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Modeling and Analysis of Biological Populations

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MODELING AND ANALYSIS OF BIOLOGICAL POPULATIONS

by

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Asymptotic and transient dynamics are both important when considering the future population trajectory of a species. Asymptotic dynamics are often used to determine whether the long-term trend results in a stable, declining or increasing population and even provide possible directions for management actions. Transient dynamics are important for estimating invasion speed of non-indigenous species, population establishment after releasing biocontrol agents, or population management after a disturbance like fire. We briefly describe here the results in this thesis.

(1) We consider asymptotic dynamics using discrete time linear population models of the form $\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t)$ where $\mathbf{A}$ is a population projection matrix or integral projection operator, and $\mathbf{n}(t)$ represents a structured population at time t. Within the model are the underlying parameters. Some of these parameters are of more interest to us: either ones which have a large confidence interval or are the easiest to manage from a conservation managers point of view. Using these parameters of interest, we next divide the parameter space into two parts: on one side the population grows and on the other side the population declines. We call this dividing hypersurface the growth-decline boundary and use this as a tool to show how senescence affects the prediction of a matrix model for the Serengeti cheetah (*Acinonyx jubatus*). We next analyze an integral projection model for thistles (*Onopordum illyricum*) again using this growth-decline boundary.

(2) We consider how temperature effects the transient (short term) dynamics for an ectothermal species such at the pea aphid (*Acyrthosiphon pisum*). We define

"transient amplification" and develop two different models to explore the effect of temperature on this concept. We estimate model parameters (survivorship and fecundity) at two different temperatures, and then scrutinize both model predictions by comparing observed and predicted transient population growth rates and the projection of population size over 20 days. Both models predict that temperature affects the short term transient amplification. The degree day model predicts no effect of temperature on the asymptotic transient amplification while the results of the ordinal day model were inconclusive.

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Contents

Chapter 1

Introduction

Matrix projection models are commonly used for predicting the dynamics of structured populations (e.g., [16, 39, 80, 98, 111]). In many cases key life history parameters like survival of fecundity are determined by continuous variables (such as size). In these cases the use of matrix projection models requires discretization of the continuous variable; because the method of discretization influences the model predictions [35], algorithms have been developed to find the most biologically meaningful discretization [96, 122]. Additionally, matrix models are often constructed with a self-perpetuating final stage, e.g. an animal could theoretically stay in the last age class indefinitely. Hence matrix models ignore the effect of senescence on population dynamics. A recently developed alternative to matrix models are integral projection models, which consider continuous stages but are discrete in time. Both of these modeling approaches require multiple parameters, and the data to accurately estimate those parameters is often lacking; as a result of insufficient data these models suffer from high parameter uncertainty. Therefore there is a need to analyze the effect of parameter uncertainty on the model's predictions. Furthermore, parameters often vary on a spatial and temporal scale, and stochastic models are even more data

hungry [34].

The first part of this dissertation entails studies of both population projection matrices (PPMs) and integral projection models (IPMs). From a mathematical point of view, PPMs and IPMs are similar, since both are compact linear operators. PPMs are analyzed using linear algebra; IPMs require the use of functional analysis. For linear PPMs and IPMs, the determination of the asymptotic growth rate of the population is the most common method for analyzing the model. For linear models, the asymptotic growth rate is the dominant eigenvalue, λ, of the model if it exists. If $\lambda > 1$, the population grows asymptotically. If $\lambda < 1$, the population declines asymptotically, and if $\lambda = 1$, the population is asymptotically stable. The growth-decline boundary of a PPM or IPM is this $\lambda = 1$ hypersurface as a function of the parameters in the model. In Chapters 2 and 3, I'll look at how changing the models' parameters effect λ and hence determine the growth-decline boundary.

There are well established methods for local perturbation analysis, such as elasticity and sensitivity of matrix transition rates or parameter values, which examine the consequences of very small perturbations of single, independent parameters [16]. Sensitivity of λ to a matrix element, a_{ij}, defined as $\dfrac{\partial \lambda}{\partial a_{ij}}$, evaluates the effect of infinitesimal perturbations of single parameters on the dominant eigenvalue. Since some matrix elements in a PPM are measured on a different scale than others, (for example, compare survivorship with fecundity), elasticity, the proportional change in λ per proportional change in the matrix element,

$$\frac{\partial \lambda}{\lambda} \bigg/ \frac{\partial a_{ij}}{a_{ij}},$$

is also used. Because both sensitivity and elasticity are partial derivatives, they inherently linearize the relationship between λ and the matrix parameter value of

interest. In some cases, this could lead to erroneous results [56, 95].

Calculations of elasticities assume that all other matrix elements remain unchanged [29], or in the case of multiple perturbations, that the transition probabilities are changed by the same proportion [95]. Sensitivity and elasticity analyses have also been used to decide which stage or age group of a population should be manipulated to improve population viability the most [29, 40], but without evaluating whether the particular management action is sufficient to achieve the management goal [26, 27, 33, 106]. If one is going to enact a conservation plan based upon the analysis of the model, one should have confidence that the model predicts success. Furthermore, elasticity analyses does not take into account uncertainty in the data. Parameter uncertainty has been incorporated into elasticity analysis by incorporating standard deviation into the definition of elasticity [40], including covariation between parameters [121], and by adding random components to the parameters [124]. Caswell [15] and de Kroon et al. [29] both give in-depth discussions of the caveats for some of these methods.

Global perturbation analysis is necessary when relatively large changes in parameters values are being considered. Large uncertainties in the parameter values often occur when the sample size is small. Management actions may also change parameter values by large amounts. Demographic and environmental stochasticity lead to mean parameter values which vary over space and time. Using sensitivity and elasticity analysis to infer the effect of large perturbations on the asymptotic population growth rate λ can result in misleading conclusions [30, 55, 56, 95, 116]. One possible approach to global perturbation analysis of matrix models is Monte Carlo analysis [116].

In Chapter 2 of this dissertation, I use an analytical alternative for matrix projection models developed by my colleagues and me to analyze the growth-decline

boundary for an endangered species. In Chapter 3, I extend this method to integral projection models. In this approach, I plot the growth-decline boundary as functions of the most significant parameters. I then use this to determine how robust λ is within the confines of the uncertainty in the parameters. This method can be applied to models for endangered (or invasive) species. Sensitivity and elasticity tells us what management strategy we should focus on in order to increase (or decrease) the asymptotic growth rate. Our method tells us how confident we are that a specific management strategy can achieve the desired population growth rate (e.g. $\lambda > 1$) in the face of both parameter and stochastic uncertainty.

The starting point for the analysis of both PPMs and IPMs is the identification of a "nominal point" in the multidimensional parameter space. The nominal point uses our best estimates for the parameters, or our best guess in the case of poorly known parameters. I am interested in both the effects of small (local) and large (global) perturbations away from the nominal point on the asymptotic growth rate, λ. In the approach I developed with my colleagues, we first calculate the hypersurface representing population stasis ($\lambda = 1$); then one side of the surface indicates the parameter space for a growing population ($\lambda > 1$), and the other side for a declining population ($\lambda < 1$). In case of an endangered species the nominal point will be on the declining side, while the nominal point for an invasive species will be on the growing side. In both cases it is important to know how sensitive the qualitative predictions are to parameter perturbations, especially when these perturbations cause a predicted growing population to decline or cause a predicted declining population to grow. This is relevant for population management, i.e. choosing a strategy that works under a range of likely environmental conditions (including temporal and or spatial variation of population parameters), or for understanding how reliably ecological factors such as predation or competition can limit population growth. The distance from the

nominal point to the hypersurface representing stasis is a measure of the robustness of the stability (or lack of stability) of the system. The larger the distance, the more robust the model predictions are to parameter perturbations, i.e. the less likely that perturbations cause a qualitative change in model predictions (e.g. achieving or not achieving a desired management goal). The distance can be evaluated numerically, or it can be evaluated graphically when there are two or three relevant parameters.

Population Projection Matrix Models (PPMs)

In these systems the population vector consists of finitely many discrete stages. If there are S stages, the population vector $\mathbf{x}$ is in $\mathbb{R}^S$, with all entries nonnegative. If the population vector during year t is denoted $\mathbf{x}(t)$, and if $\mathbf{A}$ is the S by S projection matrix for this population, then $(\mathbf{x}(t))_{t=0}^{\infty}$ satisfies the discrete time dynamical system

$$\mathbf{x}(t+1) = \mathbf{A}\mathbf{x}(t). \tag{1.1}$$

The total population is

$$\|\mathbf{x}\| := n_1 + n_2 + \ldots + n_S, \tag{1.2}$$

the 1-norm of $\mathbf{x}$.

The long term growth rate for solutions of (1.1) is determined by the eigenvalue or eigenvalues of $\mathbf{A}$ of maximum modulus. For a matrix $\mathbf{M}$, when there is only one eigenvalue of maximum modulus, we call it the *leading eigenvalue*, and refer to it as $\lambda(\mathbf{M})$. The spectral radius, $r(\mathbf{M})$, is the largest modulus of an eigenvalue of $\mathbf{M}$. If $r(\mathbf{A}) > 1$ (or $r(\mathbf{A}) < 1$), then the total population increases (or decreases) geometrically, i.e. there exists $m > 0$ and $\rho > 1$ (or $0 < \rho < 1$) such that

$$\|\mathbf{x}(k)\| \geq m\rho^k, \ (\|\mathbf{x}(k)\| \leq m\rho^k) \ \ k = 0, 1, \ldots.$$

The following is a well-known consequence of the Perron-Frobenius theorem [110]. Note that a *nonnegative* matrix is a matrix whose entries are all ≥ 0. A *primitive matrix* is a nonnegative square matrix $\mathbf{A}$ such that $\mathbf{A}^k > 0$ for some positive integer k.

Theorem 1.0.1. *(Perron-Frobenius) Let $\mathbf{A}$ be a square, nonnegative, primitive matrix. Then $\mathbf{A}$ has an eigenvalue, λ, which satisfies:*

1. *λ is real and $\lambda > 0$,*

2. *λ has a right eigenvector whose components are strictly positive, and this is the only eigenvector (up to normalization) with this property.*

3. *$\lambda > |\mu|$ for any eigenvalue $\mu \neq \lambda$,*

4. *λ is a simple root of the characteristic equation of $\mathbf{A}$.*

Integral Projection Models (IPMs)

A class of integral population projection operators is introduced in Easterling [35], Easterling, et al. [36], and Ellner and Rees [41]. Let $n(x, t)$ be the population distribution as a function of the stage x at time t. For example, x could be the size of the individual, with maximal size M_s. The matrix is replaced by an integral operator with projection kernel $k(y, x)$, yielding the integro-difference equation

$$n(y, t+1) = \int_0^{M_s} k(y, x)n(x, t)dx. \tag{1.3}$$

In particular, this kernel does two things. One, it determines the probability of transition from size x to any possible size in one time step, much the same way that the (i, j)th entry of a projection matrix determines how an individual in stage j at time t moves to state i at time $t + 1$. It also determines the number of newborns

and the probability of transition of these newborns into any possible size. Let Ω be a bounded set containing the set of possible stages y. For instance, if y is size, Ω is the interval $[0, M_s]$, where M_s is the maximum size. (We note that a size of 0 is not biologically possible.) We can write (1.3) as

$$n(y, t+1) = \int_\Omega k(y, x) n(x, t) dx. \tag{1.4}$$

The stage variable y does not have to be a scalar. In an example in Chapter 3, originally given in Ellner and Rees [41], Ω is the set of all size-age pairs, where age is measured discretely with maximum age M_a, so $\Omega = \{(x, a) \mid x \in [0, M_s], a \in \{0, 1, 2, \ldots M_a\}\}$. Then the projection model is still given by (1.4), but if Ω is not a subset of $\mathbb{R}$, dy will indicate integration with respect to a measure.

Integral equations such as (1.4) can be analyzed in much the same way as matrix-based models of the form (1.1). The Banach space $L_1(\Omega)$, which has norm

$$\|\mathbf{v}\| := \int_\Omega |\mathbf{v}(x)| dx,$$

is analogous to $\mathbb{R}^S$ with norm given in (1.2). For a population function $n(x, t)$, it is sometimes useful to distinguish between the function $n(x, t)$ of two variables and the vector $\mathbf{n}(t) = n(\cdot, t)$ which is in $L_1(\Omega)$ for a given t. Define the operator $\mathbf{A} : L_1(\Omega) \to L_1(\Omega)$ by

$$(\mathbf{A}\mathbf{v})(\cdot) := \int_\Omega k(\cdot, x) \mathbf{v}(x) dx.$$

Then the equation (1.4) is equivalent to

$$\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t), \tag{1.5}$$

which is analogous to (1.1).

Easterling [35], Easterling, et al. [36], and Ellner and Rees [41] show that for a large class of kernels k, the solution of (1.4) satisfies the conclusions of Theorem 1.0.1.

I will denote matrices and integral operators by bold capital letters, such as $\mathbf{A}$. I will denote vectors, S by 1 matrices (i.e. column vectors) and $L_1(\Omega)$ functions by bold lower case letters, such as $\mathbf{d}$. I will denote 1 by S matrices (i.e. row vectors) and functionals on $L_1(\Omega)$ by bold lower case letter with a T superscript, to denote transpose, such as $\mathbf{e}^T$.

A key modelling and analysis issue is that the matrix or operator $\mathbf{A}$ will involve parameters, for instance fecundity or survival parameters. Usually these parameters will be uncertain. These uncertainties in $\mathbf{A}$ are typically *structured*, that is, the uncertainties occur only in specific locations in the model. For example, in a Leslie matrix, it only makes biological sense to perturb the top row and/or the sub-diagonals. These uncertainties and can be described by m parameters $(p_1, p_2, \ldots, p_m)$. When $\mathbf{A}$ is a matrix, we can typically choose $m \leq S^2$, the number of entries.

Since I am interested in the effect of the uncertainties on the asymptotic growth rate λ, I denote the explicit dependence of $\mathbf{A}$ and λ on $(p_1, p_2, \ldots, p_m)$ by writing

$$\mathbf{A} = \mathbf{A}(p_1, p_2, \ldots, p_m), \qquad \lambda = \lambda(p_1, p_2, \ldots, p_m).$$

I identify a set $\mathcal{P}$ of *admissible* parameters as those $(p_1, p_2, \ldots, p_m)$ which make biological sense in the model, and if necessary, are such that $\mathbf{A}(p_1, p_2, \ldots, p_m)$ has desirable mathematical properties. I can now describe one way of analyzing the effect of changes in the parameters on λ.

Consider the subset of $\mathcal{P}$ given by

$$C := \{(p_1, p_2, \ldots, p_m) \in \mathcal{P} \mid \lambda(p_1, p_2, \ldots, p_m) = 1\}. \tag{1.6}$$

This is the set of $(p_1, p_2, \ldots, p_m)$ for which the leading eigenvalue $\lambda(\mathbf{A}) = 1$. This set is a *hypersurface*. If we are considering two uncertain parameters, then $m = 2$ and C is a curve. If we are considering three uncertain parameters, then $m = 3$ and C is an ordinary surface (that is, a two dimensional object in three dimensions).

If we are concerned with maintaining a particular growth rate, say 3%, then we would replace C by $C_{1.03}$, where for arbitrary μ,

$$C_\mu := \{(p_1, p_2, \ldots, p_m) \in \mathcal{P} \mid \lambda(p_1, p_2, \ldots, p_m) = \mu\}.$$

In many applications we would be interested in identifying the set of all parameters which lead to asymptotic growth:

$$C_+ := \{(p_1, p_2, \ldots, p_m) \in \mathcal{P} \mid \lambda(p_1, p_2, \ldots, p_m) > 1\}. \tag{1.7}$$

For other applications, we will be interested in identifying the set of all parameters which lead to asymptotic decay:

$$C_- := \{(p_1, p_2, \ldots, p_m) \in \mathcal{P} \mid \lambda(p_1, p_2, \ldots, p_m) < 1\}. \tag{1.8}$$

When the notion of "side" is made precise mathematically, we can prove that C_+ is one side of the hypersurface C and C_- is on the other side of C. This is done in [77].

My primary interest is to find a usable formula for the hypersurface C. We assume that in applications we have *nominal* values for the parameters $(p_1, p_2, \ldots p_m)$,

that is, those values that are determined by experiment or some other method. We denote these nominal values by the point $\mathbf{q}_0$ in $\mathbb{R}^m$. We also assume that it is either considered "desirable" for the population to be in asymptotic decline (for instance, for an invasive species), or "desirable" for the population to be asymptotically increasing (for instance, for an endangered species).

The following *robustness* questions can be addressed once we have a formula for C:

- If $\lambda(\mathbf{q}_0) > 1$, and it is desirable for the population to asymptotically increase, then we are interested in how much the nominal parameters can be perturbed before population growth is lost.

- If $\lambda(\mathbf{q}_0) < 1$, and it is desirable for the population to asymptotically decrease, then we are interested in how much the nominal parameters can be perturbed before population decay is lost.

The following *control*, i.e. population management, questions can be addressed once we have a formula for C:

- If $\lambda(\mathbf{q}_0) > 1$, and it is desirable for the population to asymptotically decrease, then we are interested in how much the parameters have to be perturbed before population decay is achieved.

- If $\lambda(\mathbf{q}_0) < 1$, and it is desirable for the population to asymptotically increase, then we are interested in how much the parameters have to be perturbed before population growth is achieved.

We still need to find a usable equation for C. The obvious starting point is to

consider the hypersurface Γ on which *at least one* eigenvalue of $\mathbf{A}$ is 1:

$$\Gamma = \{(p_1, p_2, \ldots, p_m) \in \mathcal{P} \mid 1 \text{ is an eigenvalue of } \mathbf{A}(p_1, p_2, \ldots, p_m)\}.$$

In the matrix case, the hypersurface Γ is obtained from inspecting the characteristic polynomial: letting I denote the $n \times n$ identity matrix,

$$\Gamma := \{(p_1, p_2, \ldots, p_m) \in \mathcal{P} \mid \det(I - \mathbf{A}(p_1, p_2, \ldots, p_m)) = 0\}. \tag{1.9}$$

More generally, we can let Γ_μ be the hypersurface on which at least one eigenvalue of A is μ:

$$\Gamma_\mu = \{(p_1, p_2, \ldots, p_m) \in \mathcal{P} \mid \mu \text{ is an eigenvalue of } \mathbf{A}(p_1, p_2, \ldots, p_m)\};$$

for matrices this is

$$\Gamma_\mu := \{(p_1, p_2, \ldots, p_m) \in \mathcal{P} \mid \det(\mu I - \mathbf{A}(p_1, p_2, \ldots, p_m)) = 0\}. \tag{1.10}$$

If $\mathbf{A}$ is a matrix, it is easy to find a formula for Γ, and if $\mathbf{A}$ is an integral operator, it is often relatively easy to approximate Γ. However, as alluded to above, there is no guarantee that Γ is the same as C because we cannot guarantee *a priori* that we have not just found a sub-dominant eigenvalue of $\mathbf{A}(p_1, p_2, \ldots, p_m)$. Therefore it would be useful to have conditions under which

$$C_\mu = \Gamma_\mu.$$

In Deines et al. (2007) this is shown for a particular matrix example, using linear

algebra techniques that are specific to the system in that paper. The following generalization was shown by Boeckner, my co-author in [77].

Theorem 1.0.2. *Suppose that* $\mathbf{A}$ *is primitive and can be written as* $\mathbf{A} = \mathbf{A}_0 + \mathbf{d}\mathbf{e}^T$ *where*

1. $\mathbf{A}_0$ *is a nonnegative matrix;*

2. $\mathbf{d}$ *is a column vector,* $\mathbf{e}^T$ *is a row vector, and at least one of them is nonnegative;*

If $\lambda > r(\mathbf{A}_0)$ *is an eigenvalue of* $\mathbf{A}$*, then* $\lambda = \lambda(\mathbf{A})$*.*

Note that in the above theorem, $\mathbf{A}_0$ may be a function of some or all the parameters $(p_1, p_2, \ldots, p_m)$, i.e. $\mathbf{A}_0 = \mathbf{A}_0(p_1, p_2, \ldots, p_m)$. If this is the case, then λ needs to be greater than $r(\mathbf{A}_0)$ for all $(p_1, p_2, \ldots, p_m) \in \mathcal{P}$.

We also showed in [77] that if $\mathbf{A}(p_1, p_2, \ldots, p_m)$ is written in the form required by Theorem 1.0.2 above, then for $\mu \geq \nu$, for some ν with $r(\mathbf{A}_0) \leq \nu$, the two hypersurfaces C_μ and Γ_μ defined by

$$C_\mu := \{(p_1, p_2, \ldots, p_m) \in \mathcal{P} \mid \lambda(p_1, p_2, \ldots, p_m) = \mu\} \tag{1.11}$$

and

$$\Gamma_\mu := \{(p_1, p_2, \ldots, p_m) \in \mathcal{P} \mid \det(\mu I - \mathbf{A}(p_1, p_2, \ldots, p_m)) = 0\} \tag{1.12}$$

are equal, i.e.

Corollary 1.0.3. *For* $\mu \geq r(\mathbf{A}_0)$*, for all* $(p_1, p_2, \ldots, p_m) \in \Gamma_\mu$*,*

$$C_\mu = \Gamma_\mu. \tag{1.13}$$

Furthermore, in [77], we showed that this curve divides the subspace, $\mathcal{P}$, into two distinct pieces:

$$C_\mu^+ := \{(p_1, p_2, \ldots, p_m) \in \mathcal{P} \mid \lambda(p_1, p_2, \ldots, p_m) > \mu\} \tag{1.14}$$

and

$$C_\mu^- := \{(p_1, p_2, \ldots, p_m) \in \mathcal{P} \mid \lambda(p_1, p_2, \ldots, p_m) < \mu\}. \tag{1.15}$$

Therefore choosing $\mu = 1$ will divide the parameter space $\mathcal{P}$ into those parameters values which result in asymptotic population growth and those which result in asymptotic population decline, i.e. $\mu = 1$ is the growth-decline boundary. This choice of μ is arbitrary; one could choose any desirable μ. For example, in the case of an invasive species, choosing a $\mu < 1$ would be a more likely management goal.

Perhaps the simplest parameterized PM is the Leslie matrix $\mathbf{L}$ of a population with S age classes. Here the parameters consist of fecundity values $f_1, \ldots, f_S$ in the top row and survival probabilities $\sigma_1, \ldots, \sigma_{S-1}$ in a sub-diagonal. The Leslie matrix $\mathbf{L}$ has only one positive real eigenvalue which is well-known, but which also follows directly from Theorem 1.0.2. Cushing and Yicang [28] showed that the asymptotic growth rate of an age-structured population, i.e. the leading eigenvalue of $\mathbf{L}$, is greater than one if, and only if, the reproductive value, $R = f_1 + f_2\sigma_1 + f_3(\sigma_1\sigma_2) + \ldots + f_s(\sigma_1 \cdots \sigma_{s-1})$ is greater than one. Hence the relationship

$$f_1 + f_2\sigma_1 + f_3(\sigma_1\sigma_2) + \ldots + f_s(\sigma_1 \cdots \sigma_{s-1}) = 1$$

characterizes the boundary between growing and declining age-structured populations. Cushing and Yicang [28] also calculated the net reproductive value for other types of population projection matrices in terms of the matrix entries. These re-

sults yield a growth-decline boundary based on the calculation for net reproductive value. In addition, given the reproductive value R, they showed that if $R < 1$, then $R \leq \lambda \leq 1$ and if $R > 1$, then $1 \leq \lambda \leq R$. However, their results do not lead to a robustness analysis of λ with respect to the nominal vital rates.

Suppose we are identifying the growth-decline boundary, but we do not have an easy way of determining whether an eigenvalue of $\mathbf{A}$ is the leading eigenvalue. This is not particularly difficult if the nominal population is declining. This is because *all* of the eigenvalues of the nominal model are less than 1 and so to seek parameters values yielding leading eigenvalues greater than one reduces to finding parameter values so that *one* eigenvalue hits 1. The same applies at more general growth-decline boundaries $\lambda = \rho$. Thus, the robustness of population decline is an 'easy' problem.

If, however, we start with a base point given by a nominal growing population, which already has *at least* one eigenvalue greater than 1, then the boundary is no longer determined simply by parameter values achieving an eigenvalue of 1. This is because we cannot guarantee *a priori* that this eigenvalue at 1 is the leading eigenvalue. We see that robustness of population growth is more subtle than robustness of population decline, and is simplified if we can easily identify when an eigenvalue is the leading eigenvalue.

In Chapter 2, I look at a specific population projection matrix for the endangered Serengeti cheetah population. The management goal for the Serengeti cheetah is to achieve a robustly stable or growing population. Using a PPM, Crooks et al. [26] showed the Serengeti cheetah population is most sensitive to adult survivorship, suggesting that conservation efforts should focus on increasing adult survivorship. One pitfall of sensitivity and elasticity analysis is they do not consider biological limits which may constrain how much a transition rate with the highest elasticity can be changed. When analyzing the survival of captive cheetahs, I found strong

age dependency in survival, indicating captive cheetahs experience senescence, i.e. the reduction in the rate of survival with age [5, 24, 104], and thus estimated the upper age limit for survival of wild cheetahs. I expand their model to incorporate senescence. I also show that my new PPM satisfies the conclusions of Theorem 1.0.2, thus in particular, $C_1 = \Gamma_1$. I then analyze the model using our robustness method which allows for multiple perturbations of different proportions, and provides a visual interpretation of the uncertainty in the data. Therefore I avoid the limitations inherent in sensitivity and elasticity analysis. By using the growth-decline boundary, I show that increasing the adult survivorship alone will not achieve the management goal of $\lambda > 1$ [78].

For integral equations with kernels of a form analogous to that in Theorem 1.0.2, I show in Chapter 3 that the curves C_μ and Γ_μ defined in equations (1.10) and (1.11) above are equal under easily checkable conditions. I also give an example of how to analyze the IPM using this method with the thistle *Onopordum illyricum*, the example originally used by Ellner and Rees [41].

In order to analyze the integral projection models, some definitions are necessary. Let $\mathcal{B}$ be a Banach space, and $\mathbf{A} : \mathcal{B} \to \mathcal{B}$ be a linear operator. The integral operators of the form (1.4) I consider in this dissertation are all bounded operators. If the function $k(\cdot, \cdot)$ is continuous and the set Ω is bounded - which is typical when Ω is the set of stages a population can take - then $\mathbf{A}$ is a Hilbert-Schmidt operator, and hence is a compact operator, see for instance Bachman and Narici [3]. One characterization of a compact operator is that it can be uniformly approximated by finite rank operators, so reliable numerical results can be obtained for these systems [50]. A consequence of compactness is that the only non-zero spectrum $\mathbf{A}$ has are eigenvalues. In order for an integral equation of the form (1.4) to satisfy the conclusions of Proposition 1.0.1, I need to make a further assumption about $\mathbf{A}$. Biologically, this assumption translates

to the need to assume that the state of the offspring is independent of the state of the parents. The following definitions can be found in many sources, including [41, 67], and [126].

In order to work with "positive operators" the same way we work with positive matrices, we first need a partial order "$\geq$" on $\mathcal{B}$.

Definition 1.0.4. *Let $\mathcal{B}$ be a Banach space. A cone is a non-empty, closed, convex subset, $K \subseteq \mathcal{B}$ provided two conditions hold:*

1. *If $x \in K$ and $\alpha \geq 0$ then $\alpha x \in K$.*

2. *If $x, -x \in K$ then $x = 0$.*

Definition 1.0.5. *A cone, K, induces a partial order on the Banach space $\mathcal{B}$, denoted by "$\geq$" (or resp. "$\leq$") where $x \geq y$ (or resp. $x \leq y$) for $x, y \in \mathcal{B}$ means $x - y \in K$ (or resp. $y - x \in K$). If we write $x > y$ (or resp. $x < y$), we mean that $x \geq y$ and $x \neq y$ (or resp. $x \leq y$ and $x \neq y$).*

Definition 1.0.6. *A cone is called reproducing if $K \ominus K = \mathcal{B}$, that is, every element in the Banach space can be written as the sum of one element in K plus the negative of another element in K.*

When $\mathcal{B} = L_1(\Omega)$, we typically use the cone K of functions which are nonnegative on Ω, which is reproducing. Hence if $f, g \in L_1(\Omega)$, then $f \leq g$ means $g - f$ is a nonnegative function on Ω, i.e. $g - f$ is in the cone K. When $\mathcal{B} = \mathbb{R}^n$, we use the cone of vectors which have nonnegative components.

Definition 1.0.7. *Let K_1 and K_2 be cones in Banach spaces $\mathcal{B}_1$ and $\mathcal{B}_2$ respectively. A bounded linear operator, $\mathbf{A}$, is called positive if it maps K_1 into the cone K_2, i.e. $AK_1 \subseteq K_2$.*

In the case where the bounded linear operator is a population projection matrix, the definition for a positive operator is analogous with the definition for a nonnegative matrix.

Definition 1.0.8. *Let $u \in K$, $u \neq 0$. A positive linear operator, $\mathbf{A}$, is called u-bounded if for each $n \in K$ there exists constants $\alpha = \alpha(n) > 0$ and $\beta = \beta(n) > 0$ such that*

$$\alpha u \leq \mathbf{A}n \leq \beta u.$$

There are two possible paths to show an integral projection model is u-bounded. Both of these methods are explained in [41]; I will summarize their explanations here. Let

$$k^{(j+1)}(y, x) = \int_\Omega k(y, x)k^{(j)}(z, x)dz, \tag{1.16}$$

where $k^{(j)}$ is the kernel for $\mathbf{A}^j$. We say that the kernel k is *power positive* if there exists some integer $j > 0$ such that $k^{(j)}(y, x) > 0$ for all $x, y \in \Omega$. This is analoguous to the definition of a primitive matrix. In kernels where $k(y, x) \geq 0$ for all $x, y \in \Omega$ this means every possible state is achievable independent of the initial conditions. For integral projection models like those in this thesis, where Ω is the product space of a continuous and discrete bounded domains and it is possible to achieve every possible state regardless of the initial condition, the kernel is a power positive kernel. Furthermore the kernel is a "uniform power positive" kernel, which has the more stringent requirement that $k^{(j)}(y, x) > c$ for all $x, y \in \Omega$ for some constant, $c > 0$. Thus for the integral projection models as discussed in this thesis, there exists some iteration of the kernel $k^m(y, x)$ which is bounded both below and above due to continuity and compactness. Hence there exists constants c and C such that $c \leq k^m(y, x) \leq C < \infty$. Letting $u(x) = 1$, $\alpha(n) = c \int_\Omega n(x)dx$ and $\beta(n) = C \int_\Omega n(x)dx$,

then

$$\alpha u \leq \int_{\Omega} k^m(y,x)n(x)dx \leq \beta u. \tag{1.17}$$

This shows $\mathbf{A}^m$ is $u-$bounded; the final steps of showing the integral operator $\mathbf{A}$ is u-bounded is given in [41].

A second method for achieving a $u-$bounded operator is if there is "mixing at birth", i.e. that all parents produce a similar distribution of offspring regardless of the state of the parents [41]. Mixing at birth leads to some iterative of the operator $\mathbf{A}$ being $u-$bounded, which in turn leads to the operator $\mathbf{A}$ itself being $u-$bounded. The mixing at birth assumption is shown to be valid for size $\times$ age domains with a finite maximum age [21] and extended to non-finite maximum age domains in species where a cohort of newborns are eventually outnumbered by their descendants for all states [41].

The following theorem is a generalization of the Perron-Frobenius theorem for matrices to compact, u-bounded operators. It is proved in [67].

Theorem 1.0.9. *Let $\mathcal{B}$ be a Banach space with a reproducing cone K which determines a partial order. Let A be a positive, compact, u-bounded linear operator on $\mathcal{B}$. Then*

1. *$\mathbf{A}$ has a positive eigenvalue, λ, whose corresponding eigenvector is an element of K. This eigenvalue is the spectral radius of $\mathbf{A}$.*

2. *This eigenvalue is simple and its corresponding eigenvector is the unique (up to normalization) eigenvector in K.*

3. *Every other eigenvalue of $\mathbf{A}$ is less in magnitude than λ.*

Transient Dynamics

The second part of this dissertation is focused on transient dynamics. Most analysis

of population dynamics literature is devoted to asymptotic dynamics, including my PPM and IPM analyses in Chapters 2 and 3, since the theory to analyze asymptotic dynamics is well established (see e.g. [16]). However, environmental disturbances like drought and fire and intervention by human activity may affect one stage or age class more than another, resulting in deviations from the stable state distribution. Thus asymptotic dynamics may in fact, be not as common as previously thought [7, 23, 42, 51, 52]. The dynamics of populations that are not at its stable state distribution, known as transient dynamics, can be significantly different from asymptotic ones.

Transient dynamics may be important for dispersal and population establishment in a new location if the dispersal is restricted to particular life history stages, such as seeds in many plants, or adults in many animals. Transient dynamics give insight into how a population may react to perturbations caused by human intervention, e.g. through the release of captive-reared animals into the wild, the relocation of a wild population, or selective culling of a specific age class. Modeling the transient behavior offers insight into whether such an management is viable [53].

Transient dynamics have been studied as perturbations from a stable state distribution or from an equilibrium. Both [18] and [19] provide theoretical framework for studying transients of a system perturbed from an equilibrium in a predator-prey model. Additionally, [118] and [119] have looked at using the Kreiss bound as an alternative method for studying perturbations from an equilibrium position. For single species models, early work focused on the length of time it took for the system to return to its stable state distribution, i.e. its damping ratio [74]. More current work has been done to calculate the sensitivity of the transient population dynamics to various life history parameters, see for example [17] and [42]. Both [64] and [125] showed for population projection matrices how the transient growth rate depends on the initial population, yet little has been done to study transient dynamics when temperature,

such as in ectothermal animals, plays an important role. In Chapter 4, I focus on the effect of temperature on the transient dynamics resulting from an invasion by a single, reproducing adult aphid, which is the dispersal stage of the aphid, and compared these dynamics with an invading population with a stable state distribution, normalized to 1.

One quantification of transient dynamics is to consider the difference between the size of a population which starts with a stable stage distribution versus one which starts with a non-stable state distribution. This has been studied by demographers (e.g. [61, 62]) in both matrix models and in continuous time models. Consider the $S \times S$ population projection matrix, $\mathbf{A}$, such that the assumptions of the Perron-Frobenius theorem, Theorem 1.0.1, are satisfied. Let $\mathbf{w}$ be $\mathbf{A}$'s leading right unit eigenvector and $\mathbf{v}$ be its leading left eigenvector normalized such that $\mathbf{v}^T \mathbf{w} = 1$. Let $\mathbf{n}(t)$ be the population vector at time t, where $\mathbf{n}(0)$ is an arbitrary (non-normalized) initial population vector. Eventually, when asymptotic behavior is reached, $\mathbf{n}(t)/\|\mathbf{n}(t)\|$ will converge to $\mathbf{w}$. The *stable equivalent*, Q, is defined as the constant such that if you begin with an initial population vector of $Q\mathbf{w}$, it asymptotically produces the same population as if you started with $\mathbf{n}(0)$. In this PPM case, $Q = \mathbf{v^T}\mathbf{n}(0)$, so Q depends on the initial population vector [62, 120]. From a different perspective, if $\mathbf{w_1}, \mathbf{w_2}, \ldots, \mathbf{w_S}$ are the (normalized) right eigenvectors with $\mathbf{w_1}$ being the eigenvector associated with the leading eigenvalue, and $\mathbf{n}(0) = c_1 * \mathbf{w_1} + c_2 * \mathbf{w_2} + \cdots + c_S * \mathbf{w_S}$, then $Q = c_1$.

Koons et al. [65] defines *population inertia* relative to a reference vector, $\mathbf{r}(t)$ as

$$I_{\mathbf{r}(0)} = \lim_{t \to \infty} \frac{\|\mathbf{n}(t)\|}{\|\mathbf{n}(0)\|} \Big/ \frac{\|\mathbf{r}(t)\|}{\|\mathbf{r}(0)\|} \tag{1.18}$$

where $\mathbf{n}(t)$ is the population at time t. For example, if the matrix is primitive,

the reference vector could be the positive eigenvector corresponding to the leading eigenvalue, i.e. the stable state distribution. In this case, population inertia, which is also called the *stable equivalent ratio*, is the ratio of the population size at time t normalized by its size at $t = 0$ to what the size of the population would be if its initial population was at its normalized stable state distribution. Additionally, if $\|\mathbf{n}(0)\| = \|\mathbf{r}(0)\|$, and $\mathbf{r}(0)$ is the positive right eigenvector associated with the leading eigenvalue, then the stable equivalent ratio is equal to Q. Koons et al's [65] population inertia is a generalization of Tuljapurkar's and Lee's deterministic stable equivalent ratio [120] and Keyfitz's population momentum [61]. Tuljapurkar and Lee [120] also defined their stable equivalent ratio for stochastically varying matrices.

Because I am interested in the transient effects caused by an invasion, I am looking in particular at how the population changes in those first days of the invasion. One frequent measure of transient dynamics is the *transient growth rate* which is defined as

$$\lambda(t) = \frac{\|\mathbf{n}(t+1)\|}{\|\mathbf{n}(t)\|} \tag{1.19}$$

where t is measured in days. Following [117], I also define *transient amplification* as

$$T_A(t) = \frac{\|\mathbf{n}(t)\|}{\lambda^t} \tag{1.20}$$

where $\mathbf{n}(t)$ is the population at time t and λ is the asymptotic population growth rate. I assume the initial population, $\|\mathbf{n}(0)\| = 1$. This definition is therefore a specific case of Koons et al.'s [65] population inertia given in (1.18) above.

Two models were constructed to study the effect of temperature on transient dynamics. Both are variations of the continuous time model given in [10]:

$$n(a,t) = \begin{cases} n(a-t,0)\dfrac{s(a)}{s(a-t)} & a > t \\ b(t-a)s(a) & a < t, \end{cases} \qquad (1.21)$$

where $n(a,t)$ is the population distribution of age a at time t, $s(a)$ is the probability an aphid will survive to age a, and $b(t)$ are the births at time t. The first line in (1.21) is the number of aphids alive at $t = 0$ and still alive at time t. The second line is the number of aphids which were born at time $t - a$ and are still alive at time t. The number of births $b(t)$ is given by

$$b(t) = \int_0^{\text{max age}} n(a,t)m(a)da, \qquad (1.22)$$

where $m(a)$ is the average offspring per aphid of age a. See Chapter 4 for more specifics on the models.

In one model, called the ordinal time model, time is measured in days and is denoted by t; while in the other model, called the degree day model, time is measured in degree days and is denoted by $\tilde{t}$. Degree days normalize the effect of temperature on insect growth and development, i.e. degree days measure physiological time. In the temperature range of interest $(18-28°C)$, the relationship (for most insects, including aphids) between temperature and rate of development is linear [75, 114, 115], i.e.

$$(\text{time to first reproduction})^{-1} = c_1 * \text{temperature}(°C) + c_2, \qquad (1.23)$$

where c_1 and c_2 are constants dependent upon the particular species. The temperature where this linear fit crosses the temperature axis is called the "lower threshold", L_T, or "threshold of development" [69, 115]. Biologically, this can be thought of the lowest temperature at which chemical reactions within the animal will occur and thus allow growth. Outside of the range of interest in this thesis, the linear relationship no

longer holds, and flattens out at lower temperatures before no development occurs, hence L_T is not a true threshold. Assuming a constant temperature, T, the number of cumulative degree days is given by

$$\text{degree days} := \widetilde{t} = (T - L_T)t, \tag{1.24}$$

where t is the elapsed number of days. [57, 92]. Using $t = 1$ converts the one day to elapsed degree days.

In both the ordinal day model and the degree day model, the maternity function, or the number of offspring produced per unit time, was measured as a function of time since from onset of reproduction, either by days or by degree days. This is the significant difference between my models and that given by (1.21) above.

To parameterize the models, I conducted empirical experiments to estimate parameter values and to test model predictions. I estimated survivorship and fecundity of aphids at two different temperatures ($20°C$ and $25°C$) and at low and medium relative humidities. The models were tested by simulating an aphid invasion in the laboratory and counting the population as it evolved in time. Temperature was included into the model in two different ways. The first method parameterized the survivorship and fecundity data for each temperature as two separate experiments. The second method combined the survivorship and fecundity data for both temperatures using the degree day conversion in (1.24) above. Statistical analyses were done to determine if humidity affected the parameterization of the model and hence the final results.

Chapter 2

Using the Growth-Decline Boundary to Determine the Effect of Senescense on Stage Structured Populations

As mentioned in the introduction, sensitivity and elasticity analysis do not consider how biological limits may constrain how much life history parameters can be manipulated [16]. Using the endangered cheetah (*Acinonyx jubatus*) as a case study I illustrate that ignoring biological limits can result in management recommendations that are unlikely to achieve the management goal, which in this case is population stasis or population increase ($\lambda_{max} \geq 1$).

Crooks et al. [26] constructed a population matrix model for Serengeti cheetahs; see Table 2.1. Their model predicts an annual population decline of 8.7%, i.e. $\lambda_{max} := \lambda = 0.913$. The long-term population growth rate is most sensitive to adult survivorship, suggesting that wildlife managers should aim to increase adult

Table 2.1: Population Projection Matrix (PPM) for wild cheetahs [26]

Age classes (months)

$0-6$	$6-12$	$12-18$	$18-24$	$24-30$	$30-36$	$36-42$	$42+$
0	0	0	0	$s_2 f_1$	$s_2 f_1$	$s_2 f_1$	$s_3 f_2$
s_0	0	0	0	0	0	0	0
0	s_1	0	0	0	0	0	0
0	0	s_1	0	0	0	0	0
0	0	0	s_2	0	0	0	0
0	0	0	0	s_2	0	0	0
0	0	0	0	0	s_2	0	0
0	0	0	0	0	0	s_2	s_2

$s_0 = 0.081$,   survival of $0-6$ month age class;
$s_1 = 0.771$,   survival of $6-12$ and $12-18$ month age classes;
$s_2 = 0.920$,   survival of $18-24, 24-30, 30-36$ and
               $36-42$ month age classes;
$s_3 = 0.879$,   survival of $42+$ month age class;
$f_1 = 1.2476$,   fecundity of $24-30, 30-36$, and
               $36-42$ month age classes;
$f_2 = 1.4994$,   fecundity of $42+$ month age class.

survival. I expand their model to include the effects of senescence on survival and fecundity.

In 1900, the cheetah (*Acinonyx jubatus*) roamed over much of Africa, Asia and the Middle East with a total population estimated at 100,000 [85]. Now barely 100 years later, there are only 12,000 to 15,000 animals left worldwide; most reside in southern Africa [88, 89, 85]. The largest concentration of cheetahs resides in Namibia, with an estimated population of 2500 felines [88, 89, 85]. The majority of the cheetahs in Namibia live outside protected areas and as a result, their demise is linked to the loss of habitat by encroaching farms, poaching, and the reduced number of prey [86, 87, 88, 89]. Approximately 300-400 cheetahs reside in the Serengeti Plains of Tanzania [14, 47]. Much of this area is a protected national park, yet the population

fails to thrive due to the high cub mortality caused by predation by lions and hyenas [13, 37, 59, 60, 72]. 92% of the newborn cheetahs die during the first six month of life, but once they can outrun predators (older than 5 months) their survival increases 10 times [26]; see also [13]. Juveniles stay with their mother for up to 18 months [13, 37, 60]. A female reaches sexual maturity at approximately 24 months, and after a gestation period of about 3 months she will give birth to one to six cubs [13, 37, 59, 60, 86]. Caro [13] considers a 23-42 month old adult cheetah to be a young adult and those older than 42 months to just be adults. If a wild female Serengeti cheetah reaches adulthood (24 months), its average life span is 6.2 years [60].

2.1 Methods

I retain Crooks et al.'s [26] original 6 month age classes as an aid to help compare models which include senescence with those that do not. The new model (see Tables 2.2 and 2.3) increases the number of age classes from 8 to 36; the last age class includes cheetahs that are 210-216 month old (18 years). Since cheetahs older than 18 years have zero fecundity, they are considered "biologically dead" and are not a factor in the cheetah's population growth, hence they are ignored in the model (Caswell, 2001). I then identify strategies that produce a growing population ($\lambda > 1$) and are robust to parameter uncertainty. First, I estimate the biological limit of adult survival. Then, within the biological meaningful range of survival scenarios, I identify the magnitude of disturbances permissible to reach the management goal; if the permissible perturbations are realistic within the confines of the variance in the data, I call the management strategy "robust".

I analyze survival data available in the 2002, 2003, and 2004 International Cheetah Studbooks [82, 83, 84]. Because the model by Crooks et al. [26] ignores males, I

Table 2.2: Population Projection Matrix (PPM) for wild cheetahs incorporating senescence.

Age classes (months)

0–6	6–12	12–18	18–24	24–30	30–36	36–42	42–48	⋯	96–102	102–108	⋯	138–144	144–150	⋯	204–210	210–216
0	0	0	0	$s_2^*f_1$	$s_2^*f_1$	$s_2^*f_1$	$s_3^*f_2$	⋮	$s_3^*f_2$	$s_4^*f_3$	⋮	$s_4^*f_2$	$s_4^*f_3$	⋮	$s_4^*f_2$	0
s_0	0	0	0	0	0	0	0	⋮	0	0	⋮	0	0	⋮	0	0
0	s_0	0	0	0	0	0	0	⋮	0	0	⋮	0	0	⋮	0	0
0	0	s_1	0	0	0	0	0	⋮	0	0	⋮	0	0	⋮	0	0
0	0	0	s_2^*	0	0	0	0	⋮	0	0	⋮	0	0	⋮	0	0
0	0	0	0	s_2^*	0	0	0	⋮	0	0	⋮	0	0	⋮	0	0
0	0	0	0	0	s_2^*	0	0	⋮	0	0	⋮	0	0	⋮	0	0
0	0	0	0	0	0	s_2^*	0	⋮	0	0	⋮	0	0	⋮	0	0
0	0	0	0	0	0	0	s_3^*	⋮	0	0	⋮	0	0	⋮	0	0
⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮
0	0	0	0	0	0	0	0	⋮	s_3^*	0	⋮	0	0	⋮	0	0
0	0	0	0	0	0	0	0	⋮	0	s_4^*	⋮	0	0	⋮	0	0
⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮
0	0	0	0	0	0	0	0	⋮	0	0	⋮	s_4^*	0	⋮	0	0
0	0	0	0	0	0	0	0	⋮	0	0	⋮	0	s_4^*	⋮	0	0
⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮
0	0	0	0	0	0	0	0	⋮	0	0	⋮	0	0	⋮	s_4^*	0

Values for variables are listed in Table 2.3

only estimate female survival. Sometimes cheetah deaths are not reported and as a result the records suggest that some of these cheetahs are older than 30 years; even though in captivity cheetahs rarely live past 21 years of age [88]. Also, since the inclusion of live cheetahs in my data analysis did not change the survivorship estimation significantly, in the survival analysis I exclude those cheetahs that are still alive and those considered "lost" or "assumed dead" by the stud keeper. This left $N = 1955$ cheetahs for my analysis. Figure 2.1 shows the Kaplan Meier curve for captive cheetah survival. The Kaplan Meier curve, also called the product-limit estimator; is probability that an individual will survive beyond a specific time [25]. The Matlab [91] computer code for these calculations is given in Appendix A.

Analogous to Crooks et al.'s [26] model, I use 6 month time intervals and calculate survivorships for $0-6$ month old (s_0^*), $6-18$ months old (s_1^*), and $18-42$ months old cheetahs (s_2^*). To account for senescence (Figure 2.1) I split the survival of the $42+$ month old cheetahs of Crooks et al's [26] model into $42-102$ months old (s_3^*) and > 102 months old (s_4^*). For cheetahs older than 156 months I use the same survivorship as for cheetahs aged $102-156$ months, even though this is an overestimation. I calculate the average survival per time step as follows:

$$s_i^* = \left(\frac{\ell(t + \delta t)}{\ell(t)}\right)^{1/n} \tag{2.1}$$

where ℓ is the Kaplan-Meier estimate, t and $(t + \delta t)$ are the start and end times of the ith stage, and n is the number of time steps in δt [16]. Using these estimates for survivorship (Table 2.3), my model predicts that once a cheetah survives to adulthood, there is a 50% chance that she will survive past $9 - 9\ 1/2$ years ($108 - 114$ months).

The model by Crooks et al. [26] assumes the same fecundity, f_2, for all $42+$ months old cheetahs. This is particularly problematic because in the wild, cheetahs do not
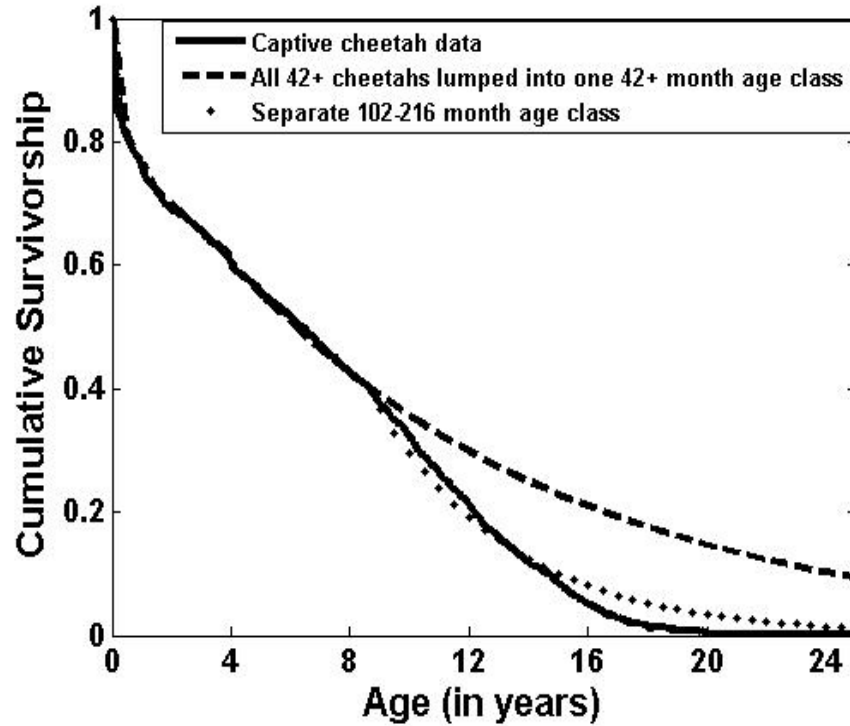
Figure 2.1: Survival data from captive female cheetahs shows the cumulative survivorship of female cheetahs with known age of death. The solid curve is the Kaplan-Meier curve using monthly time steps. The heavy dashed curve shows the cumulative female adult survivorship with all 42+ month old cheetahs lumped into one age class using the survivorship of $42 - 102$ month cheetahs ($s_3^* = 0.9567$). The heavy dotted curve divides the 42+ month old cheetahs into two age classes: $42 - 102$ months ($s_3^* = 0.9567$) and 102+ months ($s_4^* = 0.898$) with the 102+ month age class having the survivorship of $102 - 162$ month cheetahs. The 95% confidence intervals for the Kaplan-Meier curve are very tight and thus are omitted for clarity.

reproduce after 12 years of age [59, 86, 101] and even in captivity, cheetahs rarely, if at all, reproduce after they turn 18 years (216 months) (see [81, 82, 83, 84, 88]). In captivity, a cheetah's prime reproductive period is between 3 and 10 years of age [81, 82, 83, 84], but in general cheetah fecundity in captivity is lower than in the wild [101]; also compare [81, 82, 83, 84] with [59]. This is in agreement with other captive carnivorous animals [22, 68]. Because I do not have data to estimate the effect of senescence on the fecundity of wild cheetahs, I consider two different cases. In both cases, I assume fecundity of the $18 - 42$ month old cheetahs ($f_1 = 1.2476$) and the $42 - 144$ month old cheetahs ($f_2 = 1.4994$) is that given in Crooks et al. [26]. Defining f_3 to be the fecundity of the $144 - 216$ month old cheetahs, I first set f_3 equal to f_2 ($f_3 = 1.4994$), which ignores a reduction in fecundity due to senescence, and as a consequence, my model's predictions will overestimate population growth rate (Table 2.2). Second, I assume that adult cheetahs stop reproducing at the age of 12 years as is observed in wild cheetahs, ($f_3 = 0$), in which case I can remove these age classes from the model. In both cases, I assume the fecundity of cheetahs older than 216 months (18 years) is zero.

To analyze this model I examine the response of the asymptotic population growth, $\lambda_{\max}$, to large simultaneous deviations from the parameter values used in the model by Crooks et al. [26]; in particular I wish to explore if it is theoretically possible to achieve the management goal (in this paper $\lambda_{max} > 1$) by perturbing parameter values to their biological limits. First I set the fecundities and survivorships of the $102 - 216$ month old cheetahs to their biological limit (f_2^*, f_3^*, s_4^*, Table 2.3). I then identify the survivorship combinations of younger adult cheetahs (s_2^*, s_3^*) that yield a growth rate of $\lambda = 1$. Let $\mathbf{A}$ be the 36×36 population projection matrix model shown in Table 2.2 with Crooks et al.'s [26] values for the survivorships of the $0 - 6$ month cubs (s_0) and the $6 - 18$ month old cheetahs (s_1). Let $\mathbf{P}$ denote the 36 by 36 matrix

containing the deviations from the nominal values given in $\mathbf{A}$; all matrix entries of $\mathbf{P}$ that are not affected by the particular perturbation are zero. Since I am perturbing s_2^*, s_3^*, I let p_2 denote changes in s_2^*, and I let p_3 denote changes in s_3^*. Thus the first row of the matrix $\mathbf{P}$ has $p_2 f_1$ in columns 5 through 7 and $p_3 f_2$ in columns 8 through 17 where f_1 and f_2 are the fecundities of the $18 - 42$ month old and the $42 - 216$ month old cheetahs. The subdiagonal of $\mathbf{P}$ has p_2 in columns 4 through 7 and p_3 in columns 8 through 17. I call $\mathbf{A} + \mathbf{P}$ the perturbed matrix. For example, to examine the effect of changing both s_2^*, s_3^* to that given in Crooks at al. [26] I set $p_2 = -.0485$ and $p_3 = -.0468$ in the above $\mathbf{P}$. This gives $s_2^* + p_2 = s_2$ and $s_3^* + p_3 = s_3$.

My goal is to determine which (p_2, p_3) yield $\lambda(p_2, p_3) = 1$, i.e. to determine the growth-decline boundary as a function of p_2 and p_3. Unfortunately, $\mathbf{A}$ and $\mathbf{A} + \mathbf{P}$ are not primitive matrices since the last column consists entirely of zeros, therefore Theorem 1.0.2 cannot directly be used to show that if an eigenvalue, λ, of $\mathbf{A} + \mathbf{P}$ is 1, then $\lambda = \lambda(\mathbf{A} + \mathbf{P})$. In order to use Theorem 1.0.2, a modification to the Perron-Frobenius Theorem (Theorem 1.0.1) is necessary.

Theorem 2.1.1. *Let A be an $n \times n$ matrix of the form given in Table 2.3. Then* $\mathbf{A}$ *has an eigenvalue, λ, which satisfies:*

1. *λ is real and $\lambda > 0$,*

2. *λ has a unique (up to normalization) right eigenvector whose components are strictly positive,*

3. *$\lambda > |\mu|$ for any eigenvalue $|\mu| \neq \lambda$,*

4. *λ is a simple root of the characteristic equation of* $\mathbf{A}$.

Proof: Let λ be an eigenvalue of $\mathbf{A}$ and $\mathbf{v}$ its corresponding eigenvector. Consider the system

$$
\mathbf{Av} = \begin{bmatrix} & & & 0 \\ & \mathbf{B} & & \vdots \\ & & & 0 \\ 0 & \cdots & 0 & s_3^* & 0 \end{bmatrix} \begin{bmatrix} v_1 \\ \vdots \\ v_{n-1} \\ v_n \end{bmatrix} = \lambda \begin{bmatrix} v_1 \\ \vdots \\ v_{n-1} \\ v_n \end{bmatrix}, \tag{2.2}
$$

where $\mathbf{B}$ is the $n-1$ by $n-1$ submatrix of $\mathbf{A}$. It is easily seen that the eigenvalues of $\mathbf{A}$ are the same as the eigenvalues of $\mathbf{B}$ plus the addition of $\lambda = 0$. Since $\mathbf{B}$ is a square, nonnegative, primitive matrix, then the Perron-Frobenius theorem (Theorem 1.0.1) holds for $\mathbf{B}$. Let λ be the largest positive eigenvalue of $\mathbf{B}$; hence λ satisfies items (1) and (3) for $\mathbf{A}$ as required. Notice that

$$
\mathbf{B} \begin{bmatrix} v_1 \\ \vdots \\ v_{n-1} \end{bmatrix} = \lambda \begin{bmatrix} v_1 \\ \vdots \\ v_{n-1} \end{bmatrix}.
$$

By Perron-Frobenius (Theorem 1.0.1), we may assume $v_1, \ldots, v_{n-1} > 0$ and

$$
\begin{bmatrix} v_1 \\ \vdots \\ v_{n-1} \end{bmatrix} \tag{2.3}
$$

is the unique (up to normalization) positive eigenvector of $\mathbf{B}$. For $\mathbf{v}$ to be the corresponding eigenvector for $\mathbf{A}$ requires $s_3^* v_{n-1} = \lambda v_n$. Now, s_3^*, v_{n-1} and λ are all > 0. Therefore $v_n > 0$ and is uniquely defined by $v_n = s_3^* v_{n-1}/\lambda$.

In order to satisfy (2) above, I need to show that $\lambda = 0$ does not have an eigenvector, $\mathbf{v}$, whose components are strictly positive. Assume $\mathbf{v}$ is the eigenvector associated

with $\lambda = 0$ and that it has strictly positive components. Thus

$$\begin{bmatrix} & & & 0 \\ & \mathbf{B} & & \vdots \\ & & & 0 \\ 0 & \cdots & 0 & s_3^* & 0 \end{bmatrix} \begin{bmatrix} v_1 \\ \vdots \\ v_{n-1} \\ v_n \end{bmatrix} = 0. \tag{2.4}$$

It is obvious this requires $s_3^* v_{n-1} = 0$. Since both s_3^* and v_{n-1} are positive, this is a contradiction. Therefore $\mathbf{A}$ has only one eigenvector whose components are strictly positive, hence item (2) is satisfied.

To show item (4) holds, let $\det(t\mathbf{I} - \mathbf{A})$ be the characteristic equation of $\mathbf{B}$. Thus the characteristic equation of $\mathbf{A}$ is $t\det(t\mathbf{I} - \mathbf{A})$. Thus $t = 0$ is an additional root of $\mathbf{A}$'s characteristic equation. Since the Perron-Frobenius theorem (Theorem 1.0.1) holds for $\mathbf{B}$, then the leading eigenvalue λ is also a simple root of the characteristic equation of $\mathbf{A}$, hence item (4) holds. □

Corollary 2.1.2. $\mathbf{A}$ *satisfies the conclusions of Theorem 1.0.2.*

Proof: The proof follows the same as Theorem 1.0.2. I can rewrite $\mathbf{A}$ as $\mathbf{A}_0 + \mathbf{d}\mathbf{e}^T$ where $\mathbf{A}_0$ is the same as $\mathbf{A}$ except the first row is replaced with zeros, $\mathbf{d} = [1\ 0\ \cdots\ 0]^T$ and $\mathbf{e}^T$ is the first row of $\mathbf{A}$. Since $\mathbf{A}_0$ is nilpotent, $r(\mathbf{A}_0) = 0$. The proof of Theorem 1.0.2, which is similar to the proof of Theorem 3.1.1, shows $\lambda = \lambda(\mathbf{A})$. □

Therefore, if $\lambda(p_2, p_3) = 1$, then $\lambda(p_2, p_3) = 1$ is the largest eigenvalue of $\mathbf{A} + \mathbf{P}$ and the $\lambda(p_2, p_3) = 1$ curve divides the admissible parameter space into increasing and decreasing asymptotic populations. Methods for solving the equation $\det(\mathbf{I} - (\mathbf{A} + \mathbf{P})) = 0$ are further outlined in [30, 55, 56]. Because cub survival in the wild is extremely low and can theoretically be increased to a large extent I also consider the perturbations in three parameter values: $s_0, s_2^*,$ and s_3^*. The computer code for these

Table 2.3: Values* Calculated by Kaplan-Meier Analysis for Captive Cheetahs

$s_0^* = 0.8087 \pm 0.0174,$ survival of $0 - 6$ month age class;
$s_1^* = 0.9434 \pm 0.0082,$ survival of $6 - 12$ and $12 - 18$ month age classes;
$s_2^* = 0.9685 \pm 0.0047,$ survival of $18 - 24, 24 - 30, 30 - 36$ and
$36 - 42$ month age classes;
$s_3^* = 0.9567 \pm 0.0041,$ survival of $42 - 48, 48 - 56, \ldots 96 - 102$
month age classes;
$s_4^* = 0.8980 \pm 0.0091,$ survival of $102 +$ month age class.

*with 95% confidence intervals

analyses is located in Appendix A.

2.2   Results

In this study I used data for captive cheetahs as a conservative estimate of the biological limit of adult survival. The Kaplan-Meier curve (Figure 2.1) illustrates that the survival of captive cheetahs dropped after 8.5 years and that a model ignoring this largely overestimates cheetah survival (heavy dashed line). Thus, predicting the effect of increasing adult survival requires a model that includes a senescent age class (modified model, Table 2.2, and heavy dotted line in Figure 2.1). Assuming that the survival of an adult cheetah in the wild can be raised to that in captivity corresponds to an average life expectancy of $9 - 9\ 1/2$ years for those cheetahs that reach adulthood. This is four years more than in the model by Crooks et al. [26] and three years longer than calculated by Kelly et al. [60]. Still, this increase in adult survival is not sufficient to produce a growing population; the projected population growth rate, λ, is 0.998, indicating that in each 6 month interval the cheetah population decreases by 0.2% (Tables 2.2 and 2.3).
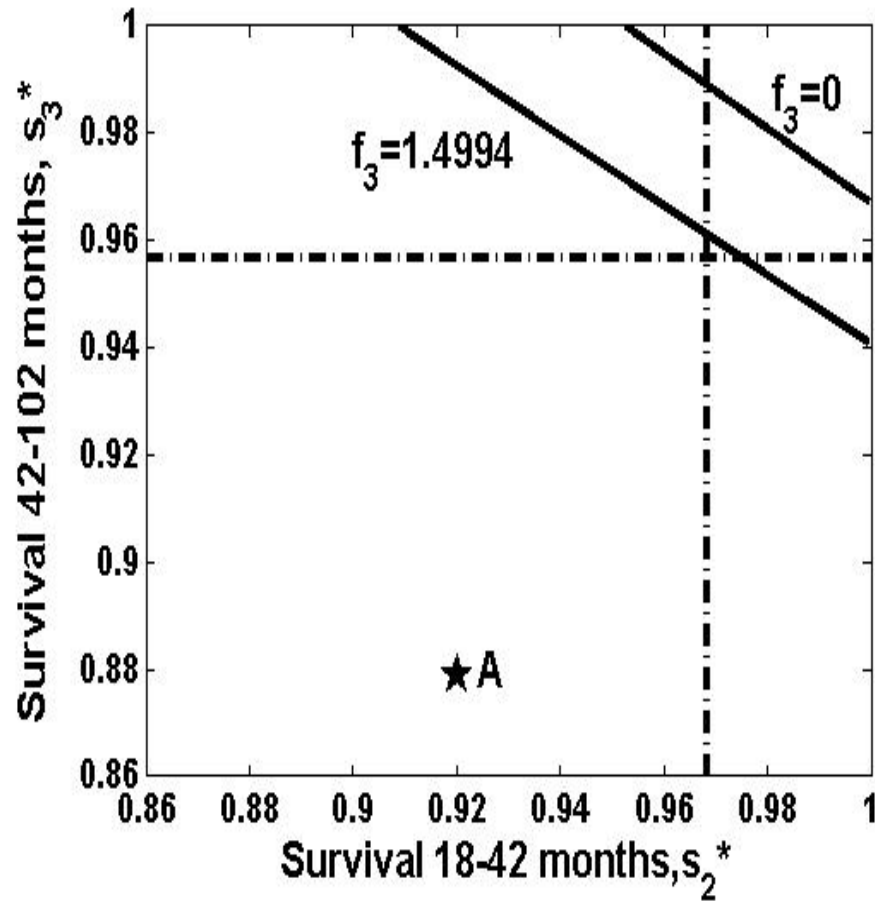
Figure 2.2: The effect of perturbing survivorships of $18 - 42$ month old adults and $42-102$ month old adults, where the $102+$ month old adult survivorships have been set to the biological limit ($s_{4}* = 0.898$). The solid curves denotes $\lambda = 1$ for two different fecundities of the $144-216$ month old cheetahs: $f_3 = 1.4994$ and $f_3 = 0$. Points above each of these curves produce positive growth; points below the curve produce negative growth. The horizontal line denotes the biological limit for the survivorship of $42-102$ months old adults ($s_{3}* = 0.9567$) and the vertical line denotes the biological limit for the survivorship of $18 - 42$ months old adults ($s_{2}* = 0.9685$). Point A marks the original, unperturbed survivorships ($s_2 = 0.92, s_3 = 0.879, \lambda = 0.9553$) reported by [26].

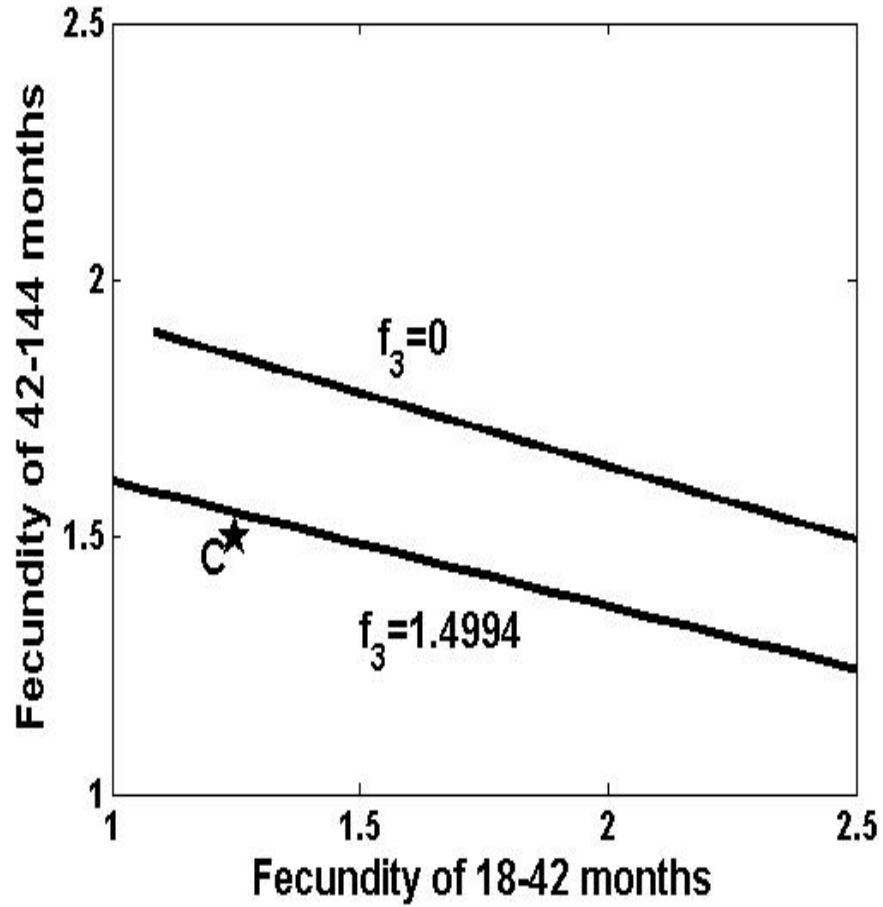Figure 2.3: Necessary fecundities required to achieve $\lambda = 1$ with all adult survivorships at their biological limits. The top curve sets the fecundity of $144 - 216$ month old to be zero ($f_3 = 0$). The bottom curve sets the fecundities of the $144 - 216$ month olds to be the same as the $42 - 102$ month old adults ($f_3 = 1.4994$). Point C shows the fecundities as calculated by Crooks et al. [26].
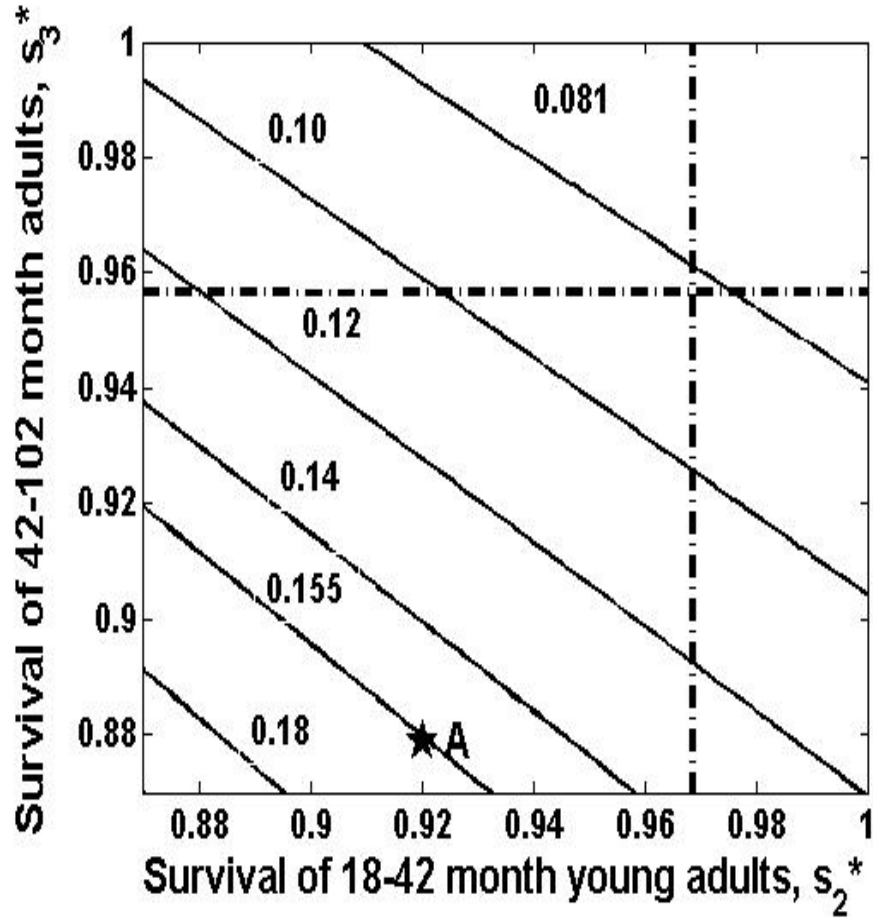
Figure 2.4: Contour graph of the perturbed survivorships of the $18 - 42$ month old adults, $42 - 102$ month old adults and $0 - 6$ month cubs. The contours are labeled by the $0 - 6$ month cub survivorship and describe the $18 - 42$ month and $42 - 102$ month survivorships necessary to achieve stasis ($\lambda = 1$). The heavy contour denotes calculated $0 - 6$ month cub survivorship ($s_0 = 0.081$). The horizontal line denotes the biological limit for the adult survivorship of $42 - 102$ month cheetahs ($s_3^* = 0.9567$). The vertical line denotes the biological limit in the $18 - 42$ month old cheetahs ($s_2^* = 0.9685$). Point **A** marks the original, unperturbed young and old adult survivorships as recorded in [26] ($s_2 = .92, s_3 = .879, \lambda = 0.9553$). In this case, the $0 - 6$ month cub survivorship must increase to 0.155 in order to obtain $\lambda = 1$.

Next I perturbed the survival of $18 - 42$ months old (s_2) and $42 - 102$ months old cheetahs (s_3) and graphed the growth-decline boundary as a function of these parameters.(Figure 2.2). Graphically, one can see how far different parameter combinations are from the $\lambda = 1$ curve. A discussion of how to quantify the distance between the chosen parameter combination and the $\lambda = 1$ curve is given in [77]. Only if both survival parameters increase to that of captive cheetahs, and if cheetah fecundity is not affected by senescence (e.g. fecundity of $12 - 18$ year old females does not differ from 4 year old ones) do the parameter values approach the $\lambda = 1$ curve (as indicated by the short distance to the $\lambda = 1$ curve). In a more realistic scenario, where females older than 12 years of age are assumed to be infertile, the distance to the $\lambda = 1$ curve is rather large. Hence within the biological meaningful parameter range it is highly unlikely to produce population stasis ($\lambda_{max} = 1$) by increasing adult survival alone (Figure 2.2). It is only possible to achieve a growing population by increasing adult survival to its biological limit if the fecundity of younger adults has been underestimated by Crooks et al. [26] (Figure 2.3).

Finally I explored the effect of increasing newborn survival (Figure 2.4), which is highly impacted by predators [13, 71]. My model suggests that increasing newborn survival from 0.081 to only 0.155, which is far below cub survival in captivity ($= 0.81$, Table 2.3), produces population stasis. The improvement in cub survival required to achieve population stasis decreases with increasing survival of older age classes.

2.3   Discussion

My results reveal that senescence plays an important role in the longevity of the captive adult cheetah. In the wild, the evidence for senescence is ambiguous [44, 104, 113] due to many reasons, including the fact that wild animals are subjected to predation,

injuries, and random environmental factors and hence rarely live to old age [24, 93]. Furthermore there is a lack of long-term monitoring which also contributes to the inability to quantify senescence [44, 76, 100]. Thus population projection matrices for wild animals rarely incorporate senescence into the model. In captivity, senescence is exhibited by increased mortality and decreased fecundity of older animals, which cannot be explained by random effects [24]. Since the survival of adult Serengeti cheetahs is already very close to the biological limit predicting the effect of increasing adult survivorship even further requires a model which takes senescence into consideration - to do otherwise will vastly overestimate adult survivorship and in turn, result in an overestimation of the population growth rate.

In this study I calculated the survivorships of the adult captive cheetah and used these to approximate the biological limit for the wild cheetah. Using captive reared animals to estimate biological limits assumes that hunting success of adult cheetahs (food availability) is independent of age and that diseases successfully treated in captivity have negligible survival consequences for wild animals. Since captive cheetahs have been known to live more than 15 years [82, 83, 84, 88], husbandry methods are not a restricting factor when determining the biological limit. I also assume that cheetahs older than 18 years were infertile. Using this model, I find that even increasing the survivorships of the wild adult cheetah to the biological limit does not result in an asymptotic growing population. Since it is highly unlikely the survivorship of the wild cheetah can reach and be sustained at these biological limits, a management strategy which only strives to increase adult survivorship will not result in a growing population.

My perturbation analysis of the model evaluated the effect of increasing the adult survivorship alone and then also in conjunction with increasing the $0 - 6$ month cub survivorship. Since there is uncertainty in all parameter estimates, where some

of these uncertainties maybe large, it is important to consider management options which will succeed in light of this uncertainty. Since I am interested in the effect of changes and/or uncertainty in two (or three) parameters, I use robustness methods described in Hodgson and Townley [55], Hodgson et al. [56], Deines et al. [30] and Lubben et al. [77]. I calculate the growth-decline boundary, i.e. the $\lambda = 1$ curve; the distance from model prediction to this curve is a measure of robustness (the larger the distance the larger the robustness). This perturbation analysis suggests that within the biological reasonable parameter space it is highly unlikely to produce a growing population by increasing adult survival alone. In contrast, increasing newborn survival to a fraction of its biological limit can achieve the management goal. The latter management strategy is robust to parameter uncertainty. The survivorship of Serengeti cubs is currently an order of magnitude smaller than both the biological limit and that of Namibian wild cubs where predation on cubs is not an issue [86]. In the Serengeti, cheetah predators are protected from culling, therefore it would be challenging to find effective management strategies ensuring better newborn survival. In addition, it is necessary to account for the relative costs of altering different parameters [4]. However these results clearly demonstrate that such strategies could dramatically improve the future prospects of Serengeti cheetah populations.

Chapter 3

The Growth-Decline Boundary of Integral Projection Models

3.1 Methods

As mentioned in the introduction, there is a class of integral operators, introduced in [41], of the form (1.4), for which there is an analog of the Perron-Frobenius Theorem. In particular, conditions on $\mathbf{A}$ are given in Theorem 1.0.9 which guarantee that (1.1) satisfies the conclusion of Proposition 1.0.1. These conditions are that $\mathbf{A}$ is *positive*, *compact*, and *u-bounded*. These three concepts were defined in the introduction.

As in the PPM case, an IPM operator $\mathbf{A}$ can usually be decomposed into the sum of a survival operator $\mathbf{A}_0$ and a fecundity operator $\mathbf{F}$. Furthermore, $\mathbf{F}$ can often be decomposed into a product $\mathbf{d}\mathbf{e}^T$: if $\mathbf{v}$ is a population vector, $\mathbf{e}^T\mathbf{v}$ is the total number of offspring from all states, and $\mathbf{d}$ distributes these offspring into the states. Therefore, $\mathbf{A} = \mathbf{A}_0 + \mathbf{d}\mathbf{e}^T$. Roughly speaking, any population where the state of the offspring is independent of the parents' state can be written in this manner. For instance, in a plant model, the seeds are the same independent of the size of the plant

that produced them.

If $\mathbf{A}$ is a positive, compact and u-bounded operator, then there are results for $\mathbf{A}$ which are analogous to Theorem 1.0.2 and Corollary 1.0.3. I assume a cone in the Banach space $\mathcal{B}$ has been defined, thus determining a definition of "positive": see Definitions 1.0.4, 1.0.5, 1.0.6 and 1.0.7 in the introduction.

Theorem 3.1.1. *Suppose that* $\mathbf{A}$ *is positive, compact and u-bounded and can be written as* $\mathbf{A} = \mathbf{A}_0 + \mathbf{d}\mathbf{e}^T$ *where*

1. $\mathbf{A}_0 : \mathcal{B} \to \mathcal{B}$ *is a positive linear operator;*

2. $\mathbf{d} : \mathbb{R} \to \mathcal{B}$, $\mathbf{e}^T : \mathcal{B} \to \mathbb{R}$, *and at least one of them is positive;*

If $\lambda > r(\mathbf{A}_0)$ *is an eigenvalue of* $\mathbf{A}$, *then* $\lambda = \lambda(\mathbf{A})$.

Proof: I first assume that $\mathbf{d}$ is positive. Suppose $\lambda > r(\mathbf{A}_0)$ is an eigenvalue of $\mathbf{A}$. Then for some nonzero $\mathbf{v} \in \mathbb{R}^n$,

$$(\mathbf{A}_0 + \mathbf{d}\mathbf{e}^T)\mathbf{v} = \lambda\mathbf{v}. \tag{3.1}$$

Since λ is not an eigenvalue of $\mathbf{A}_0$, I can re-arrange (3.1) to give:

$$\mathbf{v} = (\lambda\mathbf{I} - \mathbf{A}_0)^{-1}\mathbf{d}\mathbf{e}^T\mathbf{v}. \tag{3.2}$$

Note that if $\mathbf{e}^T\mathbf{v} = 0$, then (3.2) implies that $\mathbf{v} = 0$, which is a contradiction. Hence $\mathbf{e}^T\mathbf{v}$ or $-\mathbf{e}^T\mathbf{v}$ is a positive scalar. Without loss of generality assume that $\mathbf{e}^T\mathbf{v}$ is positive, since if $\mathbf{e}^T\mathbf{v}$ is not positive, I can replace $\mathbf{v}$ by $-\mathbf{v}$. Since $\lambda > r(\mathbf{A}_0)$, I can expand $(\lambda\mathbf{I} - \mathbf{A}_0)^{-1}$ in a power series:

$$(\lambda\mathbf{I} - \mathbf{A}_0)^{-1} = \frac{1}{\lambda}\left(\mathbf{I} + \frac{\mathbf{A}_0}{\lambda} + \frac{\mathbf{A}_0^2}{\lambda^2} + \ldots\right). \tag{3.3}$$

Since $\mathbf{A}_0$ is positive and $\mathbf{d}$ is positive, it follows that $\mathbf{A}_0^k\mathbf{d}$ is positive for all $k \geq 0$. Hence it follows from (3.3) that $(\lambda\mathbf{I} - \mathbf{A}_0)^{-1}\mathbf{d}$ is positive. Then (3.2) shows that $\mathbf{v}$ is also positive, i.e. it is in the cone. Hence λ is a positive eigenvalue of $\mathbf{A}$ with associated positive eigenvector $\mathbf{v}$. Hence by Theorem 1.0.9, λ must be the leading eigenvalue of $\mathbf{A}$, so $\lambda = \lambda(\mathbf{A})$. Since $\mathbf{A}$ is compact, its nonzero spectrum consists only of eigenvalues, so $\lambda(\mathbf{A}) = r(\mathbf{A})$.

If $\mathbf{d}$ is not positive but $\mathbf{e}^T$ is positive, I can apply the result to the adjoint $\mathbf{A}^*$ of $\mathbf{A}$. We denote the adjoint of $\mathbf{d}$ by $\mathbf{d}^T$ and the adjoint of $\mathbf{e}^T$ by $\mathbf{e}$. Then the result follows immediately from the facts that $\mathbf{A}^* = \mathbf{A}_0^* + \mathbf{e}\mathbf{d}^T$, $r(\mathbf{A}_0^*) = r(\mathbf{A}_0)$, and $\lambda(\mathbf{A}^*) = \lambda(\mathbf{A})$.

$\square$

Now suppose $\mathbf{A} = \mathbf{A}(p_1, p_2, \ldots p_m)$. We now can identify the set of admissible parameters $\mathcal{P}$ as those $(p_1, p_2, \ldots p_m)$ such that $\mathbf{A}(p_1, p_2, \ldots p_m)$ satisfy the hypotheses of Theorem 3.1.1. It follows immediately that Corollary 1.0.3 is also true for $\mathbf{A}$ which satisfy the hypotheses of Theorem 3.1.1.

3.2 Results

I will apply our methods to a model, originally given in Ellner and Rees [41], for the thistle *O. illyricum*, which can be wriiten in the form (1.4). I will consider the effect that three of the parameters in the fecundity kernel have on $\lambda(\mathbf{A})$.

O. illyricum is a monocarpic perennial across its entire current range [102]. It flourishes in fertile soils and is adapted to warmer climate with dry summers [8]. Reproduction only occurs by seed, and seeds remain viable in the seed bank for many years [46]. In its native range *O. illyricum* is attacked by a large variety of insect species (129 insect species feed on Onopordum spp. in Europe [9]), but in its introduced range like Australia, insect herbivores play a minor role in *O. illyricum* pop-

ulation dynamics. This thistle became a noxious weed in Australia after widespread pasture improvements (fertilization) [49].

The population distribution of *O. illyricum* at time t, $n(x, a, t)$, is a function of the plant size x, and the age of the plant a. The plant size is a continuous variable taking on values between 0 and M_s, the maximum size, whilst the age is a discrete variable which can take on values in $\{0, 1, \ldots, M_a\}$, where M_a is the maximum age. Let $\Omega = \{(x, a) \mid x \in [0, M_s], \ a \in \{0, 1, \ldots, M_a\}\}$, and let $d(x, a)$ denote the product measure on Ω with Lebesgue measure in x and discrete measure in a (i.e. integrate over x and sum over values of a). The kernel k in (1.4) can be written $k = p + f$, where p is the "growth and survivorship kernel" and f is the "fecundity kernel". The kernel describes how to get from state (x, a) to state (y, b), hence is a function of (y, x, b, a). The population model can be written as $\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t)$: here $\mathbf{A}$ is the operator defined on the Banach space

$$\mathcal{B} = L_1(\Omega) = \left\{ v(\cdot, \cdot) \mid \int_0^{M_s} |v(x, b)| \, dx < \infty \text{ for all } b = 0, 1, 2, \ldots M_a \right\}$$

given by

$$(\mathbf{A}v)(y, b) = \int_\Omega (p(y, x, b, a) + f(y, x, b, a))v(x, a)d(x, a). \tag{3.4}$$

Expanding the product measure, (3.4) becomes

$$(\mathbf{A}v)(y, b) = \sum_{a=0}^{M_a} \int_0^{M_s} (p(y, x, b, a) + f(y, x, b, a))v(x, a)dx.$$

The population vector $\mathbf{n}(t) = n(\cdot, \cdot, t)$ is a vector in $\mathcal{B}$ for each t.

The growth and survivorship kernel $p(y, x, b)$ is given by

$$p(y, x, b, a) = s(x, a) \left[1 - p_f(x, a)\right] g(y, x)\delta_{a,b-1}(1 - \delta_{b,0}), \tag{3.5}$$

with component terms as follows: $s(x, a) > 0$ is the yearly survivorship of a plant of size x and age a into a plant of size x and age $a + 1$; the Kronecker delta function δ_{ij} equals 1 if $i = j$, else it equals 0; the growth of a plant from size x to size y is given by $g(y, x) > 0$; and $p_f(x, a)$ is the probability of the plant of size x and age a to flower in a year. Since *O. illyricum* is a monocarpic perennial, flowering results in death. Consequently $1 - p_f(x, a) > 0$ reflects the probability of the plant not flowering. The term $\delta_{a,b-1} = 1$ when $a = b - 1$, i.e. when plants are moving from one age class into the next. This prevents plants from aging more than one year at a time and also prevents them from getting younger with time. Since plants do not grow and survive into age 0, $1 - \delta_{b,0}$ prevents this possibility. (For simplicity, these functions were not included in the original model in Ellner and Rees (2006).) Hence the growth and survival operator $\mathbf{A}_0$ is given by

$$(\mathbf{A}_0 \mathbf{v})(y, b) = \int_\Omega s(x, a) \left[1 - p_f(x, a)\right] g(y, x) \delta_{a,b-1} (1 - \delta_{b,0}) v(x, a) \; d(x, a). \qquad (3.6)$$

The fecundity kernel $f(y, x, b, a)$ contains three underlying parameters, p_e, p_1 and p_2, whose uncertainty can have a broad impact on the asymptotic population growth rate. Here, p_e is the probability of seedling establishment and $e^{p_1 + p_2 x}$ is the number of seeds per adult of size x. Since the model assumes that the state of the offspring is independent of the parents, new plants are distributed into size classes according to the probability distribution $\phi(y) > 0$. The kernel f is therefore given by

$$f(y, x, b, a) = s(x, a) p_f(x, a) p_e e^{p_1 + p_2 x} \phi(y) \delta_{b,0}. \qquad (3.7)$$

The total number of offspring produced by the population distribution $\mathbf{n}(x, b, t)$ at

time t is

$$(\mathbf{e}^T\mathbf{n})(t) = \int_\Omega s(x,a)p_f(x,a)p_e e^{p_1+p_2x}n(x,a,t) \ d(x,a). \tag{3.8}$$

These offspring are then distributed into size classes described by the vector $\mathbf{d} \in \mathcal{B}$ given by

$$\mathbf{d} = \phi(\cdot)\delta_{b,0}, \tag{3.9}$$

that is, $\mathbf{d}(1)$ is represented by the function which is $\phi(y)$ when $b = 0$ and is 0 otherwise. Thus the population distribution at time $t+1$ is

$$\mathbf{n}(t+1) = \mathbf{A}(\mathbf{n}(t)) = (\mathbf{A}_0 + \mathbf{de}^T)(\mathbf{n}(t)). \tag{3.10}$$

We need to verify that this system satisfies the condition in Theorem 3.1.1. The cone K used in Theorem 1.0.9 is the set of all positive functions $v(x,a)$ on Ω. In this example, the operator $\mathbf{A}_0 : \mathcal{B} \to \mathcal{B}$ is nilpotent, i.e. there is a positive integer m such that $\mathbf{A}_0^m = 0$. This is because $\mathbf{A}_0$ advances the age of the population distribution, and in the absence of any population input the population will die off in finite time. Nilpotent operators are well-known to have spectral radius 0, i.e. $r(\mathbf{A}_0) = 0$. An integral projection model which does not advance the age of the species may or may not have this decomposition into a nilpotent $\mathbf{A}_0$. The vector $\mathbf{d} \in \mathcal{B}$, and the operators $\mathbf{e}^T : \mathcal{B} \to \mathbb{R}$, $\mathbf{A}_0$ and $\mathbf{A}$ are clearly positive. The kernel $k(y,x,b,a) = p(y,x,b,a) + f(y,x,b,a)$ is bounded on a bounded set $[0, M_s] \otimes \{0, 1, \ldots, M_a\}$, so by the Hilbert-Schmidt theorem $\mathbf{A}$ is compact (see Bachman and Narici, 1966). It is proved in Ellner and Rees (2006) that $\mathbf{A}$ is u-bounded. Therefore, this system satisfies the hypotheses of Theorem 1.0.2 with $r(\mathbf{A}_0) = 0$, so I can conclude that any positive eigenvalue of $\mathbf{A}$ is in fact the leading eigenvalue. $\mathbf{A}$ satisfies the conditions of Theorem 1.0.2 for any positive p_e, p_1 and p_2. In addition, since p_e is a probability,

the set, $\mathcal{P}$, of admissible parameters is $\{(p_e, p_1, p_2) \mid p_e \in [0,1], p_1 > 0, p_2 > 0\}$.

Remark 3.2.1. *The kernel k in the model given in Ellner and Rees (2006) also depends on the quality q, which represents the variability between plants and is assumed to be constant throughout each plant's lifespan. To add this dependence to the model here would only require including a distribution function $\beta(q)$ to the operator $\mathbf{d}$ which distributes the newborns into quality classes much like $\phi(y)$ distributes the newborns into size classes.*

The probability of seedling establishment, p_e, cannot be calculated accurately due to the presence of a seed bank, so I expect substantial uncertainty in the value of this parameter. Suppose p_e has a nominal value of 0.025. (Note that while in Ellner and Rees (2006), $p_e = 0.025$, they use the value 0.03 in their computer code.) I take the nominal value of the fecundity intercept, p_1, to be -11.84, and the nominal value of the fecundity slope, p_2, to be 2.27. Both of these calculated numbers have the following standard errors as given in Ellner and Rees (2006): 4.43 for the fecundity intercept and 0.60 for the fecundity slope. Thus the seed production per plant has a wide range of possibilities.

I first consider the effect of p_e and p_1 on $\lambda(\mathbf{A})$, which is an easy case, since both variables can be pulled out of the integral defining $\mathbf{e}^T$. In particular, I can write

$$\mathbf{e}^T = p_e e^{p_1} \mathbf{e}_p^T, \quad \text{where } \mathbf{e}_p^T \mathbf{v} = \int_\Omega e^{p_2 x} p_f(x, a) s(x, a) v(x, a) \ d(x, a).$$

For now I assume that p_2 is fixed at its nominal value.

Theorem 3.2.2. *Suppose that $\lambda > 0$ is an eigenvalue of $\mathbf{A}$. Then*

$$p_e = \left(\frac{\lambda}{\gamma}\right) e^{-p_1}, \tag{3.11}$$

where

$$\gamma = \mathbf{e}_p^T \left(\mathbf{I} + \frac{\mathbf{A}_0}{\lambda} + \frac{\mathbf{A}_0^2}{\lambda} + \cdots + \frac{\mathbf{A}_0^{m-1}}{\lambda} \right) \phi. \tag{3.12}$$

Proof Suppose that $\lambda > 0$ is an eigenvalue of $\mathbf{A}$ with eigenvector $\eta \in \mathcal{B}$. Then

$$(\mathbf{A}_0 + \mathbf{d}\mathbf{e}^T)\eta = \lambda\eta. \tag{3.13}$$

Let $\mathbf{I} : \mathcal{B} \to \mathcal{B}$ be the identity operator, and note that $(\lambda\mathbf{I} - \mathbf{A}_0)^{-1}$ is a bounded operator since $\mathbf{A}_0$ is a compact operator with $r(\mathbf{A}_0) = 0$. After some algebraic manipulation,

$$(\lambda\mathbf{I} - \mathbf{A}_0)^{-1}\mathbf{d}\mathbf{e}^T\eta = \eta,$$

which implies that

$$\mathbf{e}^T(\lambda\mathbf{I} - \mathbf{A}_0)^{-1}\mathbf{d}\mathbf{e}^T\eta = \mathbf{e}^T\eta. \tag{3.14}$$

If the scalar $\mathbf{e}^T\eta = 0$, then (3.13) implies that λ is an eigenvalue of $\mathbf{A}_0$, which is not possible. Hence $\mathbf{e}^T\eta$ is a nonzero scalar and we can divide (3.14) by $\mathbf{e}^T\eta$ to obtain

$$\mathbf{e}^T \left(\mathbf{I} - \frac{\mathbf{A}_0}{\lambda} \right)^{-1} \mathbf{d}(1) = \lambda. \tag{3.15}$$

Since $\mathbf{A}_0^m = 0$, expanding (3.15) gives

$$\lambda = p_e e^{p_1}\mathbf{e}_p^T \left(I - \frac{\mathbf{A}_0}{\lambda} \right)^{-1} \mathbf{d}(1) = p_e e^{p_1}\mathbf{e}_p^T \left(I + \frac{\mathbf{A}_0}{\lambda} + \frac{\mathbf{A}_0^2}{\lambda} + \cdots + \frac{\mathbf{A}_0^{m-1}}{\lambda} \right) \mathbf{d}(1). \tag{3.16}$$

Note that $\mathbf{d}(1) = \phi(y)$, a probability distribution, to get (3.12). Therefore we can solve for p_e in terms of p_1 to get (3.11). $\qquad\square$

Note that γ is a real number which can be accurately approximated numerically.

If there is a particular asymptotic growth rate $\lambda > 0$ which is desired, Theorem 3.2.2 gives a formula for the curve of (p_1, p_e) values which lead to λ.

Figure 3.1 shows the curves $\{(p_1, p_e)|\lambda(p_1, p_e) = \alpha\}$ for α increasing from 0.70 to 1.3 in 0.1 increments. The nominal point computed in Ellner and Rees (2006) is $(-11.84, 0.025)$, which leads to $\lambda = 0.9878$. One can see from both the figure and from (3.16) that λ varies considerably more with larger uncertainties in the fecundity intercept p_1 than with large uncertainties in the probability for seedling establishment p_e. The graphs shows the range of p_1 within its standard error of the nominal value. In this range the variation in λ includes both values signifying dramatic asymptotic decay and values signifying dramatic asymptotic growth. Thus I do not consider λ to be robust with respect to large changes in p_1. Since the probability of seedling establishment was not measured directly (see Ellner and Rees (2006)), it is unclear whether λ is robust to changes in p_e within the unknown standard error. If p_e remains within 25% of its current values, i.e. between 0.019 and 0.031 and if the fecundity intercept remains fixed at its nominal value, -11.84, λ varies by less than 0.10. Yet if p_e increases by as much as 50% to 0.375, then λ increases by approximately 0.10. Likewise, if p_e decreases by 50% to 0.0125, then λ decreases by almost 0.20. Hence λ is more robust to increases in p_e than to decreases to p_e.

I now consider simultaneous variation in the fecundity intercept p_1, fecundity slope p_2 and probability of seedling establishment p_e. This is more difficult computationally, since p_2 cannot be pulled out of the integral defining $\mathbf{e}^T$. I use the same derivation as above, but now γ in (3.12) is the function, $\gamma(p_2)$, which needs to be calculated for every p_2. I can solve for p_e in terms of p_1 and $\gamma(p_2)$. Figure 3.2 shows the surface $\{(p_e, p_1, p_2)|\lambda(p_e, p_1, p_2) = 1\}$ for a range of admissible (p_e, p_1, p_2). This surface divides the (p_e, p_1, p_2) parameter space into those parameters above the surface, which lead to asymptotically increasing population, and those parameters below
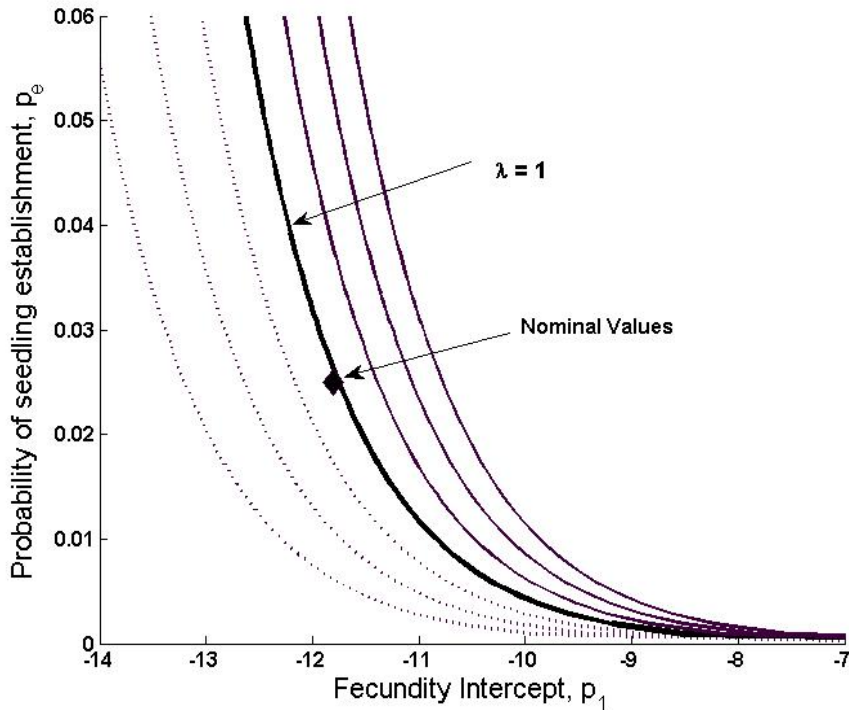
Figure 3.1: The curves show values of (p_1, p_e) for which $\lambda = .70, .80, .90, 1.0, 1.1, 1.2$, decreasing in value to the left of the $\lambda = 1$ curve and increasing in value to the right. The black diamond marks the nominal point $(-11.84, 0.025)$

the surface, which lead to asymptotic decreasing population, i.e. this is the growth-decline boundary. Notice that as p_1 and p_2 decrease within the standard error, p_e must increase exponentially to maintain $\lambda(p_e, p_1, p_2) = 1$, and eventually increases above 1, an impossibility for a probability. Figure 3.3 shows the $\lambda = 1$ contours for $p_e = .01, .03, .10, .30, .60$, and 1.0. The black diamond marks the nominal values of $(p_1, p_2) = (-11.84, 2.27)$. On the graph, one can see that if p_1 and/or p_2 are increased slightly, p_e needs only to decrease slightly in order to maintain $\lambda = 1$. On the other hand, if p_1 and/or p_2 are decreased slightly, p_e must increase to a much greater value in order to maintain $\lambda = 1$. Thus our graph shows λ is not robust at all to decreases in p_1 and p_2 and to increases in p_e.
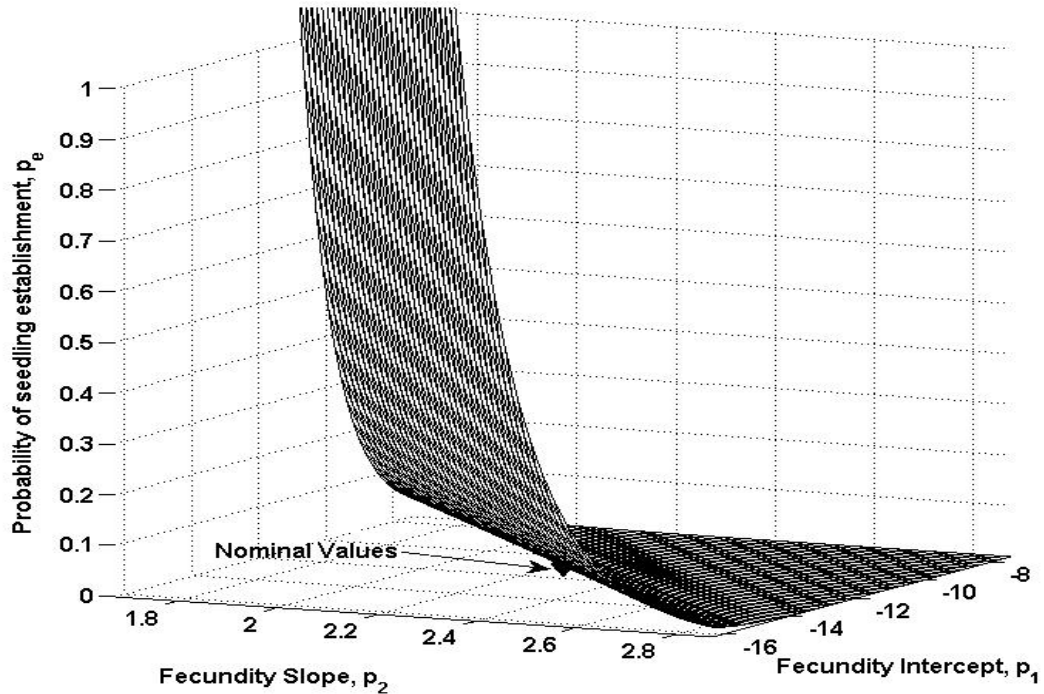
Figure 3.2: The parameter space of fecundity intercept p_1, fecundity slope p_2 and probability of seedling establishment p_e for $\lambda = 1$.

3.3 Discussion

Extending the theory given by Boeckner in [77], I identify a class of PPM's (e.g. see Chapter 2) and IPM's for which the growth-decline boundary $\lambda = \rho$ is given precisely by those parameters for which ρ is *an* eigenvalue. This means I can determine the growth-decline boundary simply by evaluating the parameterized characteristic function evaluated at $\rho = 1$. I must assume a decomposition of the parameterized operator in terms of an operator $\mathbf{A}_0$ whose dominant eigenvalue we know to be less than ρ, and a second operator which can be decomposed into two separate operators: one from the Banach space into $\mathbb{R}$ and the other from $\mathbb{R}$ into the Banach space. The existence of such a decomposition very often follows immediately from the construction of the
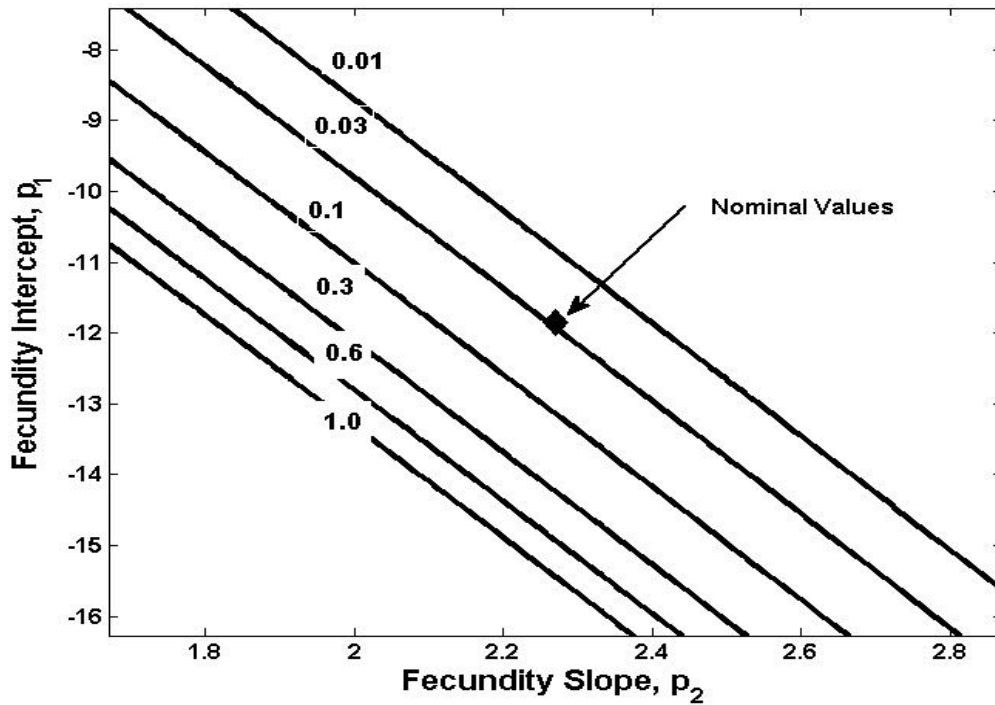
Figure 3.3: The contours are the $\lambda = 1$ curves for various values of the probability of seedling establishment p_e. The nominal values for the fecundity intercept and fecundity slope are indicated by the black diamond.

PM, and is ecologically natural. For instance, for Leslie matrices $\mathbf{A}_0$ is obtained by zeroing out the fecundities so that $\mathbf{A}_0$ has dominant eigenvalue $\lambda = 0$. For an IPM, $\mathbf{A}_0$ would be the operator containing only the growth and survival kernel. In fact, any PPM or IPM whose population advances to a new age class at every time step until it reaches some maximum age and then dies, will have nilpotent $\mathbf{A}_0$, so $r(\mathbf{A}_0) = 0$. This is true for a Leslie matrix, for my PPM example in Chapter 2 and in my IPM example in this chapter. Thus, as a special case, I get the familiar result that any PM which can be written in the general form of $\mathbf{A} = \mathbf{A}_0 + \mathbf{d}\mathbf{e}^T$, with nilpotent $\mathbf{A}_0$, will have only one positive eigenvalue.

Having identified the growth-decline boundary in such analytically simple terms,

I can then explore how "close" the nominal values are to the boundary as one, two or even all parameters are varied. Additionally, the growth-decline boundary shows the interconnectedness between all of the parameters. A management action increasing one parameter value may also have the benefit of moving the nominal point far enough on the other "side" of the $(\lambda = 1)$-hypersurface, that the uncertainties in the other parameters are no longer a major concern. Thus, in this case even with the uncertainties in the other parameters, population growth (or decline) is robust.

While this method does not explicitly address stochastically varying environments, it does allow for analysis of spatially and temporally varying environments when this variation is within some tolerance level. For example, in environments which vary slightly, the stochastic contribution to the variance of the parameters can be treated like a parameter uncertainty. These methods then can be applied in the same way as we did in [77], where the data uncertainty is due to spatial variation. If the environments vary considerably, such as in the case of hurricanes, fires or other catastrophes, then our method would not give useful information since the parameter variation is too large. However, in this case, sensitivity methods may also not be accurate [56, 95]. Our methods also do not take into consideration possible density-dependence.

Despite these shortcomings mentioned in the previous paragraph, this method generates a clear growth-decline boundary for PPMs and IPMs and points conservation managers towards a strategy which can be robust in the face of the uncertainty in more than one parameters.

Chapter 4

Effect of Temperature on Transient Dynamics

4.1 Introduction

I constructed two models to study the effect of temperature on transient dynamics. As mentioned in the introduction, one is a function of ordinal time, measured in days, and one is a function of physiological time, measured in degree days. Both are variations of a continuous time model given in [10]:

$$
n(a,t) = \begin{cases} n(a-t,0)\dfrac{s(a)}{s(a-t)} & a > t \\[2ex] b(t-a)s(a) & a < t, \end{cases} \tag{4.1}
$$

where $n(a,t)$ is the population density of age a at time t, $s(a)$ is the probability an aphid will survive to age a, and $b(t)$ are the births at time t. The first line is the number of aphids alive at $t = 0$ and still alive at time t. The second line is the number of aphids born at time $t - a$ who survived to age a. This model is shown in [66] to

be equivalent to the McKendrick-von Foerster PDE:

$$\frac{\partial n}{\partial a} + \frac{\partial n}{\partial t} = -\mu(a)n, \tag{4.2}$$

where $\mu(a)$ is the per capita mortality rate of an aphid of age a. The relationship between $\mu(a)$ and $s(a)$ is derived by first performing a change of variables. Let $a = \xi$ and $t = \xi + \nu$. Thus

$$\frac{\partial a}{\partial \xi} = \frac{\partial t}{\partial \xi} = 1$$

and

$$\frac{\partial n}{\partial \xi} = \frac{\partial n}{\partial a}\frac{\partial a}{\partial \xi} + \frac{\partial n}{\partial t}\frac{\partial t}{\partial \xi} = \frac{\partial n}{\partial a} + \frac{\partial n}{\partial t} = -\mu(\xi)n.$$

Thus

$$\frac{dn}{n} = -\mu(\xi)d\xi.$$

Let $a \leq t$ and consider following one cohort of aphids as they age from 0 to ξ. Then

$$\int_{n(0,\nu)}^{n(\xi,\nu)} \frac{d\widetilde{n}}{\widetilde{n}} = -\int_0^\xi \mu(\widetilde{\xi})d\widetilde{\xi},$$

$$\Rightarrow \quad \frac{n(\xi,\nu)}{n(0,\nu)} = \exp\left(-\int_0^\xi \mu(\widetilde{\xi})d\widetilde{\xi}\right).$$

Next, convert back to the original variables to obtain

$$\frac{n(a,t-a)}{n(0,t-a)} = \exp\left(-\int_0^a \mu(\widetilde{a})d\widetilde{a}\right),$$

$$\Rightarrow \quad s(a) = \exp\left(-\int_0^a \mu(\widetilde{a})d\widetilde{a}\right).$$

Pea aphids, *Acyrthosiphon pisum*, are ideally suited to study the effect of temperature on transient dynamics because they have a short generation time and all vital

rates (developmental time, fecundity and survival) are largely influenced by temperature [11, 12, 57, 63, 70, 97, 112]. Pea aphids are viviparous (give birth to live nymphs) and parthenogenic (reproduce asexually) [31]. In their natural environment, it is only until temperatures in the fall begin to dip that aphids produce eggs which survive until spring. The nymphs develop through four instars before reaching adulthood. If environmental conditions deteriorate as a result of high aphid density or decreasing host plant quality an increasing proportion of migrants are born; migrants develop wings in the adult stage (alate morphs) and disperse to better habitats [31]. Under good rearing conditions (e.g. good plant quality and low densities) the proportion of winged ahids is very small [31]; thus in my experiments I exclusively used wingless (apterae) morphs.

4.1.1 Model Construction

I will reference the model where time is measured in (ordinal) days by the "ordinal day", or OD, model. I will reference the second model, where time is measured in degree days as the "degree day", or DD, model. The difference between my two models and that given by (4.1) above is the maternity function, i.e. the number of offspring per unit time. In my models, the maternity function is not only a function of time, but also a function of time from the onset of reproduction. Thus the population is now a function of age, time and time since onset of reproduction where age is measured in the same units as time, either in ordinal days or degree days.

Let r be the time since onset of reproduction. The population as a function of r can be considered a step function. Nonreproducing aphids are assigned a constant, negative r value ($r = -1$) until they begin to reproduce at which point r is reassigned to $r = 0$. Once $r \geq 0$, r increases with time. Thus my OD model is

$$n(a,r,t) = \begin{cases} n(a-t,r-t,0)\dfrac{s(a)}{s(a-t)} & a > t, \ r > t \\[2mm] n(a-t,t-r,0)\dfrac{s(a)}{s(a-t)} & a > t, \ 0 \leq r \leq t \\[2mm] n(a-t,r,0)\dfrac{s(a)}{s(a-t)} & a \geq t, \ r = -1 \\[2mm] n(a-r,0,t-r)\dfrac{s(a)}{s(a-r)} & 0 \leq r < a < t \\[2mm] n(0,r,t-a)s(a) & a < t, \ r = -1. \end{cases} \qquad (4.3)$$

The first line is the number of reproducing aphids alive at $t = 0$ and still alive at time t. The second line is the number of nonreproducing aphids alive at time $t = 0$ who begin to reproduce at time $t - r$ and are still alive at time t. The third line is the number of nonreproducing aphids alive at $t = 0$ who have not yet begun to reproduce by by time t, and are still alive at time t. The fourth line is the number of reproducing aphids born at time $t - a$, who, at the age of $a - r$ began reproducing at time $t - r$ and are still alive at time t. The last line is the number of nonreproducing aphids born at time $t - a$ who are still alive at time t. Since I am modeling the invasion by a single invading, reproducing aphid, the number of reproducing aphids alive at $t = 0$ is 1, while there are no nonreproducing aphids alive at $t = 0$ except those born at time $t = 0$. For the DD model, t is replaced by $\tilde{t}$, the time measured in degree days.

In order to solve (4.3) numerically, it is best to think of beginning at time, $t = 0$, and marching forward in infinitesimal time steps of δt. Note that if $r \geq 0$, $\delta t = \delta a = \delta r$, otherwise $\delta r = 0$.

Theorem 4.1.1. *The model given by (4.3) can be programmed on the computer by using:*

$$n(a + \delta a, r + \delta r, t + \delta t) = \frac{s(a + \delta a)}{s(a)} n(a, r, t). \qquad (4.4)$$

Proof: I will prove the first case (i.e. the first line) in (4.3) above, the others are similar. Assume $a > t$ and $r > t$. Thus $\delta a = \delta r = \delta t$ and

$$n(\widetilde{a} + \delta a, r + \delta r, t + \delta t)$$

$$
\begin{aligned}
&= n(a + \delta a - t - \delta t, r + \delta r - t - \delta t, 0) \frac{s(a + \delta a)}{s(a + \delta a - t - \delta t)}, \quad \text{by (4.3)}, \\
&= n(a - t, r - t, 0) \frac{s(a + \delta a)}{s(a - t)}, \\
&= n(a - t, r - t, 0) \left(\frac{s(a)}{s(a - t)} \right) \left(\frac{s(a + \delta a)}{s(a)} \right), \\
&= n(a, r, t) \frac{s(a + \delta a)}{s(a)}, \quad \text{by (4.3)}.
\end{aligned}
$$

$\square$

The model's initial condition is

$$
n(a, 0, 0) = \begin{cases} 1 & \text{for } a = \widehat{a}, \text{ where } \widehat{a} \text{ is the age of the initial invading aphid} \\ 0 & \text{otherwise.} \end{cases} \tag{4.5}
$$

and first of the two boundary conditions is

$$
n(0, -1, t) = \left[\int_0^t \int_0^R m(r) n(a, r, t) \, dr \, da \right] + m(t) n(\widehat{a} + t, t, t) \delta a, \tag{4.6}
$$

where $m(r)$ is the maternity function as a function of days from the onset of reproduction and R the maximum time of the aphids' reproductive period. The first term in (4.6) above is the number of births by aphids born after time $t = 0$. The second term is the number of births by the initial invading aphid of age $\widehat{a} > t$. Since I assume this initial aphid begins to reproduce at $t = 0$, the time since its onset of reproduction is just t.

The boundary condition from when $r = -1$ to when r changes to $r = 0$, i.e. when an aphid first begins to reproduce, is given by

$$n(a + \delta a, 0, t + \delta t) = \frac{s(a + \delta a)}{s(a)} p_r(a) n(a, -1, t), \tag{4.7}$$

where $p_r(a)$ is the probability that an aphid of age a who has not started to reproduce will begin to reproduce by age $a + \delta a$.

Due to continuity, as $\delta t \to 0$ the numerical solution converges uniformly to the model given in (4.3). A flow chart for the computer program of this model is given in Figure 4.1 and the computer code is given in Appendix C.

4.1.2 Experimental Design and Methods

I conducted all the experiments in two temperature controlled rooms monitored every 5 minutes using Onset Corporation's HOBO U-012 data loggers (accuracy $\pm 0.35°C$). The experiments were carried out on alfalfa (*Medicago sativa* L., cv. 'Vernal') plants with 3-4 plants per 12.5 cm diameter pot. The same plant-aphid system has been used in other demographic models [48, 117]. The particular model in [117] suggests the occurrence of transient dynamics following a dispersal event of aphids, but none of them incorporates the effect of temperature on transient dynamics. The temperatures of the rooms were set at $20°C$ and $25°C$. Grow lights were set to a 16L:8D photoperiod. The relative humidity could not be controlled in our experiments, and varied significantly between summer and winter. Because the relative humidity influenced survivorship and fecundity I conducted experiments both in the summer ("medium" humidity) and winter ("low" humidity). The data loggers were placed under radiation shields near the alfalfa plants. An average daily temperature was determined by the 24-hr average of the readings from the data loggers. The two rooms used were
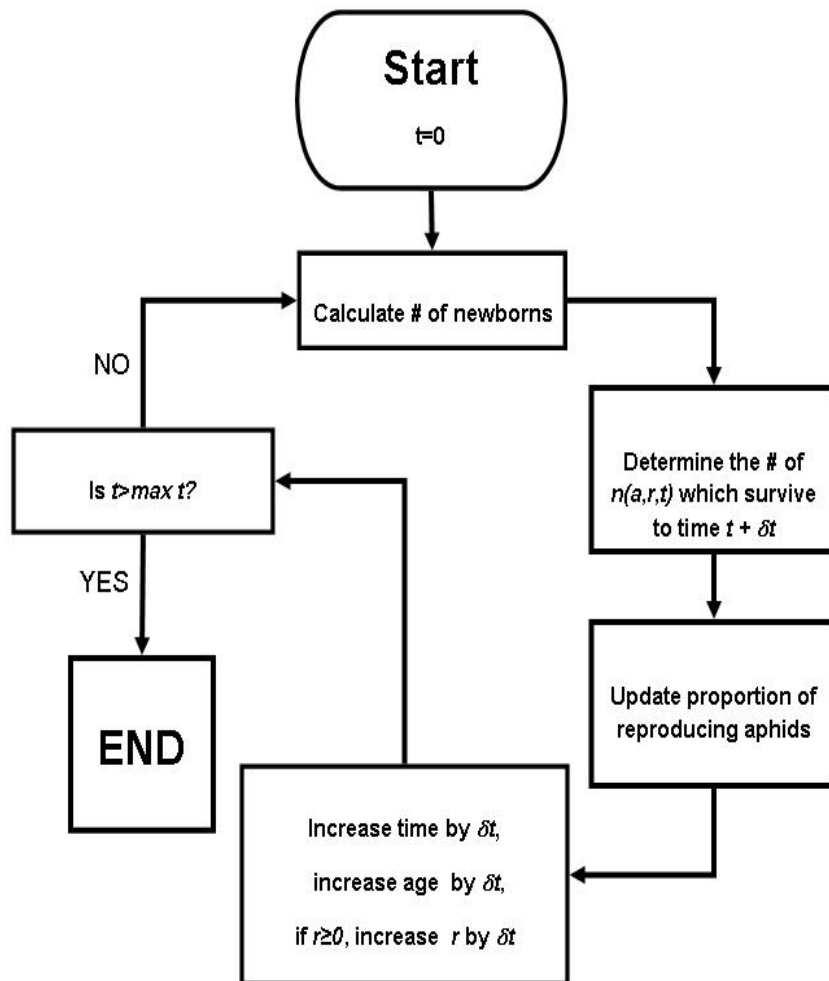
Figure 4.1: Schematics for logic flow of both models.

approximately 8.5 square meters in size and approximately square in shape.

To determine survivorship/fecundity parameters, two wingless adult aphids were placed in each clip cage (4 cm diameter) and attached to $25-35$ day old alfalfa plants. Up to 4 clip cages were used per pot of $3-4$ alfalfa plants. Seven hours later, I removed all aphids but one newborn from the clip cages. Using two adult aphids increased the probability that the clip cage would contain at least one newborn when inspected. Clip cages were monitored daily, ± 1 hours, for survivorship and fecundity and newborns were removed after counting. Each clip cage was numbered, so that I could record the fate of individual aphids from birth until death.

Next I conducted population count experiments to validate our model predictions. Because the initial population state affects transient dynamics [64] and because an aphid's fecundity is highly age dependent [6, 12], I started the experiments with aphids that newly entered the reproductive stage. I reared aphids of known age using clip cages as described above. Once aphids were 5-7 days old I transferred them to plants in larger cages with one aphid. The number of aphids was counted daily (± 3 hours) with more plants added as necessary to prevent density dependence. The change in aphid numbers was recorded in 12 cages (two runs each of 6 cages) in the low temperature, medium humidity room and in another 12 cages (two runs each of 6 cages) in the high temperature, low humidity room. Humidity was not held constant because of logistical reasons which required the experiments to be spread out over summer and winter.

Estimating Model Parameters

Clip cages were monitored daily (± 1 hours), for survivorship and fecundity. The

Table 4.1: Mean Temperatures and Humidities with 95% confidence intervals

Experiment	Temp	Mean Temp $°C$	Min Temp$°C$	Max Temp$°C$	Humidity	Mean Humidity	Min Humidity	Max Humidity
Survival/Fecundity	Low	$19.85 \pm .004$	18.0	21.3	Low	$33.11 \pm .118$	16.17	52.7
Survival/Fecundity	Low	$19.49 \pm .004$	18.6	20.84	Medium	$51.7 \pm .106$	38.0	69.68
Population Growth – Run #1	Low	$19.59 \pm .012$	18.37	20.58	Medium	$40.60 \pm .166$	29.55	72.43
Population Growth – Run #2	Low	$20.29 \pm .012$	19.20	21.18	Medium	$46.7 \pm .170$	35.5	65.61
Survival/Fecundity	High	$24.52 \pm .019$	20.53	26.33	Low	$38.46 \pm .172$	18.04	61.33
Survival/Fecundity	High	$24.57 \pm .006$	23.47	28.25	Medium	$50.75 \pm .146$	27.37	69.58
Population Growth – Run #1	High	$24.87 \pm .011$	23.09	26.92	Low	$27.47 \pm .152$	12.45	51.47
Population Growth – Run #2	High	$24.94 \pm .008$	23.81	26.33	Low	$26.74 \pm .114$	16.92	42.50

initial aphid density was 73 and 69 newborns respectively for the $20°C$ and $25°C$ experiments. Of these initial newborns, 45 and 51 survived to reproduce offspring in the $20°C$ and $25°C$ experiments respectively.

Table 4.1 lists the mean temperatures and mean humidities with 95% confidence intervals. Overall, the temperature remained constant except for brief fluctuations when the lights turned on and off. For the survival/fecundity experiment at high temperature and low humidity, the heat was shut off in the building 21 days after the beginning of the experiment, resulting in increased fluctuations in the temperature during the later part of the experiment. This had only a small effect on estimating model parameters because at that point aphid daily reproduction is only 25% of the daily reproduction during the first week of entering the reproductive period, and 43% of aphids had already died at that point. This agrees with data presented in [12] who found that in this temperature range, aphids begin to reproduce when just $6.6 - 14.5$ days old. Hence it is assumed that this instability in the temperature did not affect the fecundity of the aphids.

All model parameters were estimated using the statistical package R [105]. The methods for determining both the ordinal (OD) model's and the degree day (DD) model's parameters were similar, except for the maternity function. For the degree day (DD) model, each day was converted to degree days. I estimated the lower threshold by fitting a line to the data on a temperature vs. (time to onset of reproduction)$^{-1}$ graph (1.23) using a generalized linear model (GLM). Then I used the average temperature of each 24 hour period, to convert the day to degree days using (1.24) and converted the number of elapsed days in the experiment to elapsed degree days. The fitting routines for survival rate and probability for onset of reproduction were then used with time measured in degree days incorporating both $20°C$ and $25°C$ data sets for each humidity. The maternity function required a slightly different fitting routine

which is outlined below.

I estimated the daily survival rate using a Weibull function [103] because aphid survival is strongly age dependent. The probability that an animal of age a will survive to age $a + \delta a$, is

$$\frac{s(a + \delta a)}{s(a)} = e^{-((a+\delta a)\rho)^{\kappa} - (a\rho)^{\kappa}}, \tag{4.8}$$

where ρ is the scale parameter of the distribution and κ is the shape parameter [25].

The probability of transitioning to the reproductive stage at a particular age is a binomial process and can be analyzed using survival analysis. Because the transition probability increases with age I fitted a Weibull function to the data. Let $f(a)$ be the probability that an aphid of age a remains in the pre-reproductive stage; then an aphid who has failed to reproduce by age a will fail to reproduce by age $a + \delta a$, i.e. the aphid of age a will begin to reproduce in the time period $a + \delta a$ with probability

$$1 - \frac{f(a + \delta a)}{f(a)} = 1 - e^{-((a+\delta a)\rho)^{\kappa} - (a\rho)^{\kappa}}, \tag{4.9}$$

where ρ is the scale parameter of the distribution and κ is the shape parameter. To account for the minimum duration of the juvenile phase, I only included data where the probability of transitioning to the reproductive phase is > 0. Additionally, since the data was collected daily, reproduction began prior to the actual observation of the first offspring, up to one day earlier. Therefore, it is fair to assume that on average aphids began reproducing 1/2 day prior to the recorded observation of offspring. To account for this I assumed that on the first half-day the rate at which the aphids reproduced twice was many aphids as observed. That is, if I observed 4 aphids on the first day an aphid began reproducing, then its rate of producing offspring for the first half day is 8 aphids/day. This did not result in an increase in the total fecundity of

the individual aphid, since this rate was only maintained for 1/2 day, agreeing with the observed 4 aphids. To determine the maternity function $m(r)$ for the ordinal day (OD) model, I fit the fecundity data to a first order generalized linear model, using a Poisson error distribution with a log link, i.e. I fit the data to the curve $\exp(a + bt)$.

Determining the maternity function, $m(r)$, for the degree day (DD) model, was slightly different. If I converted the number of offspring per day to number of offspring per degree day, this would lose the characteristics of the Poisson error distribution inherent with count data. Notice that

$$\left(\frac{\text{offspring}}{\text{day}}\right) = \left(\frac{\text{offspring}}{\text{degree day}}\right)\left(\frac{\text{degree day}}{\text{day}}\right), \tag{4.10}$$

where (degree day)/day is the number of degree days in one day as calculated by (1.24). If I assume an exponentiated linear function for offspring per degree day, e.g. if I assume a first order exponentiated linear function, then

$$\frac{\text{offspring}}{\text{day}} = \exp(a + b\widetilde{t})\left(\frac{\text{degree day}}{\text{day}}\right), \tag{4.11}$$

and so

$$\ln\left[\frac{\text{offspring}}{\text{day}}\right] = (a + b\widetilde{t}) + \ln\left(\frac{\text{degree day}}{\text{day}}\right). \tag{4.12}$$

Since the number of offspring per day is a whole number, I can again use a Poisson error distribution and fit the fecundity data to a first order generalized linear model using a log link with an offset of

$$\ln\left(\frac{\text{degree day}}{\text{day}}\right).$$

Once offspring per day was calculated, determining the maternity function, i.e. the offspring per degree day was simply done by:

$$m(a, r) = \left(\frac{\text{offspring}}{\text{degree day}}\right) = \left(\frac{\text{offspring}}{\text{day}}\right)\left(\frac{\text{day}}{\text{degree day}}\right). \tag{4.13}$$

where day/(degree day) is the number of days in one degree day.

Evaluating Model Predictions

For all models, I simulated an invading aphid by setting the initial condition of the model to be one aphid just beginning to reproduce. For each of the simulated aphid population trajectories, I calculated the transient growth rate (1.19) and transient amplification (1.20). For the DD model, time was converted back to days prior to these calculations. To obtain the 95% confidence intervals for the models' predictions, I bootstrapped 10, 000 data sets (sampling with replacement, see [38]) using the same individual's demographic data to derive all three function parameters. To model demographic stochasticity, for each of the bootstrapped data sets, at each δt (or $\widetilde{\delta t}$) in each model's run, values for proportion surviving, proportion just beginning to reproduce, and the maternity function were determined randomly as follows: for both survivorship and whether the aphids will begin to reproduce, I randomly drew a number from a uniform distribution on $[0, 1]$. If this random number was smaller than the probability to survive as calculated by the Weibull distribution, then the aphids of that age survived. Similarly, the probability remaining in the pre-reproductive stage is equivalent to "surviving", so if the random number was less than that calculated by the Weibull distribution, then aphids of that age remained in the pre-reproductive stage. For the maternity function in both the OD model and the DD model, the number of offspring per day was randomly chosen from the Poisson distribution using

the calculated values mean in the Poisson pdf.

4.2 Results

4.2.1 Parameter Estimates

Comparison of Low and Medium Humidity Data

Generalized linear models were used to determine whether humidity had a statistically significant influence on parameter estimates. Table 4.2 shows the average demographic values for aphids growing at different temperature and humidity regimes.

The first day of reproduction was influenced by both humidity ($p = 6.2 \times 10^{-25}$) and temperature ($p = .000197$); furthermore there was a significant interaction between both factors ($p = .000142$). Survivorship was not influenced by temperature ($p = .0543$), nor humidity ($p = .553$), and there was no significant interaction between both parameters ($p = .613$). Total fecundity was influenced by both humidity ($p = 4.9 \times 10^{-5}$) and temperature ($p = 4.97 \times 10^{-5}$) and there was significant interac-

Table 4.2: The effect of temperature and humidity on aphid demography

Temperature	Humidity	Mean first day of reproduction*† (Days)	Average age to 50% mortality* (Days)	Mean Total Fecundity*†
$20°C$	Low	13.00(0.428)	26.5	29.22(2.43)
$20°C$	Medium	14.67(0.359)	33.5	44.4(3.16)
$25°C$	Low	9.15(0.181)	21.50	34.82(2.01)
$25°C$	Medium	11.40(0.454)	25.5	29.33(2.43)

*Values in parentheses are standard errors
†Includes only adults who have begun to reproduce

tion between temperature and humidity ($p = 7.06 \times 10^{-5}$). Fecundity was influenced by humidity ($p = .00584$) and the interaction between humidity and temperature ($p = .00631$), but temperature alone had no significance ($p = .615$). In conclusion, humidity was a significant factor in the aphids' first day of reproduction and in their fecundity. Therefore, these data sets were kept separate, and I parameterized the models for both low and medium humidity scenarios.

Vital Rates

I fitted the survival data to a Weibull distribution (where the mortality rate increases with age) and compared this with the exponential distribution (which has a constant mortality rate) and used the Akaike Information Criterion (AIC) to evaluate which distribution fits the data best (Table 4.3). When comparing models, the one with the lower AIC is generally deemed better, if the difference is greater than four [1, 2, 109]. Figures 4.2 and 4.3 shows the survivorship curve for the $25°C$, medium humidity data as a function of ordinal days and degree days, respectively. The curves for the other temperature/humidity combinations are similar and thus are not shown. Because the fit of the Weibull distribution (Table 4.4) was visually superior and had a smaller AIC value, the Weibull distribution was used in both models.

Determining whether the aphids will begin to produce was done similarly to the survivorship curves. Since I modeled the probability of beginning reproduction as a step function, the first days where no aphids reproduced was set to zero and the second part of the function was determined by the Weibull distribution. For the $20°C$, low humidity data, this was 10.5 days, for the $20°C$, medium humidity data, this was 11.5 days. For both humidities at $25°C$, no aphids reproduced in the first 7.5 days. If the age was above or equal to the minimum first day of reproduction, the Weibull

Table 4.3: Comparison of AIC Values for Survival Curves

Temp	Humidity	Exponential Distribution	Weibull Distribution
$20°C$	Low	560.67	549.06
$20°C$	Medium	542.30	512.05
$25°C$	Low	544.39	512.05
$25°C$	Medium	512.87	455.64
Degree Days	Low	991.16	909.67
Degree Days	Medium	913.5019	784.6982

Table 4.4: Weibull Distribution Parameter Values for Survival Function

Temp	Humidity	ρ	κ
$20°C$	Low	.039778	1.519531
$20°C$	Medium	.032442	2.202668
$25°C$	Low	.043407	1.721847
$25°C$	Medium	.038053	2.669978
Degree Days	Low	0.001894	3.337367
Degree Days	Medium	0.001612	5.373067

Table 4.5: Comparison of AIC Values for Failure to Reproduce Curves

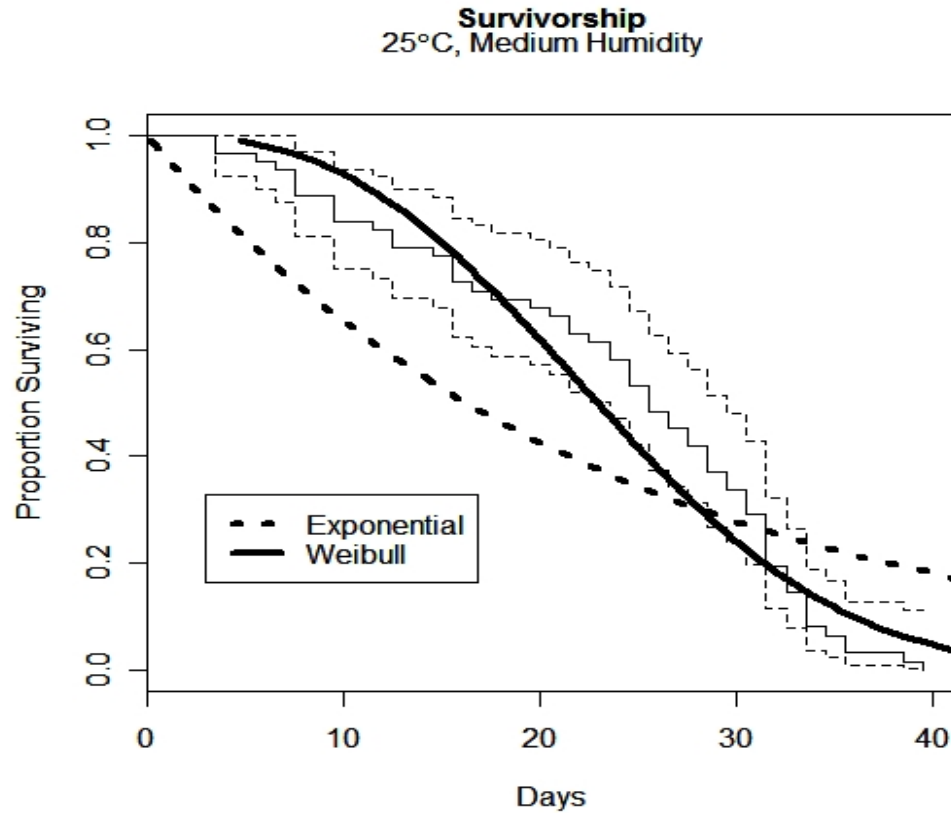| Temp	Humidity	Exponential Distribution	Weibull Distribution
$20°C$	Low	185.31	168.57
$20°C$	Medium	217.29	214.69
$25°C$	Low	171.37	164.76
$25°C$	Medium	256.06	256.73
Degree Days	Low	872.31	851.35
Degree Days	Medium	1011.92	1013.39

Figure 4.2: The Kaplan-Meier estimates for survivorship (with 95% confidence intervals) for the 25°C, medium humidity data as a function of ordinal days. Also shown are the survival curve fittings of the Weibull distribution and exponential distribution.

function determined the probability of beginning to reproduce.

The Weibull distribution was better than or equal to the exponential distribution for the "failure to reproduce" curves (Table 4.5), therefore the Weibull distribution was used in both the OD and DD models. Shown are two of the figures (Figures 4.4 and 4.5) for the proportion of not reproducing as a function of time. The curves for the other temperatures and humidities are similar and are not shown.

Figure 4.6 shows the first order maternity functions for the 25°C, low humidity
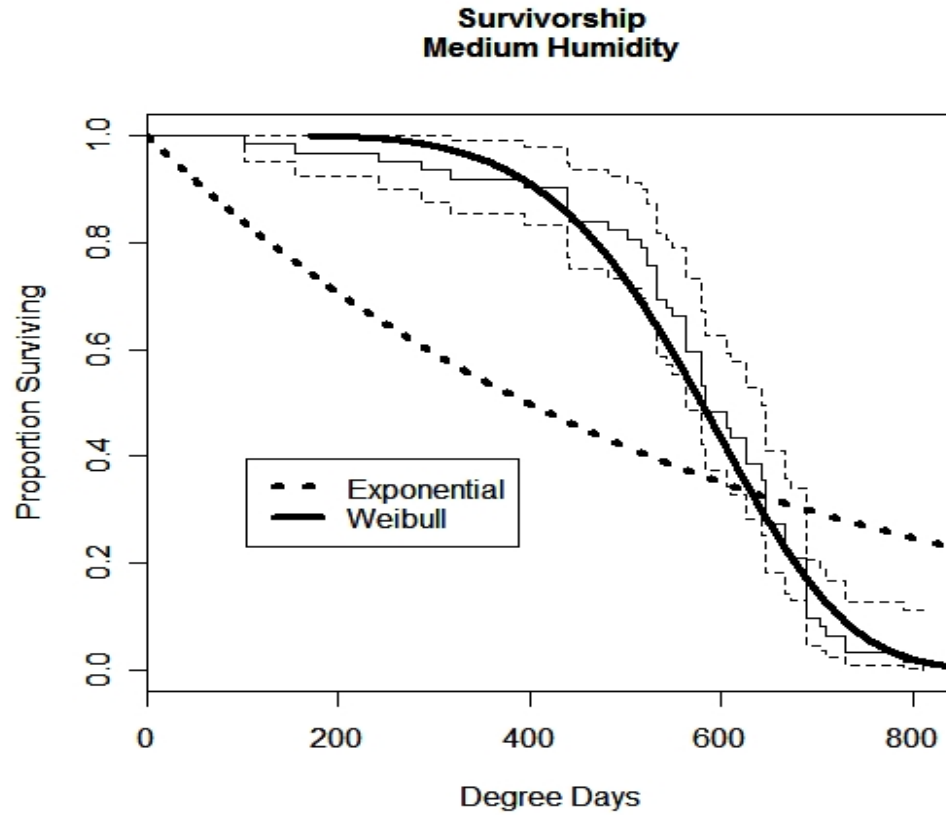
Figure 4.3: The Kaplan-Meier estimates for survivorship (with 95% confidence intervals) for medium humidity data as a function of degree days. Also shown are the survival curve fittings of the Weibull distribution and exponential distribution.

data. Figure 4.7 shows the first order maternity functions for the degree day, low humidity data.

4.2.2 Model and Empirical Results

Figures 4.8 and 4.9 show the model predictions incorporating demographic stochasticity for the transient growth rates along with the experimentally observed growth rates for the low humidity, $25°C$ data and for the medium humidity, $20°C$ data re-

Figure 4.4: The Kaplan-Meier estimates for proportion not reproducing (with 95% confidence intervals) for the 20°C, medium humidity data as a function of ordinal days from the day the aphids first began to reproduce. The shift is the day when the first aphid began to reproduce. Also shown are the curve fittings for both the Exponential and Weibull distributions.
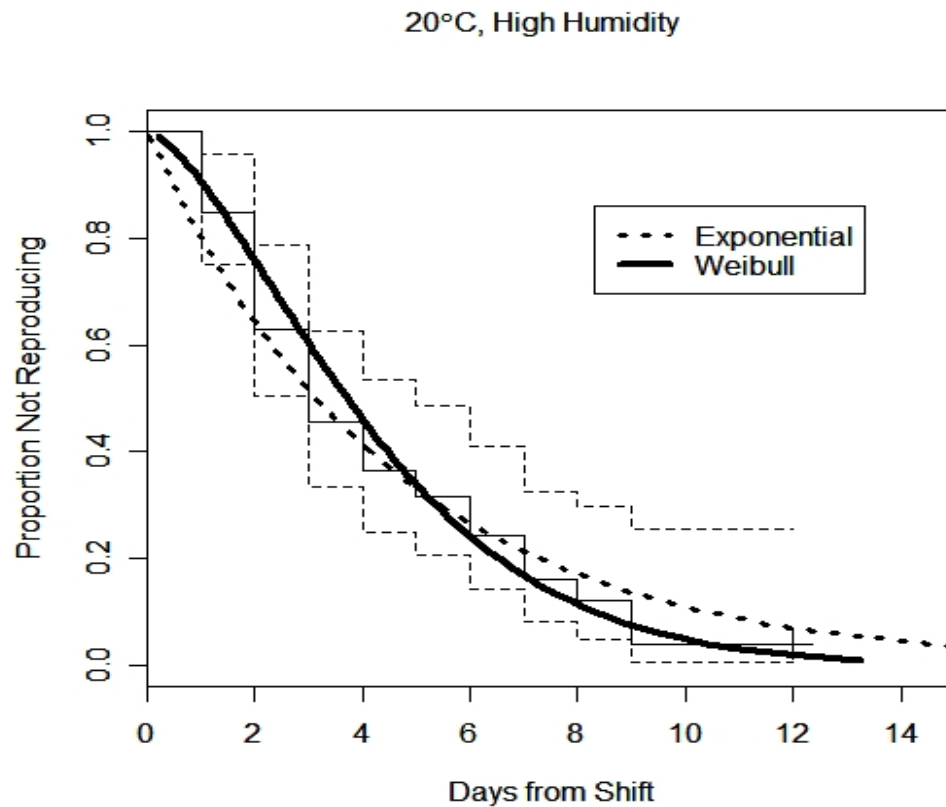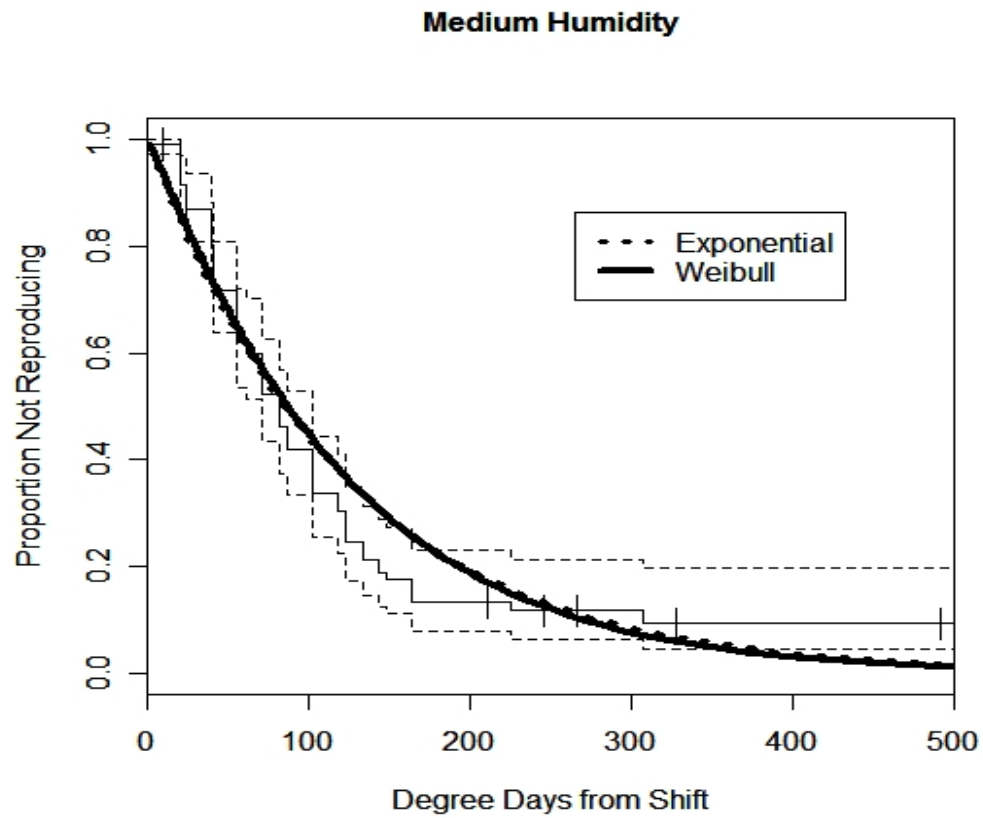
Figure 4.5: The Kaplan-Meier estimates for proportion not reproducing (with 95% confidence intervals) for the medium humidity data as a function of degree days from the day the aphids first began to reproduce. Also shown are both the curve fittings for the exponential and Weibull distribution.

Table 4.6: Weibull Distribution Parameter Values for Probability of Failing to Reproduce Function

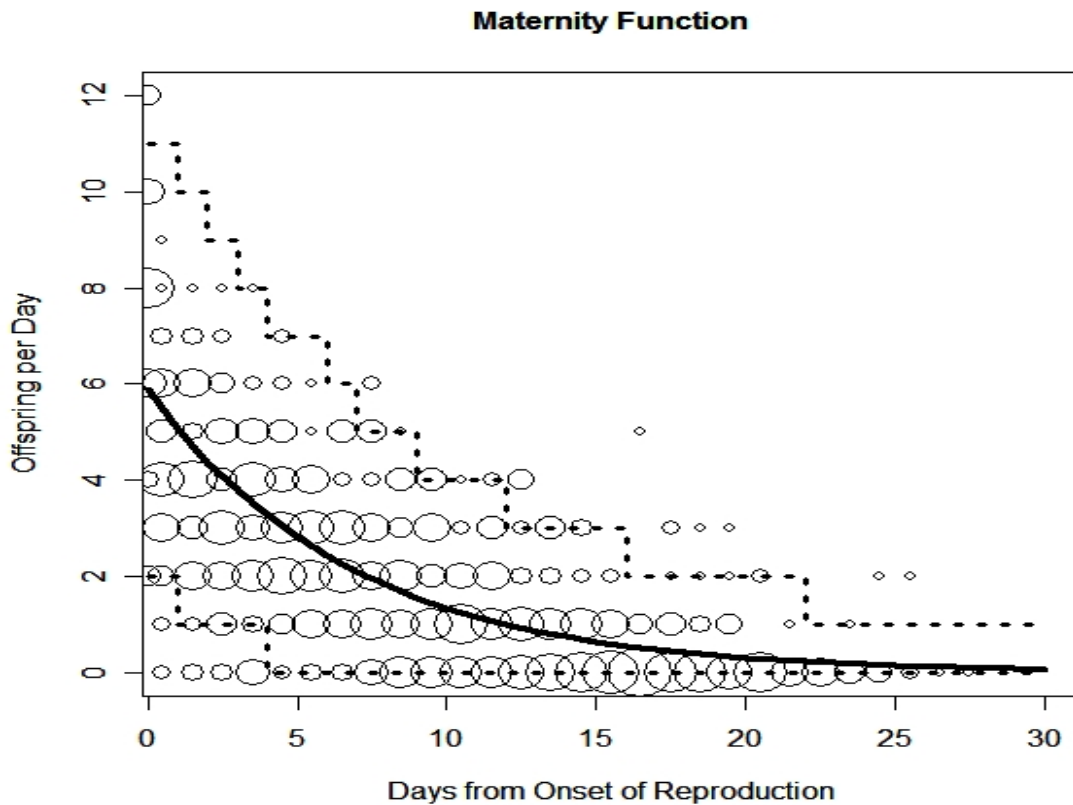| Temp	Humidity	ρ	κ
20°C	Low	0.233935	.596591
20°C	Medium	0.259200	0.762856
25°C	Low	0.550418	0.710482
25°C	Medium	0.134205	0.874164
Degree Days	Low	0.025445	0.674449
Degree Days	Medium	0.008127	1.060526

Maternity Function

Figure 4.6: The generalized linear model (with 95% confidence intervals) fitting of the maternity function to the 25°C, low humidity data. Circle represent data points with the radius of the circle proportional to number of data points.
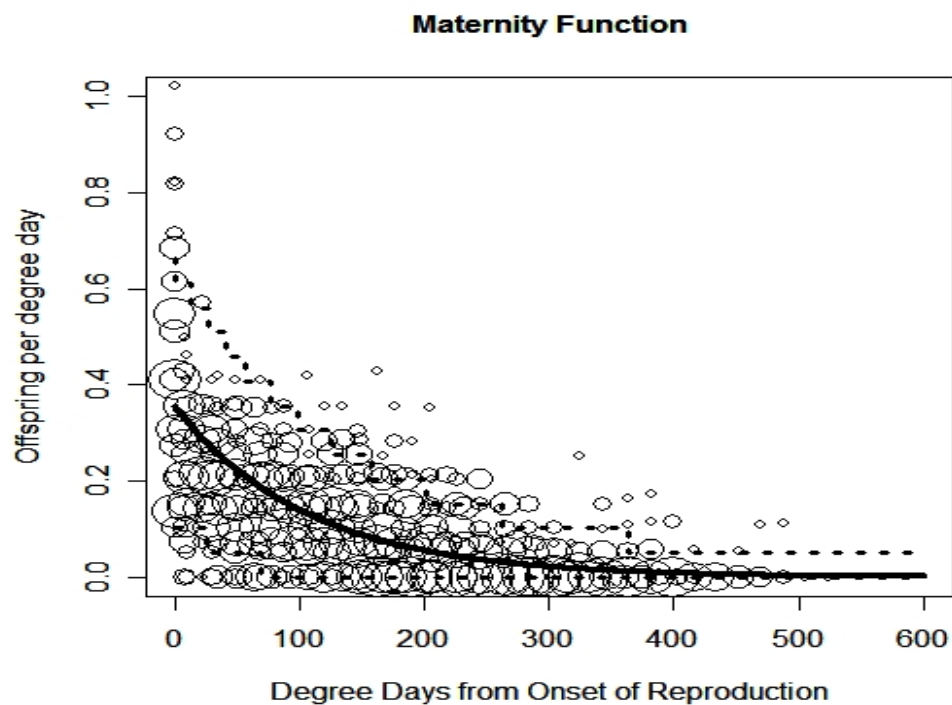
Maternity Function

Figure 4.7: The generalized linear model (with 95% confidence intervals) fitting of the maternity function to the degree day, low humidity data. Circle represent data points with the radius of the circle proportional to number of data points.

spectively. One can see that the model predictions for the low humidity, $25°C$ data fit the empirical data rather well, but that the medium humidity, $20°C$ data does not, due mainly to the difference of when the onset of reproduction began.

In the clip cages, the earliest onset of reproduction at the lower cages occurred when the aphids were 11.5 days old. From the count data of the population dynamics experiment and as can be seen in Figure 4.9, it is obvious that the first born offsprings in the large cages started reproducing at least 2 days earlier. Since the degree day model uses both temperature data to estimate the lower threshold, it does show an earlier mean onset of reproduction, by about one day, for the medium humidity, $20°C$

Figure 4.8: Comparison of the observed transient growth rates with the model predictions for the $25°C$ low humidity data. The circles are the observed population means with their 95% means. The top graph shows the model prediction using the ordinal day model. The mean prediction is the solid line with the dotted lines being its 95% confidence interval. The bottom graph shows the model prediction using the degree day model. Again, the mean prediction is the solid line with the dotted lines being its 95% confidence interval.

Table 4.7: Maternity Function, where T and L_T are the desired temperature and computed lower threshold respectively, see (1.24).

Temp	Humidity	Maternity Function
$20°C$	Low	$\exp(1.508526 - 0.139891t)$
$20°C$	Medium	$\exp(1.605473 - 0.088002t)$
$25°C$	Low	$\exp(1.774711 - 0.147828t)$
$25°C$	Medium	$\exp(1.68710 - 0.17067t)$
Degree Days	Low	$\dfrac{\exp(-1.0351707 - 0.00927430t + \ln(T - L_T))}{T - L_T}$
Degree Days	Medium	$\dfrac{\exp(-1.0960596 - 0.0074586t + \ln(T - L_T))}{T - L_T}$

data as also seen in Figure 4.9. Not shown are the actual population counts. The model predictions for population count for the $25°C$, low humidity data was consistent with the empirical observations, while the model predictions for the population count in the $20°C$, medium humidity data were much lower than the observed counts.

There are a number of possible reasons for this discrepancy between the model prediction and observation at $20°C$. The aphids used in this experiment came from a colony reared for the past two years on broad bean (*Vicia faba*) plants in a high temperature ($\geq 25°C$) room. Thus the aphids were acclimated to the higher temperature and to a different food source, which might have negatively affected aphid performance (references). This imposed stress in combination with feeding alone might have caused a delay in aphid development in the clip cages. It has been shown that it is advantageous for some aphid species to feed in groups, rather than as individuals [32, 123], though other studies have not seen this effect [54, 94]. Perhaps in pea aphids an Allee effect is only measurable under stressful conditions. Additionally, the clip cages prevented the aphids from moving to the younger, newer leaves at the
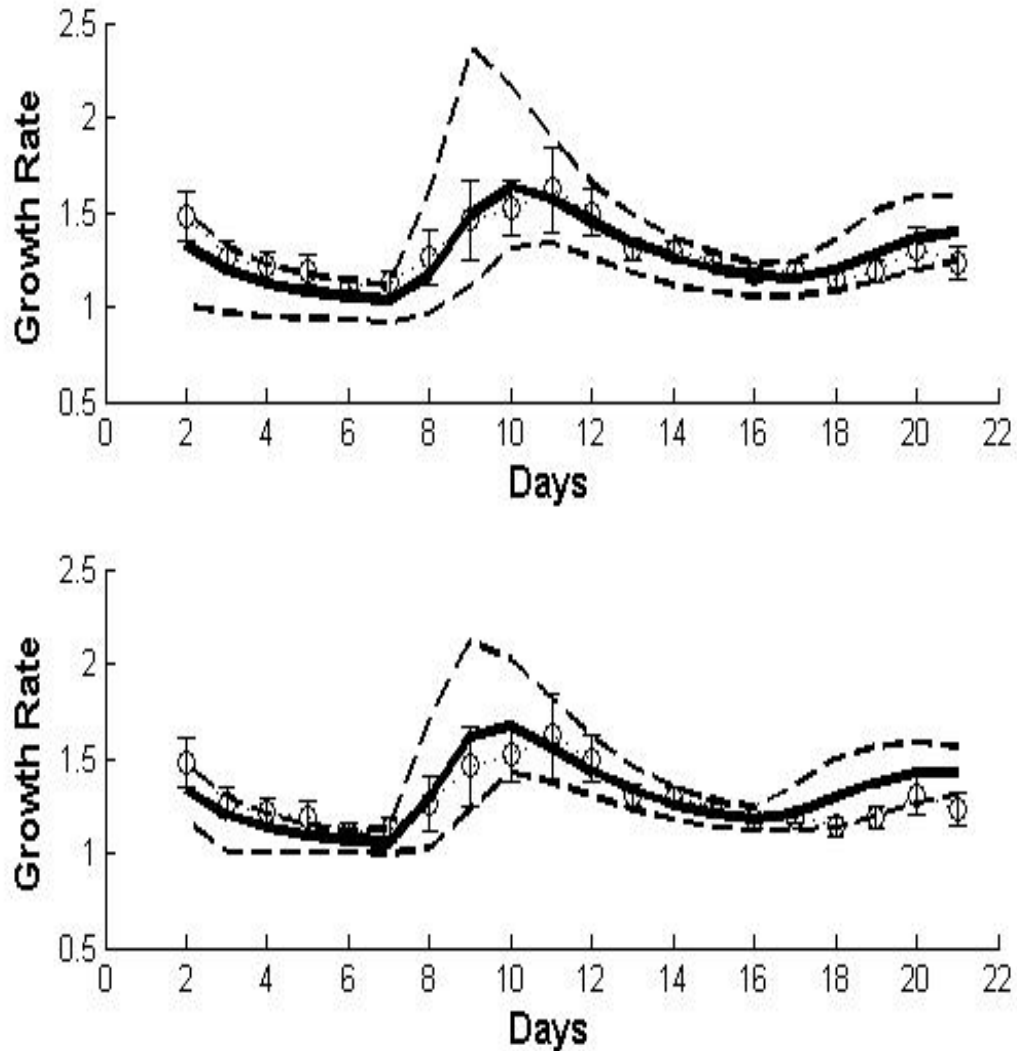
Figure 4.9: Comparison of the observed transient growth rates with the model predictions for the $20°C$ medium humidity data. The circles are the observed population means with their 95% means. The mean prediction is the solid line with the dotted lines being its 95% confidence interval. The bottom graph shows the model prediction using the degree day model. Again, the mean prediction is the solid line with the dotted lines being its 95% confidence interval.

top of the alfalfa plant as they did in the larger cages (personal observations). In the case of sycamore aphids, [20] showed that aphids feeding on older, mature leaves develop slower than those feeding on unfurling leaves. The clip cages did not impact vital rates estimates if aphids were reared at higher temperature, as there was a very good match between model prediction an observation (Figure 4.8). Therefore, I will assume the discrepancy between the model predictions and empirical observations in the $20°C$, medium humidity model case is due to the stress caused by performing the experiment at an temperature cooler than what the aphids were acclimated too.

Since the aphids began reproducing at least two days earlier in the large cages for the low temperature regime, I shifted the growth rate curve (Figure 4.9) to the left by two days by subtracting two days from the day the aphids in the clip cages began to reproduce and recalculating the parameters for the Weibull distribution for the "failure to reproduce" curve ($\rho = 0.259200$, $\kappa = 0.762856$). Then I ran the ordinal day model again with the results shown in the top graph of Figure 4.10. The predicted population count is still lower than the empirical data, but the model predictions for the transient growth rate now match the empirical data much better. This model was therefore used for the remainder of this dissertation.

I did not make any changes to the $25°C$, medium humidity data, since there is a good match between predictions and observations at this temperature regime.

Using this correction I calculated the transient amplification for both temperatures at medium humidity. The transient amplification, $T_A(t)$ as given in (1.20), is the ratio of the actual population size at time t to what the population would be if it started at its stable state distribution. Thus the greater the difference between the lines in Figure 4.11, the greater the transient amplification. I assume that the initial population size and the norm of the population at its stable state distribution are both equal to 1. Notice the y-axis is on a logarithmic scale. The transient amplification changes with
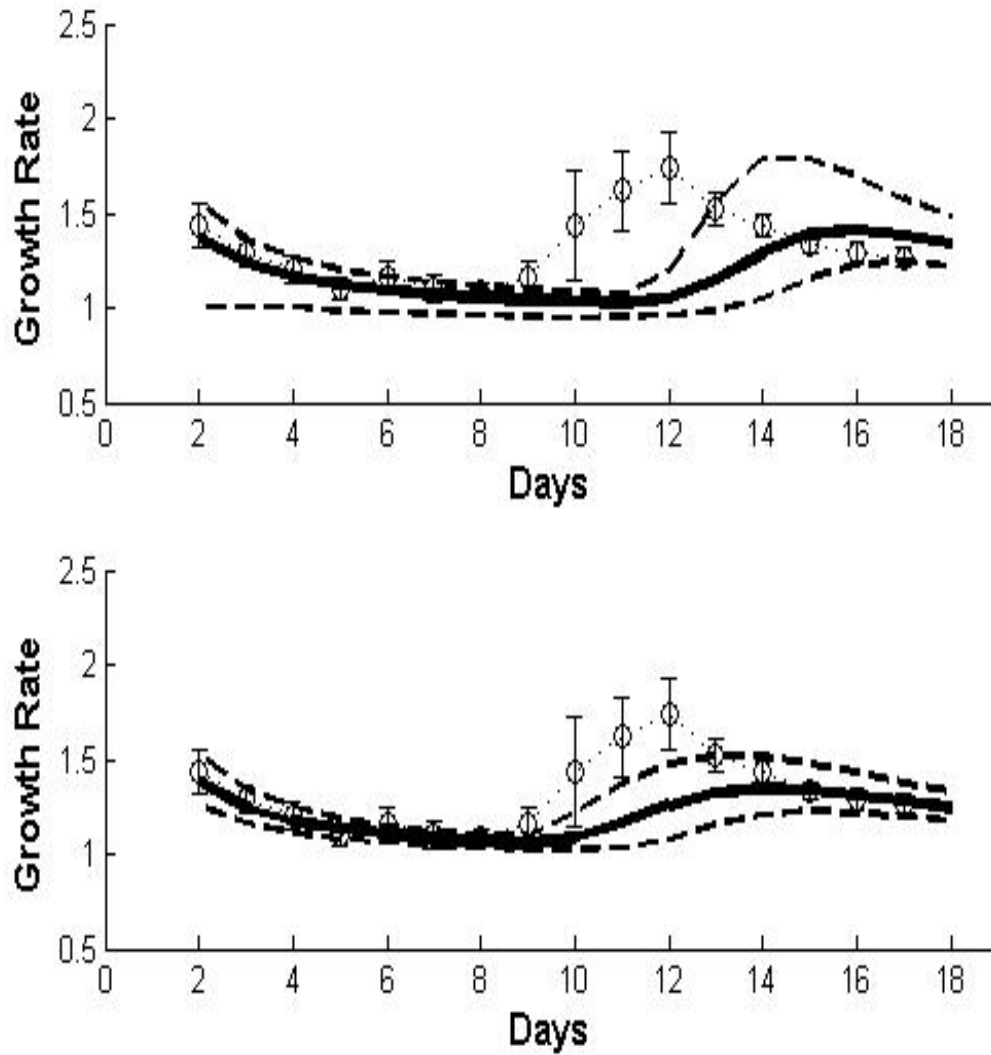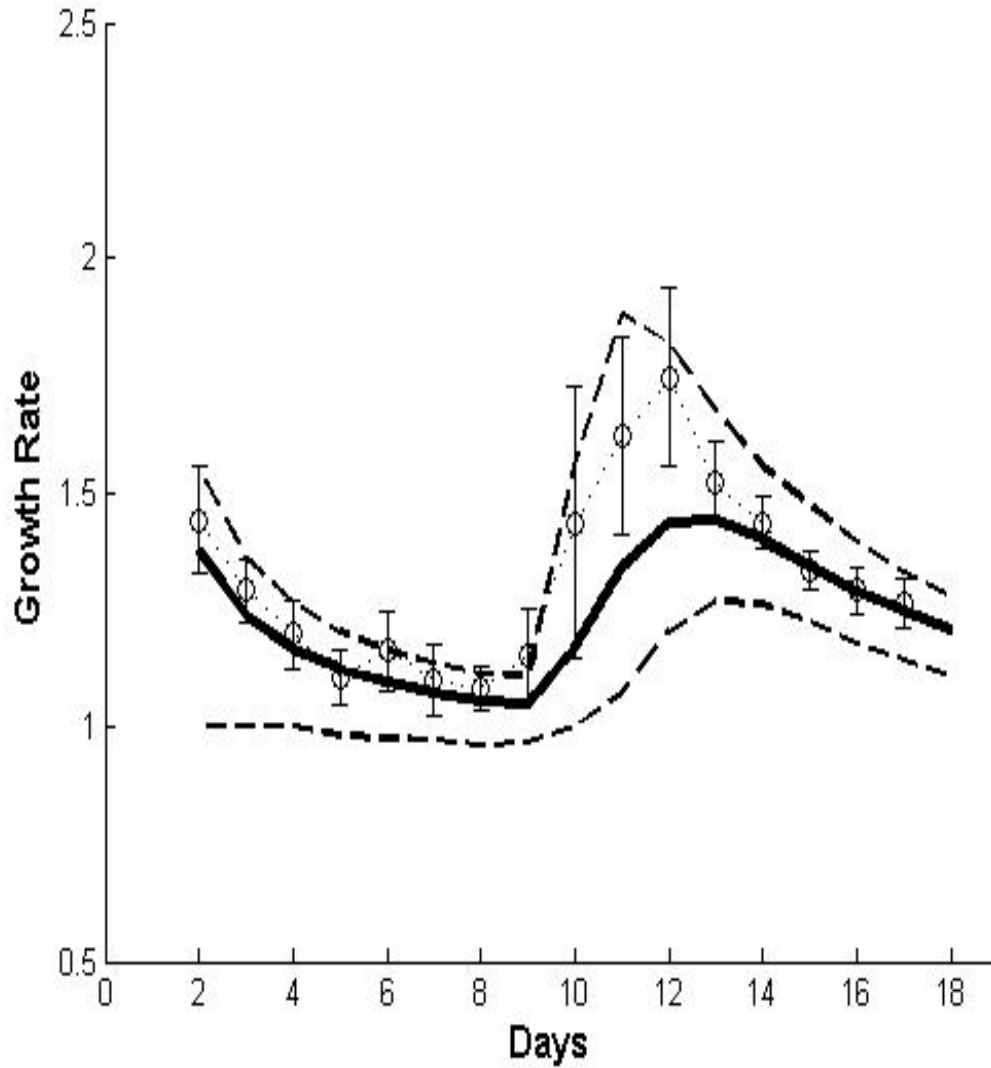
Figure 4.10: Comparison of the observed transient growth rates with the model predictions for the 20°C medium humidity data incorporating a two day shift in the onset of reproduction. The circles are the observed population means with their 95% means. The mean prediction is the solid line with the dotted lines being its 95% confidence interval.

Table 4.8: Asymptotic Rates*

Temp - Humidity	Asymptotic λ Mean lower 95% CI	Asymptotic λ Mean	Asymptotic λ Mean upper 95% CI
$20°C -$ Medium	1.1818	1.2402	1.3019
$25°C -$ Medium	1.1610	1.2333	1.3171

Temp - Humidity	Asymptotic T_A Mean lower 95% CI	Asymptotic T_A Mean	Asymptotic T_A Mean upper 95% CI
$20°C -$ Medium	1.5071	4.7809	8.1413
$25°C -$ Medium	1.7088	4.8479	9.4451

*Stochastic OD model. Mean is calculated from day 100 to day 197.

time, but stabilizes after 50 time steps. Shown is $T_A(10) = 29.96/8.64 = 3.47$.

Table 4.8 gives the asymptotic growth rate and asymptotic transient amplification for the two temperatures. While both values are similar, the higher temperature result does have a greater confidence interval.

Figure 4.12 shows the transient amplification for both the $20°C$ and $25°C$, medium humidity stochastic, ordinal day models. Notice as $t \to \infty$, the transient amplification stabilizes to a constant. For days less than 30, which temperature has the greater the transient amplification depends on the particular day. On some days (e.g. day 20), the $20°C$ model has a greater transient amplification. On other days (e.g. day 12), the $25°C$ model has greater transient amplification. The mean average peaks of the transient amplification for the two temperatures are the same; they just occur on different days. These general results, i.e. the same asymptotic transient growth rate, the same mean average peaks for transient amplification occurring on different days) are also common to the low humidity, ordinal day model and for the degree day model at both humidities (not shown). For the degree day model, the asymptotic transient amplification will always be the same, not matter what two temperatures
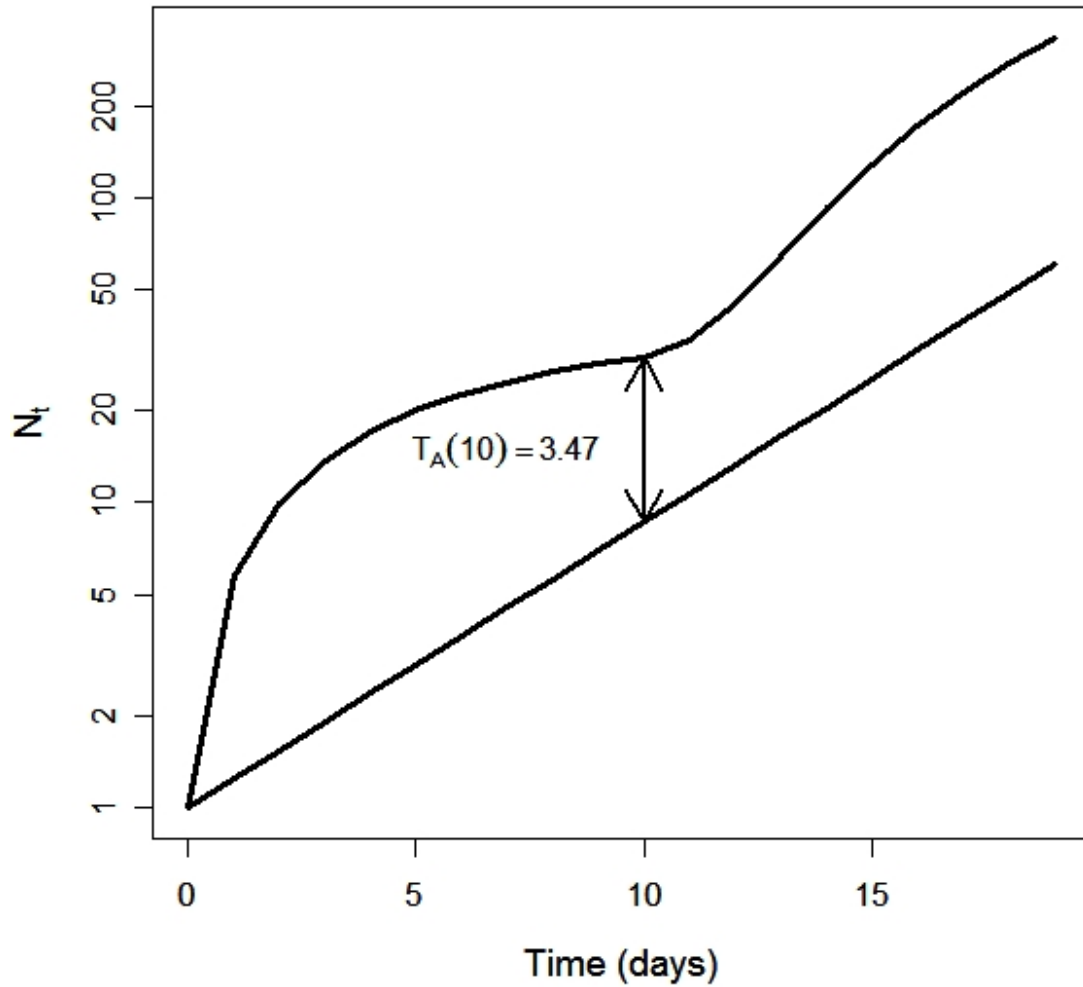
Figure 4.11: The top curve is the population trajectory assuming a single invading aphid just beginning to reproduce. The bottom curve is the population size assuming the initial population is at its stable state distribution, normalized to 1. Notice the y-axis is on a logarithmic scale. The transient amplification at time t is the ratio of the two population counts at time t.
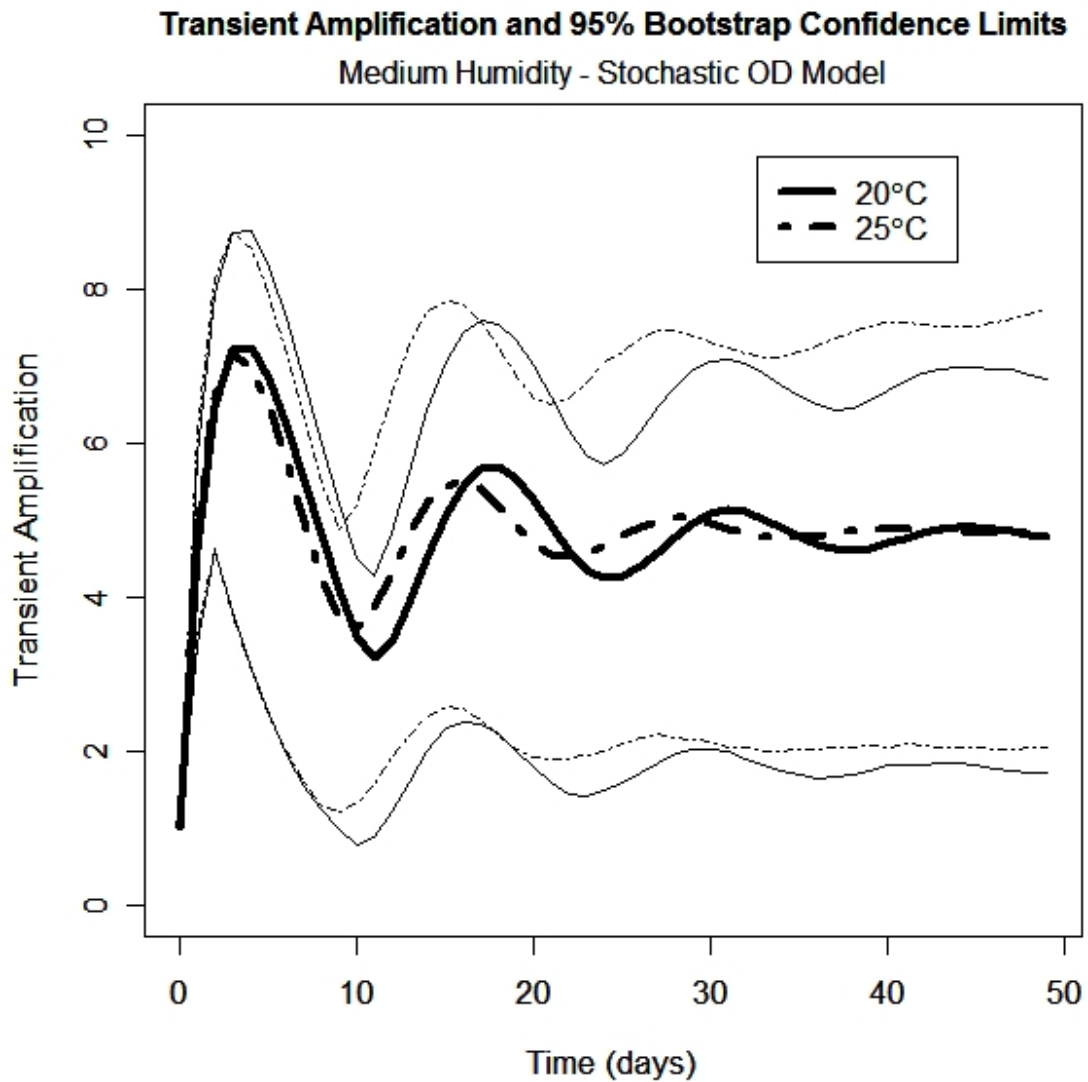
Figure 4.12: The transient amplification for the medium humidity, stochastic, ordinal day model. The lighter weight lines are the 95% confidence intervals.

are compared as the following theorem shows.

Theorem 4.2.1. *Let $n(\widetilde{t})$ be the population as a function of degree days. Then the asymptotic transient amplification for any temperature is the same.*

    Proof: Let $\widetilde{t_0}$ be a time (in degree days) such that the asymptotic dynamics

is reached. Hence I assume the aphids are reproducing exponentially and that the transient amplification at this time is constant. Let T_1 and T_2 be any two arbitrary temperatures and let L_T be the lower threshold of the degree day model. Let $\widetilde{t_1}$ and $\widetilde{t_2}$ be the degree days after one ordinal day has elapsed at temperatures T_1 and T_2 respectively. Thus $\widetilde{t_1} = \widetilde{t_0} + (T_1 - L_T)$ and $\widetilde{t_2} = \widetilde{t_0} + (T_2 - L_T)$ by (1.24). Without loss of generality, assume $\widetilde{t_1} < \widetilde{t_2}$.

Next, let $t_{01} = (T_1 - L_T)\widetilde{t_0}$ and $t_{02} = (T_2 - L_T)\widetilde{t_0}$ be the time (in ordinal days) of $\widetilde{t_0}$. Let t_{11} and t_{22} be the time (in ordinal days) of $\widetilde{t_1}$ and $\widetilde{t_2}$ respectively. Thus

$$\|n(\widetilde{t_0})\| = \|n(t_{01})\| = \|n(t_{02})\|, \tag{4.14}$$

$$\|n(\widetilde{t_1})\| = \|n(t_{11})\|, \tag{4.15}$$

$$\|n(\widetilde{t_2})\| = \|n(t_{22})\|, \text{ and} \tag{4.16}$$

$$t_{02} = t_{01}\frac{(T_1 - L_T)}{(T_2 - L_T)}. \tag{4.17}$$

Let λ_1, λ_2 be the asymptotic population growth rates at temperatures T_1 and T_2 respectively. From above and from (1.19),

$$\lambda_1 = \frac{\|n(\widetilde{t_1})\|}{\|n(\widetilde{t_0})\|} \text{ and } \lambda_2 = \frac{\|n(\widetilde{t_2})\|}{\|n(\widetilde{t_0})\|}. \tag{4.18}$$

Let r_1 and r_2 be the intrinsic rate of increase (measured in days^{-1}) at temperatures T_1 and T_2. Thus $\lambda_1 = e^{r_1}$ and $\lambda_2 = e^{r_2}$ (see [108] p. 59). Noting that the conversion from degree days to days at temperature T_1 is $(T_1 - L_T)^{-1}$, then

$$\frac{\|n(\widetilde{t_2})\|}{\|n(\widetilde{t_0})\|} = e^{r_1\frac{(\widetilde{t_2} - \widetilde{t_0})}{T_1 - L_T}}, \tag{4.19}$$

$$= e^{r_1\left(\frac{T_2 - L_T}{T_1 - L_T}\right)}. \tag{4.20}$$

Letting $s = \dfrac{T_2 - L_T}{T_1 - L_T}$, then from above,

$$\lambda_2 = \lambda_1^s, \tag{4.21}$$

and

$$\lambda_2^{t_{02}} \;\; = \;\; \left(\lambda_1^s\right)^{t_{01}\frac{(T_1 - L_T)}{(T_2 - L_T)}}, \;\; \text{by 4.17}, \tag{4.22}$$

$$= \;\; \lambda_1^{t_{01}}. \tag{4.23}$$

Let T_{A1} and T_{A2} be the asymptotic transient amplification at T_1 and T_2 respectively. Then

$$\frac{T_{A1}}{T_{A2}} \;\; = \;\; \left(\frac{\|n(\widetilde{t_1})\|}{\lambda_1^{t_{01}+1}}\right)\left(\frac{\lambda_2^{t_{02}+1}}{\|n(\widetilde{t_2})\|}\right), \tag{4.24}$$

$$= \;\; \left(\frac{\lambda_1\|n(\widetilde{t_0})\|}{\lambda_1^{t_{01}+1}}\right)\left(\frac{\lambda_2^{t_{02}+1}}{\lambda_2\|n(\widetilde{t_0})\|}\right), \tag{4.25}$$

$$= \;\; \frac{\lambda_2^{t_{02}}}{\lambda_1^{t_{01}}}, \tag{4.26}$$

$$= \;\; \frac{\lambda_1^{t_{01}}}{\lambda_1^{t_{01}}}, \;\; \text{by (4.22)}, \tag{4.27}$$

$$= \;\; 1. \tag{4.28}$$

Therefore $T_{A1} = T_{A2}$. $\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\square$

4.3 Discussion

As far as I know this study is the first study on the effect of humidity on the vital rates of aphids. I find that low humidity significantly reduces developmental time, decreases survival and reduces fecundity (at the lower temperature) of *A. pisum*

(Table 4.2). This negative effect is enhanced by increased desiccation probability at low humidity conditions: *A. pisum* drops off plants as a response to predator attack and if humidity is low aphids are more likely to die before they return to the plant [107]. Previous aphid studies on the effect of temperature on fecundity and survivorship were conducted under higher humidity conditions (e.g. [12]: $50 - 70\%$ r.h., [57]: $70-100\%$ r.h., and [112] at $70-75\%$ r.h.) than our study ($26-38\%$ r.h. and $40 - 52\%$ r.h.). Despite the higher humidity during the experimental conditions the juvenile period in the clip cages at $20°C$ was at least 4 days longer than reported in the literature ([12] 9 days, 8.5 days [57] and [112]). In contrast, aphids not constrained to clip cages (i.e., those in the large cage experiments) started reproducing 2-3 days earlier at $20°C$ than in the clip cages, which is consistent with that reported in the literature (considering the lower humidity). Therefore, in the $20°C$ model I shifted the onset of reproduction by two days.

As mentioned in the results section, this later onset of reproduction in the clip cage experiments could be due to an Allee effect caused by aphids aggregating together. Dixon and Wratten [32] showed that black bean aphids (*Aphis fabae* Scop.) feeding in groups were larger than those feeding alone and that larger apterae (non-winged) aphids not only have a greater fecundity, but they also have a shorter (one day) delay time between when the aphids molt to the adult stage and when they actually begin to reproduce. Other studies have not seen this Allee effect [54, 94]. Additionally, [20] showed that sycamore aphids (*Drepanosiphum platanoidis*) feeding on older, mature leaves developed slower than those feeding on unfurling (younger) leaves. Since the clip cages prevented the aphids from aggregating and from moving to choice feeding sites, a prolonged period of development for aphids raised in the clip cages is not unfeasible.

In general, the mean total fecundity of aphids in this experiment (30-44 aphids,

Table 4.2) was only half of that reported in the literature ([12] 93 offsprings at $20°C$, and 90 offsprings at $26°C$). In contrast, the total lifetime offspring production in this study increased with decreasing temperature under medium humidity conditions, which is consistent with the literature; both [6] and [12] found that the fecundity of pea aphids was highest at $15°C$. The overall low fecundity of these experiments in this study could be partially explained by lower host plant quality (the fecundity of pea aphids depends on plant species and plant cultivar [6, 43, 90, 97]), and to the low humidity rearing conditions. This suggests that it is rather challenging to make quantitative prediction of aphid population dynamics, however qualitative predictions should hold (e.g. fecundity decreases with increasing temperature).

For the higher temperature the predicted and observed population trajectory match perfectly, and after adjusting the parameter for the first day of reproduction for the lower temperature, the model's predicted and observed population trajectories match also. Therefore, I believe that these models can be used to examine the effect of temperature on transient and asymptotic population growth rate. Contrary to our expectations and the literature [12, 112] the asymptotic population growth rates at both temperatures are similar because, everything else equal, a quicker development increases population growth rate. In this study the time of development between the two temperature regimes differed only by one day. The positive effect of this small difference was counteracted through a reduced fecundity and survival at the higher temperature. Since the asymptotic population growth rates were similar at both temperatures, the transient amplifications should be similar as well [117]. Future experiments testing the effect of temperature on transient population dynamics should also include much lower temperature ranges resulting in a range of asymptotic population growth rates.

Transient amplification following an invasion by a single aphid exhibits damped

oscillations: the declining phase is characterized by a declining fecundity of adults and by a large number of juvenile aphids; the increasing phase is characterized by the next generation reaching the reproductive stage. Once the stable state distribution is reached (after about 50 days), the transient amplification stabilizes to a constant. This agrees with the general results derived in [65] who showed that for any single species matrix model, the transient amplification stabilizes to a constant.

The 95% confidence intervals for the transient amplification are large and indicate the range of possible transient amplifications that one might observe in real populations. Additionally, the upper bounds take much longer the longer to reach an asymptotic level (day 100, data not shown) compared to lower bounds (day 50, Figure 4.12). The lower bound of the confidence interval is always greater 1 except at the first minimum. Therefore the ordinal day model suggests that ignoring transient dynamics in the early phase after a dispersal event of *A. pisum* always results in an underestimation of population size.

The prediction of the degree day model is similar to the ordinal day model in that the transient amplification in the first days following an invasion follows a damped oscillatory pattern. As shown in the results, for any two temperatures, the asymptotic transient amplification will always be equal. For example, model runs from $15°C$ and $25°C$ still result in the temperatures having the same asymptotic transient amplification (data not shown). As with the ordinal day model, the lower bound of the confidence interval is always greater than 1. The degree day model does rely on the assumption that the conversion of survivorship and fecundity from "per day" to "per degree day" is linear. While a linear relationship between temperature and the inverse of time to development (see equation (1.23)) exists, it is unknown whether higher temperatures decrease survivorship and increase the rate of offspring produced in the same linear fashion. Therefore, it has not been tested whether this model is

justified.

My model applies to population dynamics that are not affected by density dependent processes, such as during the initial phase of population establishments following a dispersal event. In this study aphid populations take 50 time steps to reach the asymptotic growth rate, at which time the population size increased to about 25,000 individuals; in the field, density dependence would have started to affect aphid populations at much lower density. Under crowded conditions or poor host plant quality aphids increasingly produce winged morphs (alatae) that migrate to better habitats. In the field the populations of many aphid species crash two to three generations after the initial colonization (20 - 30 days), which is mostly due to mass migration [31]. This study suggests that aphid populations crash long before they reach the asymptotic population growth rate and thus studying transient dynamics is more relevant.

Studying transient dynamics is important because it influences the probability of population establishment. If the crash occurs as a result of poor plant quality (ripening plants) or because plants get harvested, the transient population growth rate determines the peak aphid population density, which in turn influences the yield reduction caused by aphids [45, 73]. Studies have been done to predict when it is necessary to apply insecticides (see e.g. [79, 99]). In particular, [79] estimates the economic threshold level. This is the pest density at which action should be taken (e.g. application of insecticide) to prevent an increasing pest population from causing economic injury to the crop, i.e. when the cost of controlling the aphids balances the lose of income due to smaller yields caused by the infestation [58]. These estimates rely on predicting aphid population growth rates because of the time lag between the application and the harvest. The transient amplification gives an indication of the magnification of the aphid population when comparing a population beginning at its

stable state distribution verses a population beginning with a different distribution such as reproducing adults. A beginning population consisting of only reproducing adults will result in a greater population than a population (with the same number of individuals) at its stable state distribution. This in turn, gives an upper bound on the population size and hence can help determine a bound on the amount of injury caused by the aphids on a field crop.

Appendix A

Chapter 2 Computer Programs

A.1 Program 1

```
% studyearKM.m
% this takes the cheetah data from studbook and calculates
% Kaplan-Meiercurve (i.e. draws Figure 1)
clear;
cheetahdata = dlmread('studbook2004.txt','\t');
ncheetah=size(cheetahdata) ;
% ncheetah(1) = number of cheetahs in database
% initialize
possibleages=transpose(linspace(1.5,30,58));
% possible ages are 18 months - 30 years
nageclass = length(possibleages);
nalive=zeros(nageclass,1) ;
% number alive at the beginning of each age class
ndied=zeros(nageclass, 1);
%  number who died in that ageclass

flag=0; % assume dead
newdata=[];
%  now do all the cheetahs
for ii=1:ncheetah(1);  % for every cheetah
    flag=0 ; % assume dead
 if cheetahdata(ii,5)~=0 % so the cheetah is dead
    yalive = cheetahdata(ii,5)-cheetahdata(ii,3);
 else
```

```
      yalive=2004 - cheetahdata(ii,3)+1;  % cheetah is alive
     flag=1;
 end

 if yalive == 0 % died same year
    malive =  cheetahdata(ii,4)-cheetahdata(ii,2);
    % # of months alive at beginning of month
 else
    malive = 12-cheetahdata(ii,2)  ;
    % number of months alive at beginning of month in first year
    malive= malive+cheetahdata(ii,4) ;
    % plus number of months alive at beginning of month in last year
    malive= malive + 12*(yalive-1);
    % plus number of months alive inbetween
    if cheetahdata(ii,5)==0 malive=malive+1;  end
    % because lived through that last month
 end
  newdata=[newdata ; ii malive flag cheetahdata(ii,3)];

end


% now calculate Kaplan Meier curve
nalive=zeros(360,1) ;
% number of cheetahs alive at beginning of month
ndied=zeros(360,1) ;
% number of cheetahs who died during that month
nc=size(newdata);
ncheetahs=0;
for jj=1:nc(1)% number of cheetahs in studbook
    if newdata(jj,3)==0  % choose only those cheetahs that died
        ncheetahs=ncheetahs+1;
        nmonths=newdata(jj,2)+1 ;
        % number of months cheetah is alive at beginning of month
      if nmonths <=360  % use only cheetahs less than 30 years old
        nalive(1:nmonths)=nalive(1:nmonths)+1;% add to total alive
        ndied(nmonths)=ndied(nmonths)+1 ;
        % number of cheetahs that died during that month
      end
    end
end

% using "Analysis of Survival Data" by D.R. Cox and D. Oakes
```

```
% now to remove age classes where there are no deaths
r=[ncheetahs];
d=[0];
age=[0];

for kk=1:length(nalive)
    if nalive(kk)~= 0  %don't do anything if no one is still alive
%        % this prevents us also from dividing by zero
        r=[r nalive(kk)];
        d=[d ndied(kk)];
        age=[age kk/12] ; % convert months to years
    end
end

% now calculate product-limit estimator
lengthr=length(r)-1; % so we don't divide by zero
KM=zeros(lengthr,1);
KM(1)=1-d(1)/r(1);
varKM=zeros(lengthr,1);
varsum=zeros(lengthr,1);
confl=zeros(lengthr,1);  % lower 95% confidence
confu=zeros(lengthr,1);   % upper 95% confidence
cinterval=zeros(lengthr,1);  % 95% confidence
for kk=2:lengthr-1
    KM(kk)=KM(kk-1)*(1-d(kk)/r(kk));
    varsum(kk)=d(kk)/(r(kk)*(r(kk)-d(kk)));
    varKM(kk)=KM(kk)^2 *sum(varsum(1:kk));
    confl(kk)=KM(kk)-1.96*sqrt(varKM(kk));
    confu(kk)=KM(kk)+1.96*sqrt(varKM(kk));
    cinterval(kk)=1.96*sqrt(varKM(kk));
end

% now plot Kaplan-Meier curve
plot(age(1:lengthr),KM,'k','LineWidth',3);
hold on
xlabel('Age (in years)','FontSize',16)
ylabel('Cumulative Survivorship','FontSize',16)
axis([0 25 0 1]);
h=findobj;
set(h(3),'FontSize',14,'FontWeight','bold');
set(h(3),'XTick',[0 4 8 12 16 20 24]);
```

```
%plot(age,confl,'k:','LineWidth',2.5)
%plot(age,confu,'k:','LineWidth',2.5)


% calculate survivorships
% 0-6 month
alive=nalive(1,1);
died=sum(ndied(1:6));
%these died before moving to next age class
surv06=(alive-died)/alive  % 6 - month survivorship

% 6-12, 12-18 month
alive=nalive(7,1);
died=sum(ndied(7:18));
 %these died before moving to next age class
surv618=(alive-died)/alive ;  % 12 - month survivorship
surv618=surv618^(1/2)

% 18-42
alive=nalive(19,1);
died=sum(ndied(19:42));
%these died before moving to next age class
surv1842=(alive-died)/alive ;
surv1842=surv1842^(1/4)  % split into 4 age classes

% 42-102
alive=nalive(43,1);
died=sum(ndied(43:102));
%these died before moving to next age class
surv42102=(alive-died)/alive ;
surv42102=surv42102^(1/10)  % split into 10 age classes

% 102-156
alive=nalive(103,1);
died=sum(ndied(103:162));
%these died before moving to next age class
surv102162=(alive-died)/alive ;
surv102162=surv102162^(1/10)  % split into 9 age classes


% now overlay plot of Kaplan-Meier curve
% surv is survivorship with cheetahs older
```

```
%     than 42 months having 42-102 survivorship
% surv2 is survivorship with 42-102, 102-162,
%     and cheetahs older than 168
%     months having same survivorship as those 102-162
age=zeros(61,1); % there are 60 - 6 month age classes
surv=zeros(61,1); % cummulative survivorship
age(1)=0;  % everybody is alive at birth
surv(1)=1;
age(2)=.5 ;
surv(2)=surv06;
age(3)=1 ;
surv(3)=surv(2)*surv618;
age(4)=1.5 ;
surv(4)=surv(3)*surv618;


for jj=5:8
  surv(jj)=surv(jj-1)*surv1842;
  age(jj)=(jj-1)*6/12;
end
surv3(1:8)=surv(1:8);

for jj=9:18
    surv(jj)=surv(jj-1)*surv42102;
    surv3(jj)=surv3(jj-1)*.9258;  % this is our average
    age(jj)=(jj-1)*6/12;
end
surv2(1:18)=surv(1:18) ;
% these are the same until month 102

for jj=19:61
    surv(jj)=surv(jj-1)*surv42102  ;%surv102;
    surv2(jj)=surv2(jj-1)*surv102162;
    surv3(jj)=surv3(jj-1)*.9258;
    age(jj)=(jj-1)*6/12;
end

 hold on
 plot(age, surv,'k--','Linewidth',3)
 plot(age, surv2,'ko','Linewidth',2.5)
```

A.2 Program 2

```
% p1f2 (Chapter 2, figure 2)
% calcuates perturbations in adult survivorship for
%      senescence matrix, sets
% s4 at biological limit, allows s2 to vary and determines s3
% necessary for lambda=1
% two cases:  fecundity of 12-18 years is biological limit
% and fecundity of 12-18 years is = 0

clear
global sw0 sw1 sw2 sw3
global s2 s3 s4 f1 f2 f3;
syms sp3 Delta P
syms p2

getinitialvalues  %
p3start = -.02 ; %
p3finish= 1 - s3;
lp3=100;  % length of p2
p3=linspace(p3start,p3finish,lp3);


% part 1: biological limit for fecundity of 12-18 years old cheetah
smat=36;  % size of matrix
A=matrixA(smat);
D=zeros(smat,14);
D(1,2:4)=f1*ones(1,3);
D(1,5:14)=f2*ones(1,10);
for nn=1:14
    D(nn+4,nn)=1;
end
E=zeros(14,smat);
for nn=1:14
    E(nn,nn+3)=1;
end
% Here is Delta
for jj=1:14
    for nn=1:14
        Delta(nn,jj)=0;
    end
end
```

```
for nn=1:4;
   Delta(nn,nn)=p2;
end
for nn=5:14
     Delta(nn,nn)=sp3;
end

% check does P=D*Delta*E ?
for jj=1:smat
     for nn=1:smat
          P(nn,jj)=0;
     end
end

P(5,4)=p2; P(6,5)=p2; P(7,6)=p2; P(8,7)=p2;
P(1,5)=f1*p2 ; P(1,6)=f1*p2; P(1,7)=f1*p2;
for jj=8:17
     P(1,jj)=sp3*f2;
     P(jj+1,jj)=sp3;
end

% check
% P-D*Delta*E

p3b=[];
p2b=[];

G = E*inv(eye(smat)-A)*D;
G1T=G(:,1:4);
G2=G;
G2(:,1:4)=zeros(14,4);

for ii=1:lp3;

HP=   eye(14)-p3(ii)*G2 ;
H=inv(HP)*G1T ;  % so H is a 14 x 4 matrix
p2poss=eigs(H(1:4,:));
p2poss=1./p2poss;
flag=0;
for kk=1:length(p2poss)  % we're looking for admissible p3
     if p2poss(kk)==real(p2poss(kk)) ;
     % only want real perturbations
```

```
        if p2poss(kk) > -s2 ;
        % minimum survivorship is 0 - but can't be =0
        %  since not primitive
            if p2poss(kk) <= 1-s2 % maximum survivorship is 1
                if flag ==1
                    disp('more than one admissible eigenvalue')
                end
                flag=1;
                p2c=p2poss(kk); % this perturbation is admissible
            end
        end
    end
end
if flag == 1   % so there is an admissible perturbation
    p2b=[p2b p2c];
    p3b=[p3b p3(ii)];
end
end

% now check lambdamax
lp2b=length(p2b);
P2=zeros(smat,smat);
for ii=1:lp2b;
    P2(5,4)=p2b(ii); P2(6,5)=p2b(ii);
    P2(7,6)=p2b(ii); P2(8,7)=p2b(ii);
    P2(1,5)=f1*p2b(ii) ; P2(1,6)=f1*p2b(ii); P2(1,7)=f1*p2b(ii);
    for jj=8:17
        P2(1,jj)=p3b(ii)*f2;
        P2(jj+1,jj)=p3b(ii);
    end

    evalue=eig(A+P2);
    imax=find(evalue==max(evalue));
    lambdamax=evalue(imax)

end
disp('Check to make sure eigenv = 1')


% now plot
p2t=p2b+ones(1,lp2b)*s2;
p3t=p3b+ones(1,lp2b)*s3;
```

```
plot(p2t,p3t,'k','LineWidth',3)

hold on

%*************************************************
 % part 2  fecundity of 12-18 years old cheetah is = 0
clear P
syms P
smat=24;  % size of matrix
A=matrixA0(smat);

D=zeros(smat,14);
D(1,2:4)=f1*ones(1,3);
D(1,5:14)=f2*ones(1,10);
for nn=1:14
    D(nn+4,nn)=1;
end
E=zeros(14,smat);
for nn=1:14
    E(nn,nn+3)=1;
end
% Here is Delta
for jj=1:14
    for nn=1:14
        Delta(nn,jj)=0;
    end
end
for nn=1:4;
  Delta(nn,nn)=p2;
end
for nn=5:14
    Delta(nn,nn)=sp3;
end

% check does P=D*Delta*E ?
for jj=1:smat
    for nn=1:smat
        P(nn,jj)=0;
    end
end
```

```
P(5,4)=p2; P(6,5)=p2; P(7,6)=p2; P(8,7)=p2;
P(1,5)=f1*p2 ; P(1,6)=f1*p2; P(1,7)=f1*p2;
for jj=8:17
    P(1,jj)=sp3*f2;
    P(jj+1,jj)=sp3;
end

% check
% P-D*Delta*E

p3b0=[];
p2b0=[];

G = E*inv(eye(smat)-A)*D;
G1T=G(:,1:4);
G2=G;
G2(:,1:4)=zeros(14,4);


for ii=1:lp3;
HP= eye(14)-p3(ii)*G2 ;
H=inv(HP)*G1T ;  % so H is a 14 x 4 matrix
p2poss=eigs(H(1:4,:));
p2poss=1./p2poss;
flag=0;

% now find the one which is an admissible perturbation
for kk=1:length(p2poss)  % we're looking for admissible p3
    if p2poss(kk)==real(p2poss(kk)) ;
     % only want real perturbations
        if p2poss(kk) > -s2 ;
        % minimum survivorship is 0 - but can't be =0
        %  since not primitive
            if p2poss(kk) <= 1-s2 % maximum survivorship is 1
                if flag ==1
                    disp('more than one admissible eigenvalue')
                end
                flag=1;
                p2c=p2poss(kk); % this perturbation is admissible
            end
        end
    end
```

```
end
if flag == 1    % so there is an admissible perturbation
    p2b0=[p2b0 p2c];
    p3b0=[p3b0 p3(ii)];
end
end


% now check lambdamax
lp2b0=length(p2b0);
P2=zeros(smat,smat);
for ii=1:lp2b0;
    P2(5,4)=p2b0(ii); P2(6,5)=p2b0(ii);
    P2(7,6)=p2b0(ii); P2(8,7)=p2b0(ii);
    P2(1,5)=f1*p2b0(ii) ; P2(1,6)=f1*p2b0(ii);
    P2(1,7)=f1*p2b0(ii);
    for jj=8:17
        P2(1,jj)=p3b0(ii)*f2;
        P2(jj+1,jj)=p3b0(ii);
    end

    evalue=eig(A+P2);
    imax=find(evalue==max(evalue));
    lambdamax=evalue(imax)

end
disp('Check to make sure eigenv = 1')


% now plot
p2t0=p2b0+ones(1,lp2b0)*s2;
p3t0=p3b0+ones(1,lp2b0)*s3;
plot(p2t0,p3t0,'k','LineWidth',3)

ylabel('Survival 42-102 months, s_3*','FontSize',16)
xlabel('Survival 18-42 months,s_2*','FontSize',16)
xstart=.86;
xfinish=1.0;
ystart=.86;
yfinish=1.0;
axis([xstart xfinish ystart yfinish])
h=findobj;
```

```
set(h(3),'FontSize',14,'FontWeight','bold');
set(h(3),'YTick',[.86 .88 .90 .92 .94 .96 .98 1.0]);
set(h(3),'XTick',[.86 .88 .90 .92 .94 .96 .98 1.0]);

%
text(.9,.975,'f_3=1.4994','FontSize',16,'FontWeight','bold');
text(.982,.98,'f_3=0','FontSize',16,'FontWeight','bold');

% now draw dotted lines showing perturbed to that of
% captive cheetahs
x1=linspace(xstart,xfinish,lp2b0);
y1=0.9567*ones(1,lp2b0);
plot(x1,y1,'k-.','LineWidth',3);
x1=0.9685*ones(1,lp2b0);
y1=linspace(ystart,yfinish,lp2b0);
plot(x1,y1,'k-.','LineWidth',3);
plot(sw2,sw3,'p', 'MarkerEdgeColor','k','MarkerFaceColor','k',...
    'MarkerSize',14)     % original values for f1 and f2
text(.92+.004,.88,'A','FontSize',16,'FontWeight','bold');
```

A.3   Program 3

```
% p1f3 (Chapter 2, figure 3)
% calcuates robustness due perturbations in
% fecundity in senescence matrix
% sets s2, s3 and s4 at biological limit
%
clear
global sw0 sw1 sw2 sw3
global s2 s3 s4 f1 f2 f3
syms fsym P detAP

smat=36;  % size of matrix A
eyemat=eye(smat);
getinitialvalues

%*********************************************
% Case 1 f3=0
% nominal value is point A on graph
smat=24;  % size of matrix A
eyemat=eye(smat);
```

```
A=matrixA0(smat);

% OK, now we are going to perturb
% fecundity f2 and solve for f1

pf2start=-.4;  %
pf2finish= .4; %
lpf2=50;  % length of f2
pf2=linspace(pf2start,pf2finish,lpf2);

pf2b=[];
pf1b=[];

for jj=1:smat
    for nn=1:smat
        P(nn,jj)=0;
    end
end
for jj=1:lpf2
    flag=0;
    for kk=5:7
        P(1,kk)=s2*fsym;
    end
    for kk=8:17
        P(1,kk)=s3*pf2(jj);
    end
    for kk=18:24
        P(1,kk)=s4*pf2(jj);
    end

detAP=det(eyemat-(A+P));
f1poss=eval(solve(detAP));
for kk=1:length(f1poss)  % we're looking for admissible f1
    if f1poss(kk)==real(f1poss(kk)) ;
    % only want real perturbations
                if flag ==1
                    disp('more than one admissible eigenvalue')
                end
                flag=1;
                pf1c=f1poss(kk); % this perturbation is admissible
    end
end
```

```
if flag == 1  % i.e. there was an admissible solution
    pf1b=[pf1b pf1c];
    pf2b=[pf2b pf2(jj)];
end

end

 % check, is this lambda max?
lpf2b=length(pf2b);

P2=zeros(smat,smat);
for jj=1:lpf2b;
    for kk=5:7
        P2(1,kk)=pf1b(jj)*s2 ;
    end
    for kk=8:17
        P2(1,kk)=pf2b(jj)*s3;
    end
    for kk=18:24
        P2(1,kk)=s4*pf2b(jj);
    end
    evalue=eig(A+P2);
    imax=find(evalue==max(evalue));
    lambdamax=evalue(imax)
end
disp('Check to make sure eigenv = 1')

figure
pf2t=pf2b+ones(1,lpf2b)*f2;
pf1t=pf1b+ones(1,lpf2b)*f1;

plot(pf1t,pf2t,'k','LineWidth',3) % This is line A
ylabel('Fecundity of 42-144 months')
xlabel('Fecundity of 18-42 months')
hold on

%************************************************
% Case 2 f3=f2
% nominal value is point A on graph

f3=f2;
```

```
smat=36;
A=matrixA(smat);
eyemat=eye(smat);
pf2b=[];
pf1b=[];

for jj=1:smat
    for nn=1:smat
        P(nn,jj)=0;
    end
end
for jj=1:lpf2
    flag=0;
    for kk=5:7
        P(1,kk)=s2*fsym;
    end
    for kk=8:17
        P(1,kk)=s3*pf2(jj);
    end
    for kk=18:24
        P(1,kk)=s4*pf2(jj);
    end
    for kk=25:smat-1
        P(1,kk)=s4*pf2(jj);  % since f3=f2
    end

detAP=det(eyemat-(A+P));
f1poss=eval(solve(detAP));
for kk=1:length(f1poss)  % we're looking for admissible f1
    if f1poss(kk)==real(f1poss(kk)) ;
     % only want real perturbations
                if flag ==1
                    disp('more than one admissible eigenvalue')
                end
                flag=1;
                pf1c=f1poss(kk); % this perturbation is admissible
    end
end

if flag == 1  % i.e. there was an admissible solution
    pf1b=[pf1b pf1c];
    pf2b=[pf2b pf2(jj)];
```

```
end

end

 % check, is this lambda max?
lpf2b=length(pf2b);

P2=zeros(smat,smat);
for jj=1:lpf2b;
    for kk=5:7
        P2(1,kk)=pf1b(jj)*s2 ;
    end
    for kk=8:17
        P2(1,kk)=pf2b(jj)*s3;
    end
    for kk=18:24
        P2(1,kk)=s4*pf2b(jj);
    end
    for kk=25:smat-1
        P2(1,kk)=s4*pf2b(jj);  % since f3=f2
    end
    evalue=eig(A+P2);
    imax=find(evalue==max(evalue));
    lambdamax=evalue(imax)
end
disp('Check to make sure eigenv = 1')

pf2t=pf2b+ones(1,lpf2b)*f2;
pf1t=pf1b+ones(1,lpf2b)*f1;

plot(pf1t,pf2t,'k','LineWidth',3)  % This is the bottom line

xstart=1;
xfinish=2.5;
ystart=1;
yfinish=2.5;
axis([xstart xfinish ystart yfinish])
text(1.5,1.3,'f_3=1.4994','FontSize',16,'FontWeight','bold');
text(1.5,1.8,'f_3=0','FontSize',16,'FontWeight','bold');
plot(f1,f2,'p', 'MarkerEdgeColor','k','MarkerFaceColor',...
      'k', 'MarkerSize',14)% original values for f1 and f2
text(f1-.07,f2-.04,'C','FontSize',16,'FontWeight','bold');
```

A.4   Program 4

```
%  p1f4  Chapter 2, figure 4
% calcuates perturbations in adult survivorship for senescence
% model sets p4 at biological limit.  Sets fecundity at
% biological limit allows p2 and p3 to vary, calculates
% necessary p0 to achieve lambda=1
clear
global sw0 sw1 sw2 sw3
global s2 s3 s4 f1 f2 f3;

getinitialvalues
smat=36;

A=matrixA(smat);
eyemat=eye(smat);

% OK, now we are going to perturb adult survivorships p2 and p3
p2start=-.14;  %
p2finish= 1-s2; % perturbations can't be greater than 1
p3start= -.12 ;
p3finish=1-s3;
lp2=100;
lp3=100;
p2=linspace(p2start,p2finish,lp2);
p3=linspace(p3start,p3finish,lp3);

p2b=[];
p3b=[]
p0b=[];

for jj=1:smat
    for nn=1:smat
        P(nn,jj)=0;  % initialize P
    end
end

for nn=1:lp3
for jj=1:lp2
    flag=0;

G = E*inv(eye(smat)-A)*D;  % so G is a 15 by 15 matrix
```

```
G1T=G(:,1);
G2=zeros(15,15);
G2(:,2:5)=G(:,2:5);
G3=zeros(15,15);
G3(:,6:15)=G(:,6:15);

HP=eye(15)-p2(jj)*G2-p3(nn)*G3 ;
H=inv(HP)*G1T ;   % so H is a 15 x 1 vector

p0b(nn,jj)=1/H(1); %

end
end

% check, is this lambda max?

%lp2b=length(p2b);
%lp3b=length(p3b)'
P2=zeros(smat,smat);

for jj=1:lp2;
    for nn=1:lp3;
    P2(5,4)=p2(jj); P2(6,5)=p2(jj); P2(7,6)=p2(jj); P2(8,7)=p2(jj);
    P2(1,5)=f1*p2(jj) ; P2(1,6)=f1*p2(jj); P2(1,7)=f1*p2(jj);
    for kk=8:17
        P2(1,kk)=p3(nn)*f2;
        P2(kk+1,kk)=p3(nn);
    end
    P2(2,1)=p0b(nn,jj);
    evalue=eig(A+P2);
    imax=find(evalue==max(evalue));
    lambdamax=evalue(imax);
    if abs(lambdamax-1) > .00001  % check tolerance
        lambdamax
    end
end
end

disp('Check to make sure eigenv = 1')

figure
p2t=p2+ones(1,lp2)*s2;
```

```
p3t=p3+ones(1,lp3)*s3;
p0t = p0b + ones(lp3,lp2)*sw0;
% adding the original survivorship to the perturbation

[cs,h]=contour(p2t,p3t,p0t,[.081 .1 .12 .14 .155 .18 .20] );
%clabel(cs,h,'fontsize',16);
colormap('gray')
caxis([4 5]);
xlabel('Survival of 18-42 month young adults, s_2*')
ylabel('Survival of 42-102 month adults, s_3*')
axis([.87 1 .87 1])
h=findobj;
set(h(3),'FontSize',14,'FontWeight','bold');

%
hold on

% now draw dotted lines showing perturbed to
% that of captive cheetahs
xstart=.8;
xfinish=1;
x1=linspace(xstart,xfinish,lp2);
y1=s3*ones(1,lp2);
plot(x1,y1,'k-.','LineWidth',3);
x1=s2*ones(1,lp2);
y1=linspace(xstart,xfinish,lp2);
plot(x1,y1,'k-.','LineWidth',3);
plot(sw2,sw3,'p', 'MarkerEdgeColor','k','MarkerFaceColor','k');
text(sw2+.004,sw3,'A','FontSize',16,'FontWeight','bold');
```

A.5   Common Subroutines

```
function getinitialvalues
% This sets the initial values
global sw0 sw1 sw2 sw3
global s2 s3 s4 f1 f2 f3 ;
sw0 = .081 ;  % survival of juvenile wild cubs age 0-6 month
sw1 = .771  ; % survival of juvenile wild cubs age 6-12 month
               % and 12-18 month
sw2 = .92;   % survival of wild 18-24, 24-30, 30-36,
             % and 36-42 month
sw3 = .879; % survival of wild adults age 42+
```

```
s2 = .9685; % biological limit for  wild young adults
             % (18-42 months)
s3 = .9567; % biological limit for wild mid age adults
             % (42-102 months)
s4 = .8980; % biological limit for wild very old adults
             % (102+ months)
f1 = 1.75*(365/256)*(1/2) ;  % from Crooks' paper -
        %fecundity of 24-42 age classes
f2 = 1.75*(365/213)*(1/2) ;  % from Crooks' paper -
        %fecundity of 42 - 144 age classes
f3 = f2; %fecundity of 144-216 month age classes (12-18 years)
          % we'll perturb this

function A=matrixA(smat)
% matrixA
% This calculates matrix A for all pictures for paper #1
% smat is size of square matrix Z
global sw0 sw1 sw2 sw3
global s2 s3 s4 f1 f2 f3;
A=zeros(smat,smat) ;

% put in survivorships into matrix
A(2,1)=sw0;
A(3,2)=sw1; A(4,3)=sw1;
A(5,4)=s2; A(6,5)=s2; A(7,6)=s2; A(8,7)=s2;
A(1,5)=f1*s2 ; A(1,6)=f1*s2; A(1,7)=f1*s2;
for jj=8:17
    A(1,jj)=s3*f2;
    A(jj+1,jj)=s3;
end
for jj=18:24
    A(1,jj)=s4*f2;
    A(jj+1,jj)=s4;
end
for jj=25:smat-1
    A(1,jj)=s4*f3;
    A(jj+1,jj)=s4;
end
A(1,smat)=0;%s4*f3;

function A=matrixA0(smat)
% matrixA
% This calculates matrix A for all pictures for paper #1 using zero
```

```
% fecundity if cheetah is over 12 years
% smat is size of square matrix Z
global sw0 sw1 sw2 sw3
global s2 s3 s4 f1 f2 f3

A=zeros(smat,smat) ;

% put in survivorships into matrix
A(2,1)=sw0;
A(3,2)=sw1; A(4,3)=sw1;
A(5,4)=s2; A(6,5)=s2; A(7,6)=s2; A(8,7)=s2;
A(1,5)=f1*s2 ; A(1,6)=f1*s2; A(1,7)=f1*s2;
for jj=8:17
    A(1,jj)=s3*f2;
    A(jj+1,jj)=s3;
end
for jj=18:smat-1
    A(1,jj)=s4*f2;
    A(jj+1,jj)=s4;
end

A(1,smat)=0;%s4*f3;
```

Appendix B

Chapter 3 Computer Programs

B.1 Program 1

```
% figure 1 in chapter 2
clear all
global n nage nquality gammaq cutq phiy

% what lambda do we deisre?
lambda = [.7 .8 .9 1 1.1 1.2 1.3 ];
[pvec,L,U,pest,withq]=getinitialvalues;

% boundary points b and mesh points y
c=0:1:n ;    % row vector
b = L+c*(U-L)/n;
y = 0.5*(b(1:n)+b(2:(n+1)));
kidsizemean=pvec(13);
kidsizevar=pvec(14);

phiy=normpdf(y,kidsizemean,sqrt(kidsizevar))/ ...
    (1-normcdf(0,kidsizemean,sqrt(kidsizevar)));
phiy=transpose(phiy);  %
%points for numerical integration of survival intercepts
cutq = linspace(-4*pvec(4),4*pvec(4),nquality);
%normalised to sum to 1
gammaq=normpdf(cutq,0,1)/sum(normpdf(cutq,0,1));

hold on
ploticon=['k',':','--'];
p2start= -.02499;  % thus p2 + pest > 0.0001 > 0
p2finish= .07;
```

```
npoints=100;
p2=linspace(p2start, p2finish,npoints);

for kk=1:3  % lambda < 1
    % now calculate triple integral
    w=D(1, withq);
    w=IminusA0inv(pvec,w,y,U,L,lambda(kk),withq);
    gamma(kk)=E(pvec,w,pest,y,U,L,withq);
    gamma(kk)=gamma(kk)/pest;
    p1=zeros(1,npoints);
    for jj=1:npoints
        p1(jj)=log(lambda(kk)/((pest+p2(jj))*gamma(kk)));
    end
    plot(p1+pvec(11),p2+pest, ':')
end
kk=4;  % lambda =1
    % now calculate triple integral
    w=D(1, withq);
    w=IminusA0inv(pvec,w,y,U,L,lambda(kk),withq);
    gamma(kk)=E(pvec,w,pest,y,U,L,withq);

    gamma(kk)=gamma(kk)/pest;
    p1=zeros(1,npoints);
    for jj=1:npoints
        p1(jj)=log(lambda(kk)/((pest+p2(jj))*gamma(kk)));
    end
    plot(p1+pvec(11),p2+pest, 'k')

for kk=5:7  % lambda >1
        % now calculate triple integral
    w=D(1, withq);
    w=IminusA0inv(pvec,w,y,U,L,lambda(kk),withq);
    gamma(kk)=E(pvec,w,pest,y,U,L,withq);

    gamma(kk)=gamma(kk)/pest;
    p1=zeros(1,npoints);
    for jj=1:npoints
        p1(jj)=log(lambda(kk)/((pest+p2(jj))*gamma(kk)));
    end
    plot(p1+pvec(11),p2+pest, '-')
end
xlabel('Fecundity Intercept, p_1','FontSize',16)
```

```
ylabel('Probability of seedling establishment, p_e','FontSize',16)
axis([-16.27 -7.41 0 .06])
plot(-11.85,0.025,'d')
```

B.2   Program 2

```
% plots figures 2 and 3 in chapter 3
clear
global n nage nquality gammaq cutq phiy
[pvec,L,U,pest,withq]=getinitialvalues;
kidsizemean=pvec(13);
kidsizevar=pvec(14);

lambda=1; % what lambda do we desire?
storepvec=pvec; % because change it later
p2start=-4.43 ;
% we're perturbing fecundity intercept (nominal value = -11.84)
p2finish=4.43 ;
p3start=  -.6 ;
% we're perturbing fecundity slope (nominal value = 2.27)
p3finish=  .6 ; %
npoints=50 ; % # of perturbations
p2=linspace(p2start, p2finish,npoints);
npointsp3=50 ; % # of perturbations
p3=linspace(p3start, p3finish,npointsp3);
p1=zeros(npoints, npointsp3);

YMIN = storepvec(11)-4.43;  % limits on graph
YMAX = storepvec(11)+4.43;
XMIN = storepvec(12)-.60;
XMAX = storepvec(12)+.60;
ZMIN = 0;
ZMAX = 1;

% boundary points b and mesh points y
c=0:1:n ;    % row vector
b = L+c*(U-L)/n;
y = 0.5*(b(1:n)+b(2:(n+1)));

if withq==0
    pvec(4)=0 ;
end
```

```
if nquality==1;
    pvec(4)=0;
end

phiy=normpdf(y,kidsizemean,sqrt(kidsizevar))/ ...
         (1-normcdf(0,kidsizemean,sqrt(kidsizevar)));
phiy=transpose(phiy);  %
%points for numerical integration of survival intercepts
cutq = linspace(-4*pvec(4),4*pvec(4),nquality);
%normalised to sum to 1
gammaq=normpdf(cutq,0,1)/sum(normpdf(cutq,0,1));
ww=D(1, withq);
% now calculate triple integral (*)
for jj=1:npoints
    w=IminusA0inv(storepvec,ww,y,U,L,lambda,withq);
    for kk=1:npointsp3
        pvec(12)=storepvec(12)+p3(kk);
        gamma(kk)=E(pvec,w,pest,y,U,L,withq);
        p1(jj,kk)=pest*((lambda/gamma(kk))*exp(-p2(jj))-1);
    end

end
xx=p3+storepvec(12);
yy=p2+storepvec(11);
zz=p1+pest;
mesh(xx,yy,zz)
hold on

colormap('gray')
zlabel('Probability of seedling establishment, p_e');
ylabel('Fecundity Intercept, p_1');
xlabel('Fecundity Slope, p_2');
% now plot nominal values
plot3(2.27,-11.84,0.025,'kd')
AXIS([XMIN XMAX YMIN YMAX ZMIN ZMAX])
%
figure
[X, Y]=meshgrid(xx,yy);
contour(X,Y,zz,'LineWidth',3,'LineColor',[0 0 0],...
    'LevelList',[0.01 0.03 0.1 0.3 0.6 1]);

colormap('gray')
```

```
xlabel('Fecundity Slope, p_2');
ylabel('Fecundity Intercept, p_1');
hold on
plot(2.27,-11.84,'kd')
```

B.3   Common Subroutines

```
function [pvec,L,U,pest,withq]=getinitialvalues
% getinitialvalues
% this gets the initial values needed for all of my matlab files
global n nage nquality gammaq cutq phiy
n=50;
nage=8;
nquality=1;
% Rounded parameter vector,
% see Table 1 in Ellner and Rees for more details.
pvec=[-1.42 1.08 -1.09 0.82 -24.01 2.91 .84 3.24 .56  ...
        42.47 -11.84 2.27 1.06 3.37 -0.71/2];
L=0;% minimum (0.9*minimum size from data)
U=9.24; % maximum sizes (1.1*maximum size from data)
%probability of seedling establishment
pest=0.025     ;
withq=0 ; % if we're using quality, otherwise =0 if not

function Aw = IminusA0inv(params,w,y,U,L,lambda,withq);
global n nage nquality gammaq cutq phiy
% computes  (I-A_0/lambda)^{-1}w
% note -  A0 is a nilpotent operator,
% thus we need to only carry out the
% summation to the nage^{th} term

Aw=w;
P=getmatrixP(params,y,U,L,withq);
if withq==1
    v=zeros(n,nage,nquality) ;% ;
    for iter=1:nage-1  % since A0 is nilpotent
        v=A0withq(params,w,y,U,L,P);
        w=v;
        Aw=Aw+w/lambda^(iter);
        % i.e. (I + A_0 /lambda + (A_0)^2/lambda + ...)w
    end
else
```

```
        v=zeros(n,nage) ;% ;
    for iter=1:nage-1  % since A0 is nilpotent
        v=A0noq(params,w,y,U,L,P);
        w=v;
        Aw=Aw+w/lambda^(iter);
        % i.e. (I + A_0 /lambda + (A_0)^2/lambda + ...)w
    end
end


function w=D(alpha,withq);
% alpha := scalar
% w := element in the Banach space
% withq =1 if adding quality
global n nage nquality gammaq cutq phiy

if withq==1  % with quality
    w=zeros(n,nage,nquality);
 % distribute into sizes
    SizeN=phiy*alpha;
 % distribute into quality classes and into the first age class
    for interb=1:nquality
        w(:,1,interb)=w(:,1,interb)+gammaq(interb)*SizeN;
    end
else
    w=zeros(n,nage);
 % now distribute into sizes
    w(:,1)=phiy*alpha;  % distribute into size classes and
                        % into the first age class
end


function nbirths=E(params,Nt,pest,y,U,L,withq);
% calculates the number of new births by population distribution Nt
% alpha := scalar
% Nt := element of the Banach space
global n nage nquality gammaq cutq phiy

storepvec=params;
if withq==1
B=zeros(n,nage,nquality);  % fecundity
%Create matrix B, looping over quality class
%  (survival intercept) and age
for inter = 1:nquality
```

```
 for age = 1:nage
%   # Calculate survival intercept for this quality class
    params(1) = storepvec(1)+cutq(inter);
%   # Calculate survival and birth matrices for
%  each quality (intercept) age combination.
    for xi=1:n
        B(xi,age,inter)=fxyt(y(xi),age,params,pest);   %
    end
end
end
B=(U-L)*B/n;  % this gives B(x);

% now evaluate triple integral
nbirths = 0;  % total number of new births
 for interp=1:nquality
  for agep=1:nage
  % number of births per size and quality
  nbirths= nbirths + transpose(B(:,agep,interp))*Nt(:,agep,interp)
   end
  end
else  % no quality
    B=zeros(n,nage);  % fecundity
%Create matrix B, looping over age
 for age = 1:nage
    for xi=1:n
        B(xi,age)=fxyt(y(xi),age,params,pest);   %
    end
end

B=(U-L)*B/n;  % this gives B(x);

% now evaluate double integral
nbirths = 0;  % total number of new births
    for agep=1:nage
      % number of births per size
      nbirths= nbirths + transpose(B(:,agep))*Nt(:,agep);
    end
end


function P=getmatrixP(params,y,U,L,withq);
% calculates matrix P which is used to estimate A0
```

```
global n nage nquality gammaq cutq phiy
if withq==1
P=zeros(n,n,nage,nquality);  % survival growth
oldpvec=params;
%Create matrix P, looping over quality class
% (survival intercept) and age
for inter = 1:nquality
    params(1) = oldpvec(1)+cutq(inter);
 for age = 1:nage
    for xi=1:n
        for yi=1:n
        P(yi,xi,age,inter)=pxyt(y(yi),y(xi),age,params);
        end
    end
 end
end
P=(U-L)*P/n;  % this gives P(y,x)   ;

else  % no quality
P=zeros(n,n,nage);  % survival growth
%Create matrix P, looping over age
 for age = 1:nage
    for xi=1:n
        for yi=1:n
        P(yi,xi,age)=pxyt(y(yi),y(xi),age,params);  %
        end
    end
end

P=(U-L)*P/n;  % this gives P(y,x)   ;

end

function w=A0noq(params,Nt,y,U,L,P);
% calculates survial and growth by population distribution Nt
% Nt := original element of the Banach space
% w := new element of Banach space
global n nage nquality gammaq cutq phiy
w=zeros(n,nage);
for age=2:nage
    w(:,age)=P(:,:,age-1)*Nt(:,age-1);
end
```

```
function w=A0withq(params,Nt,y,U,L,P);
% calculates survial and growth by population distribution Nt
% Nt := original element of the Banach space
% w := new element of Banach space
global n nage nquality gammaq cutq phiy
w=zeros(n,nage,nquality);
  for inter=1:nquality
      for age=2:nage
          w(:,age,inter)=P(:,:,age-1,inter)*Nt(:,age-1,inter);
      end
  end
```

Appendix C

Chapter 4 Computer Programs

C.1 Program 1

```
# MCday.R
# this file chooses bootstrapped parameters
# for model as a function of ordinal days
rm(list=ls())
library(survival)
changerep=0
for (datarun in 3:3){
if(datarun==1){
fecfile <- "DevFec68degreesm2.csv"
outfile="MCday68LH.csv"
shift=10.5
}
if(datarun==2){
fecfile <- "DevFec76degreesm2.csv"
outfile="MCDay76LH.csv"
shift=7.5
}
if(datarun==3){
changerep=3 # = 0  don't shift 20 C reproduction
# = 1 yes shift 20 C reproduction by one day
# = 2 change possibility of beginning to reproduce to 8.5 days
# = 3 yes shift 20 C reproduction by two days
fecfile <- "DevFec68highhumiditym2.csv"
outfile="MCday68HH.csv"
shift=11.5
if(changerep==1){
outfile="MCday68HHwithshiftv3.csv"
```

```
shift=10.5
}
if(changerep==2){
outfile="MCday68HHwithshift.csv"
shift=8.5
}
if(changerep==3){
outfile="MCday68HHwithshiftv4p2.csv"
shift=9.5
}


}
if(datarun==4){
fecfile <- "DevFec76highhumiditym2.csv"
outfile="MCday76HH.csv"
shift=7.5
}



# initialize array to print to file
# nc = number of parameters to find
# np = number of points
nc=8
np=9000



MC<-array(NA,dim=c(np,nc))
# column #1, wrho<= location(lambda) for survivorship
# column #2, wkappa <= scale(kappa) for survivorship
# column #3, rrho <= rho for first day of reproduction
# column #4, rkappa <= kappa for first day of reproduction
# column #5, shift <= shift for first day of reproduction
# column #6, c1 <= x^0 term:
#       fecundity as function of days from onset of reproduction
# column #7, c2 <= x^1 term:
#       fecundity as function of days from onset of reproduction
# column #8, set =0
#####################################
# survtoday
# converts data file into format for survival analysis
#
survtoday=function(aphid){
```

```
# make matrix for input into survfitdays
#% csurv =   column 1 = # days for this aphid since birth
#% ysurv =   column 2 = # of offspring since birth
#                               (i.e. its still alive)
#% asurv =   column 3 = aphid #

csurv=0; # initialize - I'll remove the zeros later
ysurv=0;
asurv=0;
#%

len=length(aphid);
aphid=as.matrix(aphid)
for(ii in 1:len) {  #  % for each aphid
    yesalive=0;   # initialize - I'll remove the zero later
    # find index of negative entry
     daydied=which(aphid[,ii]<0)
daydied=as.numeric(daydied)
    if (aphid[daydied,ii] == -2) {  # died on day giving birth
      yesalive=aphid[1:daydied-1,ii] ;# since died on previous day
    }
    if (aphid[daydied,ii] == -1) {# so died day after giving birth
        yesalive=aphid[1:daydied,ii];
        yesalive[daydied]=0;  # get rid of that negative
    }
    aphidnum=ii*rep(1,length(yesalive));
    lyesalive=length(yesalive);  # initialize
    cumday=seq(1,lyesalive);
    cumday=cumday-1
    # now assume only survived half the day
    cumday[lyesalive]=cumday[lyesalive]-.5
    csurv=c(csurv,cumday)  # cumulative days
    ysurv=c(ysurv,yesalive)   # yes its alive on those days
    asurv=c(asurv,aphidnum)   # aphid number
}

# get rid of those leading zeros
csurv=csurv[-1]
ysurv=ysurv[-1]
asurv=asurv[-1]
survdata=data.frame(csurv,ysurv,asurv)
```

```
return(survdata)
}


###########################################################
###########################################################

fectoday= function(aphid){
# cfecday =   column 1 = # days for this offspring since
#                      first day of reproduction
# offspring =   column 2 = # of offspring
cfecday=0; # initialize - I'll remove the zeros at the end
offspring=0 ; # initialize - I'll remove the zeros at the end

len=length(aphid);
aphid=as.matrix(aphid)
for( ii in 1:len) {  #  % for each aphid
    firstrep=which(aphid[,ii]>0) # % finds positive entries
 #   %                        doesn't reproduce - then = NA
    firstrep=as.numeric(firstrep)
daydied=which(aphid[,ii]<0)
daydied=as.numeric(daydied)
    lenfirstrep=length(firstrep)
    noffspring=0;
    # number of days in reproductive period
    days=daydied-firstrep[1]
    if ( lenfirstrep > 0 ){ # so it reproduced
  cumdays=seq(1,days,1)
  cumdays=cumdays-1  # assume born on day 0
# this next line is because I assume that when
# the aphid begins to reproduce,
# the first data point is only for a 1/2 day
if(lenfirstrep >1){
 cumdays[2:length(cumdays)]=cumdays[2:length(cumdays)]-1/2
}
        # pick off reproducing days
        noffspring=as.numeric(aphid[firstrep[1]:(daydied-1),ii]);
# note - the first data point is for one-half day, thus
# the rate fecundity/day is actually twice the observed
# offspring, so
  noffspring[1]=noffspring[1]*2
        cfecday=c(cfecday,cumdays)
        offspring=c(offspring,noffspring)
```

```
  }}

cfecday=cfecday[-1] # get rid of those leading zeros
offspring=offspring[-1]

ab=data.frame(cfecday,offspring)
return(ab)
}

############################################################

# so, for every different run
for (ii in 1:np){
#%
#% read in surv/fecundity
#% -1 = died
#% -2 = died previous day but had offspring on that day
aphid=read.csv(fecfile,header=FALSE)
# here I do my bootstrapping
aphid=sample(aphid,replace=T)


# now find survivorship parameters
survdata = survtoday(aphid)
days=  survdata$csurv # first column
offspring=survdata$ysurv # second column
ind=survdata$asurv # third column
fecundity=data.frame(days,offspring,ind)
fec.freq = data.frame(table(days,offspring))
fec.freq$days = as.numeric(levels(fec.freq$days))[fec.freq$days]
fec.freq$offspring =
    as.numeric(levels(fec.freq$offspring))[fec.freq$offspring]

surv.times = tapply(fecundity$days,fecundity$ind,max)
surv.times = tapply(fecundity$days,fecundity$ind,max)
surv.mod1 = survreg(Surv(surv.times)~1,dist="weibull")
rho = 1/exp(surv.mod1$icoef[1])
kappa = 1/exp(surv.mod1$icoef[2])
MC[ii,1]=rho
MC[ii,2]=kappa
############################################################
# find age when the sampled aphids first reproduced
```

```
whenrep=0
status=0

ncol=length(aphid[1,])
for (jj in 1:ncol) { # for each aphid
# find when reproduced
index=which(aphid[,jj]!= 0)
if (aphid[index[1],jj]<0){  # died before giving birth
status=c(status,0)
whenrep=c(whenrep,index[1])
}
if (aphid[index[1],jj]>0){
status=c(status,1)
whenrep=c(whenrep,index[1])
}
}
#
whenrep=whenrep[-1] # get rid of the leading zero

status=status[-1]
whenrep=whenrep-1.5 # because when I wrote down the data,
   #    I started with day=1,
         # but in all my programming, I start with day==0
# shifting the onset of reproduction by one day
if(changerep==1) whenrep=whenrep-0.99
# use 0.99 because of survreg
# shifting the onset of reproduction by two days
if(changerep==3) whenrep=whenrep-1.99
# use 0.99 because of survreg
whenrep=whenrep-shift
index=which(whenrep>=0)
whenrep=whenrep[index]

status=status[index]


rep.mod2 = survreg(Surv(whenrep)~1,dist="weibull")
rho = 1/exp(rep.mod2$icoef[1])
kappa = 1/exp(rep.mod2$icoef[2])
MC[ii,3]=rho
MC[ii,4]=kappa
MC[ii,5]=shift  # shift is the # of initial days
```

```
                              # when no aphids gave birth


#######################################################
# find the parameters for
# fecundity as a function of days from onset of reproduction
#

fecdata <- fectoday(aphid)
days= fecdata$cfecday # first column
offspring=fecdata$offspring # second column
fecundity=data.frame(days,offspring)

fec.model1 =
     glm(offspring~days,family=poisson(link="log"),data=fecundity)
xx=fec.model1$coef

MC[ii,6]=xx[1]
MC[ii,7]=xx[2]
MC[ii,8]=0
}

write.csv(MC,file=outfile,row.names=FALSE)
}
```

C.2   Program 2

```
# MCdd.R
# this file chooses bootstrapped parameters for degree day model
#

rm(list=ls())

library(survival)
changerep=1 # = 0  don't shift 20 C reproduction
# = 1 yes shift 20 C reproduction by 1 day
# = 2 just change possibility of first reproduction to 8.5 days

for (datarun in 2:2){
```

```
if(datarun==1){
# low humidity data
avgtemp76=25.37
avgtemp68=19.85
# read in daily average temperature
tempdata76=read.csv("RoomAApr21May30.csv", header=FALSE)
tempdata68=read.csv("RoomBFeb21Apr6.csv", header=FALSE)


fec68file <- "DevFec68degreesm2.csv"
fec76file <- "DevFec76degreesm2.csv"
outfile="MCddLH.csv"
shift68=10.5
shift76=7.5
}
if(datarun==2){
# high humidity data
avgtemp76=24.51
avgtemp68=19.52
# read in daily average temperature
tempdata76=read.csv("RoomASep18Oct28.csv", header=FALSE)
tempdata68=read.csv("RoomBSep18Nov3.csv", header=FALSE)


fec68file <- "DevFec68highhumiditym2.csv"
fec76file <- "DevFec76highhumiditym2.csv"
outfile="MCddHH.csv"
if(changerep==1){outfile="MCddHHwithshiftv3p2.csv"}
if(changerep==2){outfile="MCddHHwithshift.csv"}
shift68=11.5
if(changerep==1){shift68=10.5}
if(changerep==2){shift68=8.5}
shift76=7.5
}


# initialize array to print to file
# nc = number of parameters to find
# np = number of points
nc=9
np=9000
```

```
MC<-array(NA,dim=c(np,nc))
# column #1, wrho<= location(lambda) for survivorship
# column #2, wkappa <= scale(kappa) for survivorship
# column #3, rrho <= rho for first day of reproduction
# column #4, rkappa <= kappa for  first day of reproduction
# column #5, shift <= shift for first day of reproduction
# column #6, c1 <= x^0 term:
#     fecundity as function of days from onset of reproduction
# column #7, c2 <= x^1 term:
#      fecundity as function of days from onset of reproduction
# column #8, c3 <= 0 not used
# column #9, lowerthres


######################################################################
######################################################################
# survtoday subroutine
# converts data file into format for survival analysis
#
survtoday=function(aphid,lowerthres,tempdata){

# make matrix for input into survfitdays
#% csurv = column 1 = # days for this aphid since birth
#% ysurv = column 2 = # of offspring since birth so still alive
#% asurv = column 3 = aphid #

csurv=0; # initialize - I'll remove the zeros later
ysurv=0;
asurv=0;



#convert daily temperature to degree days
dailyavgtem=tempdata$V6
index=which(is.na(dailyavgtem)==0)

avgtemp=dailyavgtem[index];
# avgtemp(1) = average temp from birth noon next day
#              (day 0 to day 1)
# avgtemp(2) = average temp from day 1 to day 2
# avgtemp(3) = average temp from day 2 to day 3 etc.

len=length(aphid);
```

```
aphid=as.matrix(aphid)
for(ii in 1:len) {  #  % for each aphid
    yesalive=0;   # initialize - I'll remove the zero later
     daydied=which(aphid[,ii]<0) # finds index of negative entry
daydied=as.numeric(daydied)

  if (aphid[daydied,ii] == -2) {# died on day giving birth
     yesalive=aphid[1:daydied-1,ii];# since died on previous day
  }
  if (aphid[daydied,ii] == -1) {  # so died day after giving birth
    yesalive=aphid[1:daydied,ii];
     yesalive[daydied]=0;  # get rid of that negative
  }

    aphidnum=ii*rep(1,length(yesalive));
    lyesalive=length(yesalive);  # initialize
    cumdays=seq(1,lyesalive);
    cumdays=cumdays-1
    #assume only survived half the day
    cumdays[lyesalive]=cumdays[lyesalive]-.5
# first find elapsed degree days per day
#no elapsed degree days have elapsed at beginning of experiment
dd=0
for(kk in 2:length(cumdays)){
dd=c(dd,(avgtemp[kk-1]-lowerthres)*(cumdays[kk]-cumdays[kk-1]))
}
##convert cumdays to degree days
edd=dd # initialize
for(jj in 2:length(dd)){
edd[jj]=edd[jj-1]+edd[jj] # elapsed cumulative degree days
}

        csurv=c(csurv,edd)  # cumulative degree days
  ysurv=c(ysurv,yesalive)# yes its alive on those days
               #(gives # of offspring)
  asurv=c(asurv,aphidnum) # aphid number
}

# get rid of those leading zeros
csurv=csurv[-1]
ysurv=ysurv[-1]
asurv=asurv[-1]
survdata=data.frame(csurv,ysurv,asurv)
```

```
return(survdata)
}


################################################################

fectoday= function(aphid,lowerthres,tempdata,temp){

len=length(aphid[1,]);
aphid=as.matrix(aphid)
# cdegday =    column 1 =  cumulative degree days for
#            this offspring since first day of reproduction
# offspringdd =   column 2 = # of offspring per degree day
# offspring day = column 3 = # of offspring per day
# dailydegday = column 4 = daily degree days for this offspring
cdegday=0; # initialize - I'll remove the zeros at the end
offspringdd=0; # initialize-I'll remove the zeros at the end
offspringday=0; # initialize-I'll remove the zeros at the end
dailydegday = 0; # initialize-I'll remove the zeros at the end

#convert daily temperature to degree days
dailyavgtem=tempdata$V6
index=which(is.na(dailyavgtem)==0)

avgtemp=dailyavgtem[index];
# avgtemp(1) = average temp from birth noon next day
#       (day 0 to day 1)
# avgtemp(2) = average temp from day 1 to day 2
# avgtemp(3) = average temp from day 2 to day 3 etc.

for( ii in 1:len) {  #  % for each aphid
firstrep=which(aphid[,ii]>0) # % finds positive entries -
#                                 if doesn't reproduce - then = NA
firstrep=as.numeric(firstrep)
daydied=which(aphid[,ii]<0)
daydied=as.numeric(daydied)
      lenfirstrep=length(firstrep)
      noffspring=0;
      days=daydied-firstrep[1]
      # number of days in reproductive period
   if(lenfirstrep >0) { # gave birth at least one day
    cumdays=seq(1,daydied,1)
 # assume born when zero degree days have elapsed
```

```
   cumdays=cumdays-1
        # pick off reproducing days
        noffspring=as.numeric(aphid[firstrep[1]:(daydied-1),ii]);
# this next line is because I assume that when
# the aphid begins to reproduce,
# the first data point is only for a 1/2 day
   cumdays[firstrep[1]]=cumdays[firstrep[1]]-1/2
if(days>1){
 cumdays[(firstrep[1]+1):length(cumdays)]=
        cumdays[(firstrep[1]+1):length(cumdays)]-1
}
# get rid of days not reproducing
cumdays=cumdays[(firstrep[1]):length(cumdays)]
# convert from offspring per day to offspring per degree day
# first find degree days per day on the days it reproduced
dd=0 # initialize
for(kk in 1:length(cumdays)-1){
dd=c(dd,(avgtemp[kk]-lowerthres)*
                    (cumdays[kk+1]-cumdays[kk]))
}
dd=dd[-1]


## find cumulative elapsed degree days
edd=0 # initialize
for(jj in 1:(length(dd))){
edd=c(edd, (edd[jj]+dd[jj])) # elapsed cumulative degree days
}

# now convert from offspring per day to offspring per degree day
  noffspringday=noffspring
  noffspringdd=noffspring
# note - the first data point is for one-half day, thus
# the rate fecundity/day is actually twice the observed
#  offspring, so
  noffspringday[1]=noffspringday[1]*2
# this is automatically taken into account when converting to
# degree days since dd[1] is only 1/2 day
        noffspringdd=noffspring/dd[1:length(noffspring)]
        if(days == 1){
cdegday=c(cdegday, dd[1])
dailydegday=c(dailydegday,dd[1])
```

```
  }
  if(days > 1) {
cdegday=c(cdegday, edd[1:length(edd)-1])
dailydegday=c(dailydegday,dd[1:length(edd)-1])
  }
        offspringday=c(offspringday,noffspringday)
        offspringdd=c(offspringdd,noffspringdd)
}}

cdegday=cdegday[-1] # get rid of those leading zeros
offspringdd=offspringdd[-1]
offspringday=offspringday[-1]
dailydegday=dailydegday[-1]
ab=data.frame(cdegday,offspringdd,offspringday,dailydegday)
return(ab)
}



############################################################
############################################################

# so, for every different run
for (ii in 1:np){
#%
#% read in surv/fecundity
#% -1 = died
#% -2 = died previous day but had offspring on that day
aphid68=read.csv(fec68file,header=FALSE)
aphid76=read.csv(fec76file,header=FALSE)
# here I do my bootstrapping
#
aphid68=sample(aphid68,replace=T)
aphid76=sample(aphid76,replace=T)
whenrep68=0
ncol=length(aphid68[1,])
for (jj in 1:ncol) { # for each aphid
xx=which(aphid68[,jj]!=0)
if(aphid68[xx[1],jj]>0){# so it reproduced before dying
whenrep68=c(whenrep68,xx[1])
}
}
whenrep68=whenrep68[-1]
```

```
if(changerep==1){whenrep68=whenrep68-0.99}
whenrep76=0
ncol=length(aphid76[1,])
for (jj in 1:ncol) { # for each aphid
xx=which(aphid76[,jj]!=0)
if(aphid76[xx[1],jj]>0){ # so it reproduced before dying
whenrep76=c(whenrep76,xx[1])
}
}
whenrep76=whenrep76[-1]

whenrep=c(whenrep68, whenrep76)
t68=whenrep68*0+1 #trick to make t68 the same length as whenrep68
t68=t68*avgtemp68
t76=whenrep76*0+1 #trick to make t76 the same length as whenrep68
t76=t76*avgtemp76
temp=c(t68,t76)
# find out what adult aphids didn't reproduce
nooffspring=match(whenrep,c(0))
# find what indices of whenrep where the aphid does reproduce
index=which(is.na(nooffspring))
  # vector of only those that reproduce
yeswhenrep=as.numeric(whenrep[index])

yeswhenrep=yeswhenrep-1.5 # because when I wrote down the data,
#       I started with day=1,
# but in all my programming, I start with day==0
# Also, on average begin to reproduce 1/2 before I see babies.

yeswhenrep=1/yeswhenrep
temp2=temp[index]
temp2=as.numeric(temp2)
birthdata=data.frame(temp2,yeswhenrep)
# assuming normal distribution of errors
m1 = glm(yeswhenrep~temp2,data=birthdata)
slope=m1$coefficients[2]
intercept=m1$coefficients[1]
lowerthres=-intercept/slope
MC[ii,9]=lowerthres


##############################################################
```

```
# find age when the sampled aphids first reproduced
# convert to degree days
whenrep68=0
status68=0

ncol=length(aphid68[1,])
for (jj in 1:ncol) { # for each aphid
# find when reproduced
index=which(aphid68[,jj]!= 0)
if (aphid68[index[1],jj]<0){  # died before giving birth
status68=c(status68,0)
whenrep68=c(whenrep68,index[1])
}
if (aphid68[index[1],jj]>0){
status68=c(status68,1)
whenrep68=c(whenrep68,index[1])
}
}
#
whenrep68=whenrep68[-1] # get rid of the leading zero
status68=status68[-1]
whenrep76=0
status76=0

ncol=length(aphid76[1,])
for (jj in 1:ncol) { # for each aphid
# find when reproduced
index=which(aphid76[,jj]!= 0)
if (aphid76[index[1],jj]<0){  # died before giving birth
status76=c(status76,0)
whenrep76=c(whenrep76,index[1])
}
if (aphid76[index[1],jj]>0){
status76=c(status76,1)
whenrep76=c(whenrep76,index[1])
}
}
#
whenrep76=whenrep76[-1] # get rid of the leading zero
status76=status76[-1]

whenrep68=whenrep68-1.5
```

```
  # change onset of reproduction
if (changerep==1){whenrep68=whenrep68-0.99}
whenrep76=whenrep76-1.5
whenrep68=(avgtemp68-lowerthres)*whenrep68
whenrep76=(avgtemp76-lowerthres)*whenrep76
whenrep=c(whenrep68,whenrep76)
status=c(status68,status76)

index=which(status!=0)

# convert earliest day of reproduction to degree days
shift1=(avgtemp68-lowerthres)*shift68
shift2=(avgtemp76-lowerthres)*shift76
shift3=min(whenrep[index])
shift=min(shift1,shift2,shift3)



whenrep=whenrep-shift+.001
index=which(whenrep>=0)
whenrep=whenrep[index]
status=status[index]



rep.mod2 = survreg(Surv(whenrep,status)~1,dist="weibull")
rho = 1/exp(rep.mod2$icoef[1])
kappa = 1/exp(rep.mod2$icoef[2])
MC[ii,3]=rho
MC[ii,4]=kappa
MC[ii,5]=shift  # shift is the # of initial days
                   # when no aphids gave birth

##################################################
# now find survivorship parameters
survdata68 = survtoday(aphid68,lowerthres,tempdata68)
survdata76 = survtoday(aphid76,lowerthres,tempdata76)
survdata=merge(survdata68,survdata76,all=T)
degdays=  survdata$csurv # first column
offspring=survdata$ysurv # second column
ind=survdata$asurv # third column
fecundity=data.frame(degdays,offspring,ind)
fec.freq = data.frame(table(degdays,offspring))
```

```
fec.freq$degdays =
     as.numeric(levels(fec.freq$degdays))[fec.freq$degdays]
fec.freq$offspring =
     as.numeric(levels(fec.freq$offspring))[fec.freq$offspring]

surv.times = tapply(fecundity$degdays,fecundity$ind,max)
surv.mod1 = survreg(Surv(surv.times)~1,dist="weibull")
rho = 1/exp(surv.mod1$icoef[1])
kappa = 1/exp(surv.mod1$icoef[2])
MC[ii,1]=rho
MC[ii,2]=kappa
##############################################################

# find the parameters for
# fecundity as a function of days from onset of reproduction
#
tempdata=tempdata68
avgtemp=avgtemp68
fecdata68 <- fectoday(aphid68,lowerthres,tempdata,avgtemp68)
tempdata=tempdata76
avgtemp=avgtemp76
fecdata76 <- fectoday(aphid76,lowerthres,tempdata,avgtemp)
# now merge dataframe
fecdata=merge(fecdata68,fecdata76,all=T)
days=fecdata$cdegday# first column
offspringdd=fecdata$offspringdd # second column
offspringday=fecdata$offspringday # third column
Ddays=fecdata$dailydegday # fourth column
fecundityday=data.frame(days,offspringday,Ddays)
fec.freq = data.frame(table(days,offspringdd))
fec.freq$days = as.numeric(levels(fec.freq$days))[fec.freq$days]
fec.freq$offspring =
     as.numeric(levels(fec.freq$offspring))[fec.freq$offspring]
fec.model1p = glm(offspringday~days+offset(log(Ddays)),
     family=poisson(link="log"),data=fecundityday)
xx=fec.model1p$coefficients
MC[ii,6]=xx[1]
MC[ii,7]=xx[2]
MC[ii,8]=0
}

write.csv(MC,file=outfile,row.names=FALSE)
```

```
}
```

C.3 Program 3

```
% MCdays.m
% determines aphid population as a function of days
% written in Matlab
clear all
warning('off','MATLAB:dispatcher:InexactMatch')
global npop  %
% fecundity as a function of days since onset of reproduction
global c1 c2 c3
global wrho wkappa  % weibull distribution for survivorship
% weibull distribution for first day of reproduction
global shift rrho rkappa
global degday lowerthres temp

maxa=50 ; % max age in  days
MC=1% MC = 1 assume demographic stochasticity
        % MC = 0 run model with calculated parameters
getinitialvalues=dlmread('MCday68HHwithshiftv4.csv');
getinitialvalues=getinitialvalues(8001:10000,:);
modeln='shiftv4HHm8001_10000.csv'
temp=68%
if MC==1
    basepopfile='MCpopd';
else
    basepopfile='DetPopd';
end
nMC=size(getinitialvalues);
ntrials=nMC(1);
enddays=200 % number of days to run model
kk=2 % need maxa*10 for convergence
% I concatenate the rest of the file name below
basepopfile=strcat(basepopfile,int2str(enddays));
basepopfile=strcat(basepopfile,'t');
stringtemp=int2str(temp);
basepopfile=strcat(basepopfile,stringtemp);
popfile=strcat(basepopfile,modeln);

plotday=2;
```

```
t=0:1:enddays; % used for plotting
temp=(temp-32)*5/9;   %
mina=0;  % minimum age
% number of time divisions in endtime days - depends on kk
nn=[maxa maxa*10 maxa*20 maxa*50  maxa*100];

timestart = 0;  % start after 0 elapsed days
% used when I ran through all nn to check convergence
cline=['g','r','b','k','y', 'm'];
% keep track of total population by days
npopmatrix=zeros(enddays, ntrials);


n=nn(kk);
% set up for integral
h=(maxa-mina)/n;  % length of age interval
c=0:1:n;
age = mina + c*h; %
nage=length(age) ;  % should = n+1

for trial=1:ntrials
   trial
wrho=getinitialvalues(trial,1);
wkappa=getinitialvalues(trial,2);
rrho=getinitialvalues(trial,3);
rkappa=getinitialvalues(trial,4);
shift=getinitialvalues(trial,5);
c1=getinitialvalues(trial,6);
c2=getinitialvalues(trial,7);
c3=getinitialvalues(trial,8);


initialage=shift;  % earliest age of reproduction

endtime=enddays;  % number of days in experiment
time=timestart:h:endtime;  % time at each time step
ntime=length(time);
iage=find(age >= initialage);
iage=iage(1);  % index of earliest reproducing age class
numrepageclass=nage-iage+1;% number of reproducing age classes
npop=zeros(ntime,1);% keeps track of total population over time
% keeps track of population distribution
```

```
pop=zeros(nage,numrepageclass+1);
% so popdist is age X age since first reproduction
% i.e. row 20 column 15 is number of aphids of age(20)
% and who have been reproducing for age(15) days the
% last column are those which have not started to reproduce
pop(iage,1)=1;  % initial first population distribution

npop(1)=1;  % we start with one aphid
degday=0;  % since not the degree day model
if MC == 1
% popdist is final population distribution
    pop=PDEfunc(pop,ntime,nage,age,h,MC) ;
else
    pop=PDEfuncnoMC(pop,ntime,nage,age,h,MC) ;
end
% convert to days

% find population for each 24 hour day
index=1:1:enddays+1;
index=index*(1/h)-(1/h-1);
npopdays=npop(index);

npopdaysp1=npopdays(2:length(npopdays));
npopdays=npopdays(1:length(npopdays)-1);
npopmatrix(:,trial)=npopdays;
plot(t(plotday:length(npopdays)), ...
        npopdays(plotday:length(npopdays)),cline(kk))
hold on
if floor(trial/10)==trial/10
    dlmwrite(popfile,npopmatrix);  % create data file
end


end

ylabel('N_t')
xlabel('Days')
dlmwrite(popfile,npopmatrix);  % create data file

figure
%hold on
ylabel('N_{t+1}/N_t')
xlabel('Days')
```

```
grmatrix=findgr(npopmatrix,1);
run100=mean(grmatrix,2);  %
std100=std(grmatrix')';
E = std100.*ones(size(run100));
plot(t(plotday:length(run100)),run100(plotday:length(run100)));
```

C.4   Program 4

```
% MCdegdays.m
% determines aphid population as a function of degree days
% written in Matlab
clear all
warning('off','MATLAB:dispatcher:InexactMatch')
global npop  %
% fecundity as a function of days since onset of reproduction
global c1 c2 c3
global wrho wkappa  % weibull distribution for survivorship
% weibull distribution for first day of reproduction
global shift rrho rkappa
global degday lowerthres temp %used in PDEfunc for DD model

degday=1; % since using deree day model

maxadays=50 ; % max age in  days

MC=1 % MC = 1 assume demographic stochasticity
        % MC = 0 run model with calculated parameters
getinitialvalues=dlmread('MCddHH.csv');
getinitialvalues=getinitialvalues(71:3000,:);
modeln='HHm71_3000.csv'
temp=77%
enddays=200 % number of days to run model

if MC==1
    basepopfile='MCpopdegd';
else
    basepopfile='Popdegd';
end
nMC=size(getinitialvalues);
```

```
ntrials=nMC(1);
kk=3 % need maxa*10 for convergence
% I concatenate the rest of the file name below
basepopfile=strcat(basepopfile,int2str(enddays));
basepopfile=strcat(basepopfile,'t');
stringtemp=int2str(temp);
basepopfile=strcat(basepopfile,stringtemp);
popfile=strcat(basepopfile,modeln);

plotday=2;
temp=(temp-32)*5/9;  %
mina=0;  % minimum age
% number of time divisions in endtime days - depends on kk
nn=[maxadays maxadays*5 maxadays*10 maxadays*15];

timestart = 0;  % start after 0 elapsed days
% used when I ran through all nn to check convergence
cline=['g','r','b','k','y', 'm'];
% keep track of total population by days
npopmatrix=zeros(enddays-1, ntrials);


n=nn(kk);

for trial=1:ntrials
    trial
wrho=getinitialvalues(trial,1);
wkappa=getinitialvalues(trial,2);
rrho=getinitialvalues(trial,3);
rkappa=getinitialvalues(trial,4);
shift=getinitialvalues(trial,5);
c1=getinitialvalues(trial,6);
c2=getinitialvalues(trial,7);
c3=getinitialvalues(trial,8);
lowerthres=getinitialvalues(trial,9);
% number of degree days in experiment
endtime=(temp-lowerthres)*enddays;
maxa=(temp-lowerthres)*maxadays;  % maximum age in degree days

% set up for integral
h=(maxa-mina)/n;  % length of age interval (in degree days)
c=0:1:n;
```

```
age = mina + c*h; %
nage=length(age) ;  %
initialage=shift;  % earliest age of reproduction

time=timestart:h:endtime;  % time at each time step
ntime=length(time);
iage=find(age >= initialage);
iage=iage(1);  % index of earliest reproducing age class
numrepageclass=nage-iage+1; % number of reproducing age classes
npop=zeros(ntime,1);% keeps track of total population over time
% keeps track of population distribution
pop=zeros(nage,numrepageclass+1);
% so popdist is age X age since first reproduction, i.e.
% row 20 column 15 is number of aphids of age(20) and who have
% been reproducing for age(15) days the
% last column are those which have not started to reproduce
pop(iage,1)=1;  % initial first population distribution

npop(1)=1;  % we start with one aphid
if MC == 1
% popdist is final population distribution
    pop=PDEfunc(pop,ntime,nage,age,h,MC) ;
else
    pop=PDEfuncnoMC(pop,ntime,nage,age,h,MC) ;
end

% convert to days
% find population for each 24 hour day
timedays=time/(temp-lowerthres);

npopdays=zeros(enddays,1);
npopdays(1)=1;
for mm=2:enddays-1
    index=find(timedays >= mm-1);% because starting on day 0
% assume population is linear between degree days
    slope=(npop(index(1))-npop(index(1)-1))/ ...
            (timedays(index(1))-timedays(index(1)-1));
    intercept=npop(index(1))-timedays(index(1))*slope;
    npopdays(mm)=slope*(mm-1)+intercept;
end

npopdaysp1=npopdays(2:length(npopdays));
```

```
npopdays=npopdays(1:length(npopdays)-1);

lmatrix=min(length(npopdays),length(npopmatrix(:,1)));
npopmatrix(1:lmatrix,trial)=npopdays(1:lmatrix);
t=0:1:enddays; % used for plotting
plot(t(plotday:lmatrix),npopdays(plotday:lmatrix),cline(kk))
hold on
if floor(trial/10)==trial/10
    dlmwrite(popfile,npopmatrix);  % create data file
end


end

ylabel('N_t')
xlabel('Days')
dlmwrite(popfile,npopmatrix);  % create data file

figure
%hold on
ylabel('N_{t+1}/N_t')
xlabel('Days')

grmatrix=findgr(npopmatrix,1);
    run100=mean(grmatrix,2);  %
    std100=std(grmatrix')';
    E = std100.*ones(size(run100));
    plot(t(plotday:length(run100)),run100(plotday:length(run100)));
```

C.5   Common Subroutines

```
function popdist=PDEfunc(pop,ntime,nage,age,h,MC)
% given a population distribution for each day,
% computes total population at time enddays
% written in Matlab

global npop  %
% fecundity as a function of days since onset of reproduction
global c1 c2 c3
global wrho wkappa  % weibull distribution for survivorship
% weibull distribution for first day of reproduction
global shift rrho rkappa
global degday lowerthres temp
```

```
% since calling this then MC =1
% aphids reproduce first, then age

index=find(age >= shift);%find index when old enough to reproduce
index=index(1);
numrepageclass=nage-index+1;%number of reproducing age classes
if degday ==0
% maternity function by days since onset of reproduction
    mfec= ...
    transpose(exp(c1+c2*(age(index:nage)-age(index))));
    convdd=1;
else % maternity function by degree days since onset of reproduction
 mfec= ...
   exp(c1+c2*(age(index:nage)-age(index))+ log(temp-lowerthres));
        mfec=transpose(mfec);
        convdd=temp-lowerthres;
end
% ages of aphids who are old enough to reproduce
age1=[age age(nage)+h];

% compute hazard function for reproduction,
% i.e. give proportion of aphids
% which will reproduce at age a provided
% they have not begun to reproduce
rep=((age1(index+1:nage+1)-age(index)).^rkappa)- ...
((age1(index:nage)-age(index)).^rkappa);
% proportion which will NOT begin to reproduce
nnotrep=transpose(exp(-((rrho^rkappa)*rep)));
s1=(wrho*age1(2:nage+1)).^wkappa;  % Wiebull distribution
s1=exp(-s1);
s2=(wrho*age1(1:nage)).^wkappa;
s2=exp(-s2);
surv=s1./s2;
nsurv=surv';
% reproduce first then survive
% note:  population is already vectorized (see lines 70-71)
for ii=2:ntime
    fec=poissrnd(mfec) ; % pick random maternity
    % pick if will reproduce randomly
    randrep=unifrnd(0,1,numrepageclass,1) ;
    notrep=(randrep>(1-nnotrep)) ;
```

```
      % if = 1, these age classes will not begin to reproduce
      % if = 0, these age classes will begin to reproduce
   % pick if will survive randomly
   randsurv=unifrnd(0,1,length(age),1) ;
   xx=(randsurv>nsurv) ;
   surv = 1-xx ;  % if = 1, these age classes will survive
                  % if = 0, these age classes will not survive
   fec=fec/convdd;   % final conversion for degree day model
   surv=surv(1:nage,:)*ones(1,numrepageclass+1);
   poptplus1=zeros(nage,numrepageclass+1,1);
   % total fecundity:  Equation 4.6 in thesis
   sumfec=0;
% note, the two conditional statements below are
% the same as line 80.  Removing
% these conditional statement made the program run faster
%  if ii >= index % so second generation is beginning to
      % reproduce since elapsed time = age(ii)
% \int_(age) \int_(rep age) fec(rep age)*n(age,rep age) dr da
% = \int_(rep age) fec(rep age) ( \int_(age) *n(age,rep age) da ) dr
% the inner integral is just the total number of aphids between age 0
% and age=current time (= age(ii))
% the sum(pop) below is population by age of onset of reproduction
%        jj=min(ii,nage);
%        sumfec=sum(pop(index:jj,1:numrepageclass)*fec)*h;
%    end
   % now add in offspring from initial aphid
%  if ii < nage-index+1  % so initial aphid is younger than max age
%        sumfec=sumfec + pop(ii+index-2,ii-1)*fec(ii)*h;
%    end
    sumfec=sum(pop(index:nage,1:numrepageclass)*fec)*h;


   pop(1,numrepageclass+1)=sumfec;  % put newborns into age class 0
 % figure out those that will survive to next timestep
   pop=pop.*surv;
% now figure out how many need to be reproducing at next time step
   % total # non-reproducing adults by age
   tnotrep=pop(index:nage,numrepageclass+1);
   % find proportion that will not reproduce in next timestep
   norep=tnotrep.*notrep;  %
   % thus proportion that will reproduce is
   yesrep=tnotrep-norep;
```

```
    % advance days since onset of reproduction
    pop(index:nage,2:numrepageclass)= ...
            pop(index:nage,1:numrepageclass-1);
    pop(index:nage,1)=yesrep;
    pop(index:nage,numrepageclass+1)=norep;
    poptplus1(2:nage,:)=pop(1:nage-1,:); % advance age
    npop(ii)=sum(sum(poptplus1));
    pop=poptplus1;
end

popdist=pop;  % returns population distribution
```

Bibliography

[1] H. Akaike. Information theory and an extension of the maximum likelihood principle. In B.N. Petrov and F. Csaki, editors, *2nd International Symposium on Information Theory*, pages 268–281. Publishing House of the Hungarian Academy of Sciences, Budepest, 1973.

[2] H. Akaike. Information theory and an extension of the maximum likelihood principle. In S. Kotz and N. Johnson, editors, *Breakthroughs in Statistics*, volume 1, pages 610–624. Springer-Verlag, New York, 1993.

[3] G. Bachman and L. Narici. *Functional Analysis*. Academic Press, New York, 1966.

[4] P.W.J. Baxter, M.A. McCarthy, H.P. Possingham, P.W. Menkhorst, and N. McLean. Accounting for management costs in sensitivity analyses of matrix population models. *Conservation Biology*, 20:893–905, 2006.

[5] G. Bell. Evolutionary and nonevolutionary theories of senescence. *The American Naturalist*, 124:600–603, 1984.

[6] M. Bieri, J. Baumgärtner, G. Bianchi, V. Delucchi, and R. von Arx. Development and fecundity of pea aphid (*Acyrthosiphon pisum* Harris) and by pea varieties. *Bulletin de la Société Entomologique Suisse*, 56:163–171, 1983.

[7] P. Bierzychudek. Looking backwards: assessing the projections of a transition matrix model. *Ecological Applications*, 9:1278–1287, 1999.

[8] D.T. Briese, W.J. Pettit, A. Swirepik, and A. Walker. A strategy for the biological control of *Onopordum* spp. thistles in south-eastern Australia. *Biocontrol Science and Technology*, 12:121–136, 2002.

[9] D.T. Briese, A.W. Sheppard, H. Zwölfer, and P.E. Boldt. Structure of the phytophagous insect fauna of *Onopordum* thistles in the northern Mediterranean basin. *Biological Journal of the Linnean Society*, 53:231–253, 1994.

[10] N.F. Britton. *Essential Mathematical Biology*. Springer-Verlag, London, 2003.

[11] A. Campbell and M. MacKauer. Thermal constants for development of the pea aphid (Homoptera: Aphididae) and some of its parasites. *Canadian Entomologist*, 107:419–423, 1975.

[12] A. Campbell and M. MacKauer. Reproduction and population growth of the pea aphid (Homoptera: Aphididae) under laboratory and field conditions. *The Canadian Entomologist*, 109:277–284, 1977.

[13] T.M. Caro. *Cheetahs of the Serengeti Plains: Group Living of an Asocial Species*. University of Chicago Press, Chicago, 1994.

[14] T.M. Caro and D.A. Collins. Male cheetahs of the Serengeti. *National Geographic Research*, 2:75–86, 1986.

[15] H. Caswell. Prospective and retrospective perturbation analyses: their roles in conservation biology. *Ecology*, 81:619–627, 2000.

[16] H. Caswell. *Matrix Population Models: Construction, Analysis and Interpretation*. Sinauer Associates, Inc., Sunderland, Massachusetts, second edition, 2001.

[17] H. Caswell. Sensitivity analysis of transient population dynamics. *Ecology Letters*, 10:1–10, 2007.

[18] H. Caswell. Perturbation analysis of nonlinear matrix population models. *Demographic Research*, 18:59–116, 2008.

[19] H. Caswell and M.G. Neubert. Reactivity and transient dynamics of discrete-time ecological systems. *Journal of Difference Equations and Applications*, 2:295–310, 2005.

[20] R.J. Chambers, P.W. Wellings, and A.F.G. Dixon. Sycamore aphid numbers and population density. II. Some processes. *Journal of Animal Ecology*, 54:425–442, 1985.

[21] D.Z. Childs, M. Rees, K.E. Rose, P.J. Grubb, and S.P. Ellner. Evolution of complex flowering strategies: an age- and size-structured integral projection model. *Proc. R. Soc. Lond. B*, 270:1829–1838, 2003.

[22] R. Clubb and G.J. Mason. Natural behavioral biology as a risk factor in carnivore welfare: How analysing species differences could help zoos improve enclosures. *Applied Animal Behavioral Science*, 102:303–328, 2007.

[23] T.H. Clutton-Brock and T. Coulson. Comparative ungulate dynamics: the devil is in the detail. *Phil. Trans. R. Soc. Lond. B*, 357:1285–1298, 2002.

[24] A. Comfort. *The Biology of Senescence.* Elsevier, New York, third edition, 1979.

[25] D.R. Cox and D. Oakes. *Analysis of Survival Data (Monographs on Statistics and Applied Probability).* Chapman and Hall, London, 1984.

[26] K.R. Crooks, M.A. Sanjayan, and D.F. Doak. New insights on cheetah conservation through demographic modeling. *Conservation Biology*, 12:889–895, 1998.

[27] L.B. Crowder, D.T. Crouse, S.S. Heppell, and T.H. Martin. Predicting the impact of turtle excluder devices on loggerhead sea turtle populations. *Ecological Applications*, 4:437–445, 1994.

[28] J.M. Cushing and Z. Yicang. The net reproductive value and stability in matrix population models. *Natural Resource Modeling*, 8:297–333, 1994.

[29] H. de Kroon, J. van Groenendael, and J. Ehrlén. Elasticities: A review of methods and model limitations. *Ecology*, 81:607–618, 2000.

[30] A. Deines, E. Peterson, D. Boeckner, J. Boyle, A. Keighley, J. Kogut, J. Lubben, R. Rebarber, R. Ryan, B. Tenhumberg, S. Townley, and A.J. Tyre. Robust population management under uncertainty for structured population models. *Ecological Applications*, 17:2175–2183, 2007.

[31] A.F.G. Dixon. *Aphid Ecology: An Optimization Approach.* Chapman and Hall, London, 1998.

[32] A.F.G. Dixon and S.D. Wratten. Laboratory studies on aggregation, size and fecundity in the black bean aphid, *Aphis fabae* scop. *Bulletin of Entomological Research*, 61:97–111, 1971.

[33] D. Doak, P. Kareiva, and B. Klepetka. Modeling population viability for the desert tortoise in the western Mojave desert. *Ecological Applications*, 4:446–460, 1994.

[34] D.F. Doak, K. Gross, and W.F. Morris. Understanding and predicting the effects of sparse data on demographic analyses. *Ecology Letters*, 86:1154–1163, 2005.

[35] M.R. Easterling. *The integral projection model: theory, analysis and application.* PhD thesis, North Carolina State University, Raleigh, 1998.

[36] M.R. Easterling, S.P. Ellner, and P.M. Dixon. Size-specific sensitivity: Applying a new structured population model. *Ecology*, 81:694–708, 2000.

[37] R.L. Eaton. *The Cheetah: The Biology, Ecology, and Behavior of an Endangered Species.* Van Nostrand Reinhold, New York, 1974.

[38] B. Efron and R.J. Tibshirani. *An Introduction to the Bootstrap.* Chapman and Hall, New York, 1993.

[39] J. Ehrlén. The dynamics of plant populations: Does the history of individuals matter? *Ecology*, 81:1675–1684, 2000.

[40] J. Ehrlén and J. van Groenendael. Direct perturbation analysis for better conservation. *Conservation Biology*, 12:470–474, 1998.

[41] S.P. Ellner and M. Rees. Integral projection models for species with complex demography. *The American Naturalist*, 167:410–428, 2006.

[42] G.A. Fox and J. Gurevitch. Population numbers count: Tools for near-term demographic analysis. *American Naturalist*, 156:242–256, 2000.

[43] B.D. Frazer. Population dynamics and recognition of biotypes in the pea aphid (Homoptera: Aphididae). *Canadian Entomologist*, 104:1729–1733, 1972.

[44] J.-M. Gaillard, D. Allainé, D. Pontier, N.G. Yoccoz, and D.E.L. Promislow. Senescence in natural populations of mammals: a reanalysis. *Evolution*, 48:509–516, 1994.

[45] K.S. George and R. Gair. Crop loss assessment on winter wheat attacked by the grain aphid, *Sitobion avenae* (F.), 1974-1977. *Plant Pathology*, 28:143–149, 1979.

[46] W.L. Goss. The vitality of buried seeds. *Journal of Agricultural Research*, 29:349–362, 1924.

[47] P.M. Gros. The status and conservation of the cheetah *Acinonyx jubatus* in tanzania. *Biological Conservation*, 106:177–185, 2002.

[48] K. Gross, B.A. Craig, and W.D. Hutchison. Bayesian estimation of a demographic matrix model from stage frequency-data. *Ecology*, 83:3285–3298, 2002.

[49] R.H. Groves, J.J. Burdon, and P.E. Kaye. Demography and genetics of *Onopordum* in southern New South Wales. *Journal of Applied Ecology*, 78:47–55, 1990.

[50] W. Hackbusch. *Integral Equations, Theory and Numerical Treatment.* Birkhäuser Verlag, Basel, 1995.

[51] A. Hastings. Transients: The key to long-term ecological understanding. *Trends Ecol. Evolution*, 19:39–45, 2004.

[52] A. Hastings and K. Higgins. Persistence of transients in spatially structured ecological models. *Science*, 263:1133–1136, 1994.

[53] C.E. Hauser, E.G. Cooch, and J.-D. Lebreton. Control of structured populations by harvest. *Ecological Modelling*, 196:462–470, 2006.

[54] D.J. Hodgson and H.C.J. Godfray. The consequences of clustering by *Aphis fabae* foundresses on spring migrant production. *Oecologia*, 118:446–452, 1999.

[55] D.J. Hodgson and S. Townley. Linking management changes to population dynamic responses: the transfer function of a projection matrix perturbation. *Journal of Applied Ecology*, 41:1155–1161, 2004.

[56] D.J. Hodgson, S. Townley, and D. McCarthy. Robustness: Predicting the effects of life history perturbations on stage-structured population dynamics. *Theoretical Population Biology*, 70:214–224, 2006.

[57] W.D. Hutchison and D.B. Hogg. Demographic statistics for the pea aphid (Homoptera: Aphididae) in Wisconsin and a comparison with other populations. *Environmental Entomology*, 13:1173–1181, 1984.

[58] Iowa State University-University Extension. `http://www.ipm.iastate.edu/ipm/icm/node/2551/print`.

[59] M.J. Kelly and S.M. Durant. Viability of the Serengeti cheetah population. *Conservation Biology*, 14:786–797, 2000.

[60] M.J. Kelly, M.K. Laurenson, C.D. FitzGibbon, D.A. Collins, S.M. Durant, G.W. Frame, B.C.R. Bertram, and T.M. Caro. Demography of the Serengeti cheetah (*Acinonyx jubatus*) population: the first 25 years. *Journal of Zoology, London*, 244:473–488, 1998.

[61] N. Keyfitz. On the momentum of population growth. *Demography*, 8:71–80, 1971.

[62] N. Keyfitz and H. Caswell. *Applied Mathematical Demography*. Springer, New York, third edition, 2005.

[63] L. Kilian and M.W. Nielson. Differential effects of temperature on the biological activity of four biotypes of the pea aphid. *Journal of Economic Entomology*, 64:153–155, 1971.

[64] D.N. Koons, J.B. Grand, B. Zinner, and R.F. Rockwell. Transient population dynamics: relations to life history and initial population state. *Ecological Modelling*, 185:283–287, 2005.

[65] D.N. Koons, R.R. Holmes, and J.B. Grand. Population inertia and its sensitivity to changes in vital rates and population structure. *Ecology*, 88:2857–2867, 2007.

[66] M. Kot. *Elements of Mathematical Ecology*. Cambridge University Press, Cambridge, 2001.

[67] M.A. Krasnosel'skij, Je.A. Lifshits, and A.V. Sobolev. *Positive Linear Systems - The Method of Positive Operators*. Heldermann Verlag, Berlin, 1989.

[68] L. Laikre. Conservation genetics of Nordic carnivores: lessons from zoos. *Hereditas*, 130:203–216, 1999.

[69] R.J. Lamb. Developmental rate of *Acyrthosiphon pisum* (Homoptera: Aphididae) at low temperatures: Implications for estimating rate parameters for insects. *Environmental Entomology*, 21:10–19, 1992.

[70] R.J. Lamb, P.A. MacKay, and G.H. Gerber. Are development and growth of pea aphids, *Acyrthosiphon pisum*, in North America adapted to local temperatures? *Oecologia*, 72:170–177, 1987.

[71] M.K. Laurenson. Implications of high offspring mortality for cheetah population dynamics. In A.R.E. Sinclair and P. Arcese, editors, *Serengeti II: Dynamics, Management, and Conservation of an Ecosystem*, pages 385–399. University of Chicago Press, Chicago, 1995.

[72] M.K. Laurenson, T. Caro, and M. Borner. Female cheetah reproduction. *National Geographic Research and Exploration*, 8:64–75, 1992.

[73] G. Lee, D.J. Stevens, S. Stoke, and S.D. Wratten. Duration of cereal aphid populations and the effects on wheat yield and breadmaking quality. *Annals of Applied Biology*, 98:169–178, 1981.

[74] L.P. Lefkovitch. Some comments on the invariants of population growth. In G.P. Patil, E.C. Pielou, and W.E. Water, editors, *Statistical Ecology, Vol. 2*, pages 337–360. Pennsylvania State University Press, University Park, Pennsylvania, 1971.

[75] J.A. Logan, D.J. Wollkind, S.C. Hoyt, and L.K. Tanigoshi. An analytic model for description of temperature dependent rate phenomena in arthropods. *Environmental Entomology*, 5:1133–1140, 1976.

[76] A. Loison, M. Festa-Bianchet, J.-M. Gaillard, J.T. Jorgenson, and J.-M. Jullien. Age-specific survival in five populations on ungulates: evidence of senescence. *Ecology*, 80:2539–2554, 1999.

[77] J. Lubben, D. Boeckner, R. Rebarber, S. Townley, and B. Tenhumberg. Parameterizing the growth-decline boundary for uncertain population projection models. *Theoretical Population Biology*, 75:85, 2008.

[78] J. Lubben, B. Tenhumberg, A. Tyre, and R. Rebarber. Management recommendations based on matrix projection models: The importance of considering biological limits. *Biological Conservation*, 141:517–523, 2008.

[79] G.A. Maiteki and R.J. Lamb. Spray timing and economic threshold for the pea aphid *Acyrthosiphon pisum* (Homoptera: Aphididae), on field peas in Manitoba. *Journal of Economic Entomology*, 78:1449–1454, 1985.

[80] M.C. Mandujano, C. Montaña, M. Franco, J. Golubov, and A. Flores-Martínez. Integration of demographic annual variability in a clonal desert cactus. *Ecology*, 82:344–359, 2001.

[81] L. Marker. *1999 Cheetah (Acinonyx jubatus) Studbook*. Cheetah Conservation Fund, Namibia, 1999.

[82] L. Marker. *2002 Cheetah (Acinonyx jubatus) Studbook*. Cheetah Conservation Fund, Namibia, 2004.

[83] L. Marker. *2003 Cheetah (Acinonyx jubatus) Studbook*. Cheetah Conservation Fund, Namibia, 2006.

[84] L. Marker. *2004 Cheetah (Acinonyx jubatus) Studbook*. Cheetah Conservation Fund, Namibia, 2006.

[85] L. Marker, D. Kraus, D. Barnett, and S. Hurlbut. *Cheetah Survival on Namibian Farmlands*. Cheetah Conservation Fund, Windhoek, 1996.

[86] L.L. Marker, A.J. Dickman, R.M. Jeo, M.G.L. Mills, and D.W. Macdonald. Demography of the Namibian cheetah, *Acinonyx jubatus jubatas*. *Biological Conservation*, 114:413–425, 2003.

[87] L.L. Marker, A.J. Dickman, M.G.L. Mills, and D.W. Macdonald. Aspects of the management of cheetahs *Acinonyx jubatus jubatas* trapped on Namibian farmlands. *Biological Conservation*, 114:401–412, 2003.

[88] L. Marker-Kraus. History of the cheetah *Acinonyx jubatus* in zoos 1829-1994. *International Zoo Yearbook*, 35:27–43, 1997.

[89] L. Marker-Kraus and D. Kraus. Conservation strategies for the long-term survival of the cheetah *Acinonyx jubatus* by the Cheetah Conservation Fund, Windhoek. *International Zoo Yearbook*, 35:59–66, 1997.

[90] M. Markkula and K. Roukka. Resistance of plants to the pea aphid *Acyrthosiphon pisum* Harris (Homoptera: Aphididae). *Annales Agriculturae Fenniae*, 10:33–37, 1971.

[91] MathWorks, Inc. Matlab R2007a, 2007.

[92] B.P. McCornack, D.W. Ragsdale, and R.C. Venette. Demography of soybean aphid (Homoptera: Aphididae) at summer temperatures. *Journal of Economic Entomology*, 97:854–861, 2004.

[93] P.B. Medawar. *An Unsolved Problem in Biology.* H.K. Lewis, London, 1952.

[94] F.J. Messina. Effect of initial colony size on the per-capita growth-rate and alate production of the Russian wheat aphid (Homoptera: Aphididae). *Journal of the Kansas Entomological Society*, 66:365–371, 1993.

[95] L.S. Mills, D.F. Doak, and M.J. Wisdom. Reliability of conservation actions based on elasticity analysis of matrix models. *Conservation Biology*, 13:815–829, 1999.

[96] K.A. Moloney. A generalized algorithm for determining category size. *Oecologia (Berlin)*, 69:176–180, 1986.

[97] D. Morgan, K.F.A. Walters, and J.N. Aegerter. Effect of temperature and cultivar on pea aphid, *Acyrthosiphon pisum* (Hemiptera: Aphididae) life history. *Bulletin of Entomological Research*, 91:47–52, 2001.

[98] W.F. Morris and D.F. Doak. *Quantitative Conservation Biology; Theory and Practice of Population Viability Analysis.* Sinauer Associates, Sunderland, Massachusetts, 2002.

[99] S.W. Myers, D.B. Hogg, and J.L. Wedberg. Determining the optimal timing of foliar insecticide applications for control of soybean aphid (Hemiptera: Aphididae) on soybean. *Journal of Economic Entomology*, 98:2006–2012, 2005.

[100] J.D. Nichols, J.E. Hines, and P. Blums. Tests for senescent decline in annual survival probabilities of common pochards, *Aythya ferina. Ecology*, 78:1009–1018, 1997.

[101] K. Nowell and P. Jackson, editors. *Wild Cats, Status Survey and Conservation Action Plan.* IUCN, Gland, Switzerland, 1996.

[102] W.J. Pettit, D.T. Briese, and A. Walker. Aspects of thistles population dynamics with reference to *Onopordum. Plant Protection Quarterly*, 11:232–235, 1996.

[103] J.E. Pinder III, J.G. Wiener, and M.H. Smith. The Weibull distribution: a new method of summarizing survivorship data. *Ecology*, 59:175–179, 1978.

[104] D.E.L. Promislow. Senescence in natural populations of mammals: a comparative study. *Evolution*, 45:1869–1887, 1991.

[105] R Development Core Team. R: A programming environment for data analysis and graphics, version 2.4.1, 2006.

[106] J. Ratsirarson, J.A. Silander, Jr., and A.F. Richard. Conservation and management of a threatened madagascar palm species, *Neodypsis decaryi*, Jumelle. *Conservation Biology*, 10:40–52, 1996.

[107] B.D. Roitberg and J.H. Myers. Behavioral and physiological adaptations of pea aphids (Homoptera: Aphididae) to high ground temperatures and predator disturbances. *Canadian Entomology*, 111:515–519, 1979.

[108] J. Roughgarden. *Primer of Ecological Theory*. Prentice Hall, Upper Saddle River, New Jersey, 1998.

[109] Y. Sakamoto, M. Ishiguro, and G. Kitagawa. *Akaike Information Criterion Statistics*. KTK Scientific Publishers and D. Reidel Publishing, Tokyo and Dordrecht, 1987.

[110] E. Seneta. *Non-negative Matrices and Markov Chains*. Springer-Verlag, New York, NY, 1981.

[111] H. Seno and H. Nakajima. Transition matrix model for persistence of monocarpic perennial plant population under periodically ecological disturbance. *Ecological Modelling*, 117:65–80, 1999.

[112] W.H. Siddiqui, C.A. Barlow, and P.A. Randolph. Effects of some constant and alternating temperatures on population growth of the pea aphid, *Acyrthosiphon pisum* (Homoptera: Aphididae). *Canadian Entomologist*, 105:145–156, 1973.

[113] N.A. Slade. Failure to detect senescence in persistence of some grassland rodents. *Ecology*, 76:863–870, 1995.

[114] R.E. Stinner, A.P. Gutierrez, and G.D. Butler, Jr. An algorithm for temperature-dependent growth rate simulation. *The Canadian Entomologist*, 106:519–523, 1974.

[115] F. Taylor. Convergence to the stable age distribution in populations of insects. *American Naturalist*, 113:511–530, 1979.

[116] B. Tenhumberg, S. M. Louda, S.O. Eckberg, and M. Takahashi. Monte carlo analysis of parameter uncertainty in matrix models of the weed *Cirsium vulgare*. *Journal of Applied Ecology*, 45:438–447, 2008.

[117] B. Tenhumberg, A.J. Tyre, and R. Rebarber. Model complexity affects predicted transient population dynamics following a dispersal event: A case study with *Acyrthosiphon pisum. Ecology*, 2009. In press.

[118] S. Townley, D. Carslake, O. Kellie-Smith, D. McCarthy, and D. Hodgson. Predicting transient amplification in perturbed ecological systems. *Journal of Applied Ecology*, 44:1243–1251, 2007.

[119] S. Townley and D. Hodgson. Erratum et addendum: transient amplification and attenuation in stage-structured population dynamics. *Journal of Applied Ecology*, 45:1836–1839, 2008.

[120] S. Tuljapurkar and R. Lee. Demographic uncertainty and the stable equivalent population. *Mathematical and Computer Modelling*, 26:39–56, 1997.

[121] P.H. van Tienderen. Life cycle trade-offs in matrix population models. *Ecology*, 76:2482–2489, 1995.

[122] J. Vandermeer. Choosing category size in a stage projection matrix. *Oecologia (Berlin)*, 32:79–84, 1978.

[123] M.J. Way and C.J. Banks. Intra-specific mechanisms in relation to the natural regulation of numbers of *Aphis fabae* Scop. *Annales of Applied Biology*, 59:189–205, 1967.

[124] M.J. Wisdom and L.S. Mills. Sensitivity analysis to guide population recovery: prairie-chickens as an example. *J. of Wildlife Management*, 61:302–312, 1997.

[125] J.M. Yearsley. Transient population dynamics and short-term sensitivity analysis of matrix population models. *Ecological Modelling*, 177:245–258, 2004.

[126] P.P. Zabreyko, A.I. Koshelev, M.A. Krasnosel'skii, S.G. Mikhlin, L.S. Rakovshchik, and V.Ya. Stet'senko. *Integral Equations - A Reference Text.* Noordhoff International, Leyden, The Netherlands, 1975.