further validation of the time dependent matrix model for the brown ear tick by including more field based estimates of the model parameters.

(b) Extension of the compartmental model along the lines of stochastic population models to take care of the variability in the transition rates in the model.

(c) Investigation into more robust estimation methods for the transition probabilities in the generalised time dependent matrix model, particularly under field conditions.

(d) Analysis of the stochastic dynamical model suggested here by handling the tick dynamics as a birth, immigration and death process.

(e) Linking the population models for the brown ear tick developed here to the corresponding East Coast fever disease models.

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