

Guaranteeing population growth under uncertainty for structured population models*

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Abstract

Structured population models are increasingly used in decision making, but typically have many entries that are unknown or highly uncertain. We present an approach for the systematic analysis of the effect of uncertainties on long-term population growth or decay. Many decisions for threatened and endangered species are made with poor or no information. We can still make decisions under these circumstances in a manner that is highly defensible, even without making assumptions about the distribution of uncertainty or limiting ourselves to discussions of single, infinitesimally small changes in the parameters. Suppose that the model (determined by the data) for the population in question predicts long-term growth. Our goal is to determine how uncertain the data can be before the model loses this property. Some uncertainties will maintain long-term growth, and some will lead to long-term decay. The uncertainties are typically structured, and can be described by several parameters. We show how to determine which parameters maintain long-term growth. We illustrate the advantages of the method by applying it to a peregrine falcon population. The US Fish and Wildlife Service recently decided to allow minimal harvesting of peregrine falcons after their recent removal from the Endangered Species List. Based on published demographic rates, we find that population growth ($\lambda > 1$) is guaranteed with 5% harvest rate up to 3% error in adult survival if no two year olds breed, and up to 11% error if all two year olds breed. If a population growth rate of 3% or greater is desired, the acceptable error in adult survival decreases to between 1 and 6% depending of the proportion of two year olds that breed. These results clearly show the interactions between uncertainties in different parameters, and suggest that a harvest decision at this stage may be premature without solid data on adult survival and the frequency of breeding by young adults.

1. Introduction

Decision making under uncertainty is a pervasive characteristic of conservation biology. Sometimes, the scientific uncertainty can be so severe that it paralyzes decision making, or causes decisions to be made solely on social grounds, without being informed by science. Current quantitative approaches to decision making usually rely on being able to construct models or scenarios that illuminate the consequences of decisions for various stakeholders. Managers of wildlife populations use population projection matrices (Caswell 2001) to assess decisions with increasing frequency, but pa-

rameters in these matrices are inherently uncertain. Unfortunately, the standard tools for assessing the effects of parameter uncertainty on matrix models require better data than is typically available in the management of threatened or endangered species. The method of sensitivity and elasticity analysis is only accurate for small perturbations of single parameters, and in fact might be misleading for large perturbations (see Hodgson and Townley 2004 and 2005). Another standard approach is to use Monte Carlo simulations, where the data is assumed to be substantial enough to determine parameter estimates of the distributional form of random variables. In the management of threatened or endangered species, where information can be extremely scarce, it is unlikely that the perturbations are small, or that there is enough information available to know the distribution of uncertainties. Scarcity of data particularly impacts estimates of the variance, possibly leading to underestimates of the probability of extreme values. In this paper we present an alternate approach for the systematic analysis of the effect of uncertainties on long-term population growth or decay. This approach does not require the perturbations to be small, can handle simultaneous uncertainty in several parameters, and does not require strong distributional assumptions.

Suppose that the model (determined by the data) for the population in question predicts long-term growth. Our goal is to determine how uncertain the data can be before the model loses this property. Roughly speaking, the *robustness* of a desired property (such as long-term population growth) to uncertainty or perturbation of data is a measure of how much the data can be changed before the desired property is destroyed. The techniques of robustness analysis, which have been developed in the field of control theory, have been applied to population problems in Hodgson *et al.* (2004, 2005). Our approach differs from theirs in several ways; in particular we consider population growth to be the desired property, instead of population decay, so we cannot use established techniques. In addition, we describe *all* acceptable uncertainties, while they give the answer in terms of the stability radius, which gives a distance that the data can be changed before causing the desired property to be lost.

The methods presented here are generalizable to all population projection matrices, but we illuminate the method with a particular problem: the decision to allow limited harvesting of a

recently recovered endangered species. Peregrine falcons were placed on the endangered species list in 1970 (U.S. Fish and Wildlife Service 2003), due to DDT, habitat loss, hunting, and other factors. In addition to the ban on DDT, the implementation of fostering, hacking (young falcons slowly reintroduced to the wild in stages), and the release of over 6000 peregrines helped populations recover (Craig, White and Enderson 2004).

With over 2000 breeding pairs in the United States, the population is again increasing, and falcons were removed from the endangered species list in 1999. There is renewed interest in harvesting peregrine falcons for falconry, and in May 2001 the US Fish and Wildlife Service allowed states west of the 100 deg longitude line (from North Dakota through Texas) to allow harvesting of up to 5% of their state's population (U.S. Fish and Wildlife Service 2001). Falconers as a group have considerable interest in the outcome, as they contributed a huge, voluntary effort to foster and hack young birds during the recovery phase. For them, the new harvest permits are the payoff of a long and significant investment.

In July 2005 controversy arose over the number of falcons currently being harvested in Oregon. The Audubon Societies of Portland and Denver, the Center for Biological Diversity, and the New Mexico Audubon Council questioned the decision of the US Fish and Wildlife Service allowing harvesting of the peregrine falcon population. In particular, the plaintiffs claimed that the US Fish and Wildlife Service's calculations of the margin of error misrepresented the data, and consequently harvesting exposed peregrine falcon populations to unnecessary risk of decline. These concerns were dismissed and 5% of the population are still allowed to be harvested (*Audubon Society of Portland v. United States Fish and Wildlife Service* 2005). The key issue on which this case hinged was whether or not the incorporation of uncertainty into the calculations of the allowable harvest rate was done appropriately.

This is not the first time a group of stakeholders used scientific uncertainty to force or prevent a change in management for an endangered species. For example, the US Fish and Wildlife Service found that water control operations along sections of the Missouri River by the US Army Corps of Engineers jeopardized the recovery of the Pallid Sturgeon (*Scaphirhynchus albus*) and other en-

dangered species, and required the Corps to increase spring flows by 2003 (U.S. Fish and Wildlife Service 2000). The need for a more natural hydrological regime along the Missouri River was later confirmed by a scientific review panel from the National Academy of Sciences (National Research Council 2000). During the spring of 2003, however, the Corps did not increase spring water flows along sections of the Missouri River despite a federal court order to do so, resulting in potential fines of \$500,000 a day (American Rivers vs. Army Corps of Engineers 2003). In late 2003, the Corps released its own Biological Assessment (U.S. Army Corps of Engineers 2003) in which they argued that it was unreasonable to alter spring flows because of the scientific uncertainties associated with the response of Pallid Sturgeon populations to altered flows. There are means to reduce these uncertainties through monitoring and experimentation, but for endangered species the asymmetric risk of extinction may make this delayed management untenable. How can the available scientific information, while admittedly sparse, be fairly evaluated in these decision contexts?

After we apply our methods to the model for peregrine falcon population growth, we incorporate harvest effects into the population model to assess how different levels of harvesting reduce the robustness to uncertainty. How much uncertainty is tolerable is a value judgement, but the methods used in this paper make direct connections between uncertainty and maintenance of population growth under different management choices, without assuming that uncertainties are tiny or that errors have particular distributions.

2. Methods

2.1 General Method for Classifying Perturbations

For an arbitrary matrix \mathbf{M} , let $\lambda(\mathbf{M})$ be the eigenvalue of \mathbf{M} of largest modulus. Let \mathbf{A} denote the population projection matrix for the population in question. We assume that $\lambda(\mathbf{A}) > 1$, which implies that the population is increasing (see subsection A.1 of the Appendix), if \mathbf{A} accurately models the population dynamics. The parameters used in this matrix are estimated from the

available data, and are referred to as the *nominal values*, and \mathbf{A} is referred to as the *nominal matrix*. The actual values of the parameters could differ by unknown amounts from the nominal values, due to data collection errors and changes over time, so the actual population may not in fact be growing. We will explore the effects of this uncertainty on the population. It is not difficult to determine how far a single parameter can be perturbed before the population experiences negative population growth; one method is given in subsection A.2 of the Appendix. However, it is more difficult to determine the effect of independent perturbations of two or more underlying parameters. It is our goal to determine which combinations of perturbations maintain population increase, and which lead to population decline.

We denote the actual population projection matrix by $\tilde{\mathbf{A}}$, and we write

$$\tilde{\mathbf{A}} = \mathbf{A} + \mathbf{P},$$

where \mathbf{P} is called the perturbation matrix. We do not know \mathbf{P} , and hence do not know $\tilde{\mathbf{A}}$ exactly. The nonzero entries of \mathbf{P} correspond to the uncertain entries of \mathbf{A} . If the actual matrix is close to the nominal matrix (i.e. the data is accurate), the the entries of \mathbf{P} will be small, but this is not guaranteed. The long-term population growth rate is directly determined by $\lambda(\tilde{\mathbf{A}})$, which we denote by λ .

If the dimension of the population vector is n , then the matrices \mathbf{A} , $\tilde{\mathbf{A}}$ and \mathbf{P} have n^2 entries. The uncertainties are typically *structured*, and can be described by m parameters (p_1, p_2, \dots, p_m) , where $m \leq n^2$. The smaller the number of parameters we consider, the more tractable the analysis will be, so this approach will be easier if we consider only the most significant parameters, for instance, the parameters which affect λ the most, or the most uncertain parameters. We say that (p_1, p_2, \dots, p_m) is *admissible* if $\mathbf{A} + \mathbf{P}$ is an acceptable projection matrix, and we let S be the set of admissible (p_1, p_2, \dots, p_m) . We can denote the explicit dependence of $\tilde{\mathbf{A}}$ and λ on (p_1, p_2, \dots, p_m) by writing

$$\tilde{\mathbf{A}} = \tilde{\mathbf{A}}(p_1, p_2, \dots, p_m), \quad \lambda = \lambda(p_1, p_2, \dots, p_m).$$

Now consider the subset of S given by

$$C := \{(p_1, p_2, \dots, p_m) \in S \mid \lambda(p_1, p_2, \dots, p_m) = 1\}. \quad (2.1)$$

This is the set of (p_1, p_2, \dots, p_m) which lead to a leading eigenvalue of 1. Mathematically, 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). The $m = 2$ case is illustrated in the peregrine falcon model. When $m = 2$ or 3, it is clear what it means for a particular (p_1, p_2, \dots, p_m) to be on one side or another of C ; for larger m , the notion of the side of a hyperplane can be made precise mathematically. Since we are assuming that the unperturbed matrix \mathbf{A} has $\lambda(\mathbf{A}) = \lambda(0, 0, \dots, 0) > 1$, the “population growth” side of C is the one containing $(0, 0, \dots, 0)$. Hence we consider all “good” perturbations to be those which are on the population growth side of C . Since the nominal model corresponds to $(p_1, p_2, \dots, p_m) = (0, 0, \dots, 0)$, one measure of robustness is how far $(0, 0, \dots, 0)$ is from C . In the case where $m = 2$ or 3, we get stronger results, since we get a graphical representation showing exactly which combinations of uncertainties maintain and destroy population growth.

If we are concerned with maintaining a particular growth rate, say 3%, then we would replace C by

$$C_{1.03} := \{(p_1, p_2, \dots, p_m) \in S \mid \lambda(p_1, p_2, \dots, p_m) = 1.03\}.$$

Furthermore, it should be pointed out that for some applications we will be interested in maintaining population decay, in which case the good perturbations will be on the side of C which guarantees that $\lambda(p_1, p_2, \dots, p_m) < 1$.

It still remains to find an equation for C . It is easy to find the hyperplane on which **some** eigenvalue of $\tilde{\mathbf{A}}$ is 1: Letting I denote the $n \times n$ identity matrix, this hyperplane is

$$\Gamma := \{(p_1, p_2, \dots, p_m) \in S \mid \det(I - \mathbf{A}(p_1, p_2, \dots, p_m)) = 1\}. \quad (2.2)$$

For the peregrine falcon model, we give a method, found in Appendix A3, for showing that Γ is in fact the same curve as C . Even if Γ is not the same as C (or cannot be proved to be the same as C), it is still useful. For (p_1, p_2, \dots, p_m) on Γ , the eigenvalue of largest modulus $\lambda(p_1, p_2, \dots, p_m)$ must be greater than 1, since some eigenvalue of $\tilde{\mathbf{A}}((p_1, p_2, \dots, p_m)$ is equal to 1. Hence for (p_1, p_2, \dots, p_m) on side of Γ which contains $(0, 0, \dots, 0)$, it is guaranteed that $\lambda(p_1, p_2, \dots, p_m) > 1$; however, it is not guaranteed that on the other side of Γ we have $\lambda(p_1, p_2, \dots, p_m) < 1$.

2.2 Falcon Population Model

In this section we consider a model for an endangered peregrine falcon population, and show how different kinds of uncertainties can be simultaneously, and globally, analyzed. We use a standard age structured population projection model (Caswell 2001) with three age classes - birds less than one year old, birds older than one year and less than or equal to two years old, and birds older than two years. We refer to these as x_1 , x_2 and x_3 , respectively, and the population vector is

$$\mathbf{x} = \begin{bmatrix} x_1 \\ x_2 \\ x_3 \end{bmatrix}.$$

The population vector during year k is denoted \mathbf{x}_k , and $(\mathbf{x}_k)_{k=0}^{\infty}$ satisfies the discrete time equation

$$\mathbf{x}_{k+1} = \mathbf{A}\mathbf{x}_k, \tag{2.3}$$

where \mathbf{A} is the population projection matrix. The nominal population projection matrix we use is a correction of the post-breeding model derived in Craig, White and Enderson (2004); the published matrix incorrectly includes an additional juvenile age class, although the reported model results are from the correct model (Gary C. White, personal correspondence). The model parameters are: S_0 , the survivorship from birth to age one; S_1 , the survivorship from age one to age two; S_2 , the yearly survivorship for all older birds. The fecundity F is assumed to be the same for all breeding pairs. Birds under 2 years old may or may not breed. We quantify this by letting B represent the

proportion of birds in the second age class that breed. R denotes the proportion of birds that are female. In terms of these parameters, the nominal population projection matrix is

$$\mathbf{A} = \begin{pmatrix} 0 & FRBS_1 & FRS_2 \\ S_0 & 0 & 0 \\ 0 & S_1 & S_2 \end{pmatrix}. \quad (2.4)$$

We use parameter values estimated from the peregrine falcons in Colorado, USA (Table 1; Craig, White and Enderson 2004).

Symbol	Meaning	Estimate	Sensitivity	Elasticity
F	Nestlings fledged per pair	1.660	0.0954	0.1539
R	Proportion of female nestling	0.500	0.3166	0.1539
S0	Survival of nestling to age 1	0.544	0.2910	0.1539
S1	Survival of 1 year old birds	0.670	0.2363	0.1539
S2	Survival of bird \geq 2	0.800	0.8901	0.6922
B	Proportion of 2 year old birds that breed	0	0.058	0

Table 1: Nominal Matrix Parameters

We need to incorporate harvesting into the population projection matrix. We introduce the variable h , which represents the proportion of nestlings harvested, so the term $(1 - h)$, denoting the proportion of nestlings remaining in the wild population, is included in the matrix \mathbf{A} by multiplying this term by the fecundities (Caswell 2001). The amount of harvesting is assumed to be the same in both age classes since for many birds the age cannot be determined. Let

$$\mathbf{A}_h = \begin{pmatrix} 0 & (1 - h)FRBS_1 & (1 - h)FRS_2 \\ S_0 & 0 & 0 \\ 0 & S_1 & S_2 \end{pmatrix}. \quad (2.5)$$

Harvesting can effect the nesting habits of the parents and the survivorship of the remaining nestlings. Peregrine falcons are known to re-nest (lay another clutch) if a clutch is lost early (Ratcliffe 1993). However, by US Fish and Wildlife Service regulations, nestlings may not be harvested prior to 10 days of age (U.S. Fish and Wildlife Service 2001); thus removing nestlings

will not cause the parents to re-nest. Removing a nestling could increase the survivorship of remaining nestlings due to less work for the parents. However, removing nestlings only minimally improves the survivorship of the remaining young (Thomas Cade, The Peregrine Fund, personal correspondence), thus, in modeling the worst case we may ignore this.

The US Fish and Wildlife Service found $\lambda = 1.03$ (*Audubon Society of Portland v. United States Fish and Wildlife Service*), indicating long-term growth of 3%. This is consistent with our nominal model, which has largest eigenvalue 1.0288. However, much of the data in \mathbf{A} is uncertain.

2.3 Data Uncertainties

For the purpose of demonstrating the method, we will focus on the two parameters contributing the most to the uncertainty of λ . We choose one of the parameters to be the most uncertain one, and the other parameter to be the one that affects the long-term population growth rate λ the most.

We note that B is completely unknown, and varies substantially between different populations. If a population is close to carrying capacity then 2 year old birds are less likely to find a nesting site and so are less likely to breed (Hunt 1988). However, if the population is growing, then a high percent of 2 year old birds will breed as there is less competition. Hence we consider B to be the most uncertain of the parameters.

In Figure 1, we see how λ is affected by changes in each of the parameters. When determining the effect of a parameter on λ , we can think of λ as a function of each parameter while the other parameters stay fixed at the nominal values. Figure 1 gives $\lambda(p)$ for each parameter. The value of p (shown on the x -axis) represents the proportional change in the parameter from the nominal value (e.g. $p = -.1$ represents a 10% decrease in the parameter). The y axis gives the value of λ obtained when that entry is changed and other entries are not changed. These curves are obtained using equation (A.3) in subsection A.2 of the Appendix. From these graphs we see that changes in S_2 are more important to λ than changes in S_1 or S_0 . Since the long-term growth rate λ is most sensitive

to S_2 , and B is the most uncertain parameter, we look at how λ is affected by simultaneous changes in B and S_2 . In particular, we will determine what changes can be tolerated in B and S_2 without destroying the conservation property $\lambda > 1$.

The traditional approach to analyzing the affect of a change of p to a parameter a on λ is via sensitivity analysis. The sensitivity of λ to a is the instantaneous rate of change in λ with respect to a , i.e. it is $d\lambda/da$ evaluated at the nominal value of a (see Table 1). Even though sensitivity analysis is only guaranteed accurate for small p , in this case the sensitivities in Table 1 lead to the same conclusion as the graphs in Figure 1.

We now analyze the effect of simultaneous changes in both B and S_2 . We parameterize the change in B by p_1 , and the change in S_2 by p_2 , where p_1 is an absolute change and p_2 is a relative change. In particular, we want the perturbed matrix to be

$$\tilde{\mathbf{A}} = \mathbf{A} + \mathbf{P}_1 + \mathbf{P}_2 = \begin{pmatrix} 0 & FRS_1 p_1 & FRS_2(1 + p_2) \\ S_0 & 0 & 0 \\ 0 & S_1 & S_2(1 + p_2) \end{pmatrix}. \quad (2.6)$$

As in subsection A.2 of the Appendix, we write

$$\mathbf{P}_1 = p_1 \mathbf{D}_1 \mathbf{E}_1, \quad \mathbf{P}_2 = p_2 \mathbf{D}_2 \mathbf{E}_2,$$

where

$$\mathbf{D}_1 = \begin{pmatrix} FRS_1 \\ 0 \\ 0 \end{pmatrix}, \quad \mathbf{E}_1 = (0 \ 1 \ 0) \quad (2.7)$$

and

$$\mathbf{D}_2 = \begin{pmatrix} FRS_2 \\ 0 \\ S_2 \end{pmatrix}, \quad \mathbf{E}_2 = (0 \ 0 \ 1). \quad (2.8)$$

The admissible range of p_1 is 0 to 1, where $p_1 = 1$ implies all 2 year old females breed. The admissible range of p_2 is constrained so that the term $S_2(1 + p_2)$, which is a probability, is between

0 and 1, so p_2 ranges from -1 to 0.25 . Thus the set of admissible perturbations is described by

$$S = \{(p_1, p_2) \mid 0 \leq p_1 \leq 1, \quad -1 \leq p_2 \leq .25\}.$$

We wish to find the set of (p_1, p_2) in S so that $\lambda > 1$. We can easily find a curve in the (p_1, p_2) plane on which some eigenvalue (*not* necessarily the largest eigenvalue λ) is equal to one. Hence on this curve λ must be greater than or equal to 1. If we can prove that on this curve $\lambda = 1$, then the curve breaks up the set S of admissible perturbations into two regions, one of which corresponds to $\lambda > 1$, while the other region corresponds to $\lambda < 1$. In subsection A.3 of the Appendix we find the equation of the curve using a method which *guarantees* that $\lambda = 1$ for (p_1, p_2) on this curve. The curve is shown in Figure 2, on a coordinate system with p_1 on the horizontal axis and p_2 on the vertical axis. The nominal values of (B, S_2) are represented by $(p_1, p_2) = (0, 0)$. The shaded area in Figure 2 represents those (p_1, p_2) which correspond to $\lambda > 1$.

Figure 2 shows us how much error is acceptable in B and S_2 , and more importantly shows the interplay between uncertainties in the two variables. For instance, for any value of B , S_2 can tolerate a negative error of 4% (or, of course, any positive error). If $B = 1$, S_2 can tolerate a negative error of 13% or less. This illustrates an important principle - new information about one parameter often changes the robustness to uncertainty in other parameters.

2.4 The effect of harvesting on long-term growth

We now examine the effect of harvesting on the largest eigenvalue λ of the modified population projection matrix \mathbf{A}_h (see (2.5)). As a simple example, let \mathbf{A}_h use the nominal values of B and S_2 ; we find that the smallest value of h which gives an eigenvalue of 1 is .1714. Therefore, since λ varies continuously with h and the nominal matrix \mathbf{A} with $h = 0$ has largest eigenvalue 1.0288, any value of h less than .1714 gives a largest eigenvalue of A_h greater than 1. Thus even with no 2-year old falcons breeding, if there is no uncertainty 17.41% may be harvested while maintaining a growth rate of $\lambda = 1$.

However, this does not take into account uncertainties in B and S_2 . Hence we again let p_1 be the uncertainty in B and p_2 be the uncertainty in S_2 . As in the analysis of \mathbf{A} in subsection A.3 of the Appendix, for several values of h we find curves in the (p_1, p_2) plane on which the largest eigenvalue λ for \mathbf{A}_h is 1. For $h = 0, .05, .1, .15, .1714$ and 2, these curves are shown in Figure 3. The region above each curve gives the values of (p_1, p_2) for which $\lambda > 1$ for \mathbf{A}_h .

Now suppose that we wish to identify all (p_1, p_2) which guarantee a long term growth rate of at least 3%. Then we simply replace 1 in our computations with 1.03. For several values of h we find curves in the (p_1, p_2) plane on which λ for \mathbf{A}_h is 1.03. For $h = 0, .05, .1, .15,$ and 2, these curves are shown in Figure 4 below. Using the technique in subsection A.3 of the Appendix, we can show that these curves indeed give values of (p_1, p_2) for which $\lambda = 1.03$ for \mathbf{A}_h for the given value of h . The region above each curve gives the values of (p_1, p_2) for which $\lambda > 1.03$ for \mathbf{A}_h .

3 Discussion

We can write the uncertainties in a population projection matrix \mathbf{A} as a perturbation \mathbf{P} of that matrix, and \mathbf{P} can be described by parameters (p_1, p_2, \dots, p_m) which lie in an admissible set S . The admissible set can be decomposed into

$$\{(p_1, p_2, \dots, p_m) \in S \mid \lambda(p_1, p_2, \dots, p_m) > 1\}$$

and

$$\{(p_1, p_2, \dots, p_m) \in S \mid \lambda(p_1, p_2, \dots, p_m) < 1\},$$

which are separated by the hyperplane C given in (2.1). It is easy to find the hyperplane Γ given by (2.2), and it is often possible to prove that $\Gamma = C$. Once we have an equation for C , we can use this decomposition to analyze the effect of simultaneous perturbations on the asymptotic growth or decay of the population.

This approach is used study the effect of uncertainties on an endangered peregrine falcon pop-

ulation. This population is currently on the rise, which is reflected in the fact that the largest eigenvalue λ of the nominal population projection matrix is greater than 1. However, the data collected for this population is highly uncertain and variable, and hence the long term growth rate computed from the population projection matrix is uncertain. Using our techniques, we analyze the effect of these uncertainties on the property that $\lambda > 1$. We then include the effect of harvesting on λ . The survivorship S_2 of the older birds is the parameter which is most influential to the growth rate, and the proportion B of 2 year birds which breed is the most uncertain parameter. Each of these occurs in two entries in the population projection matrix. We examine in detail the effect of simultaneous uncertainties in these two variables on λ . In the model without harvesting, the range of uncertainty keeping $\lambda > 1$ is given by all (p_1, p_2) above the curve shown in Figure 2 with the end points of $(0, -0.0418)$ and $(1, -0.1284)$. Most of this is mathematically straightforward; the mathematically novel part is to show that the graphed curves correspond to the largest eigenvalue $\lambda = 1$, rather than *some* eigenvalue being equal to 1, so the region above the curve represents all (p_1, p_2) for which $\lambda > 1$, rather than just some of them.

We then did the same analysis when a proportion h of the falcons are harvested. The relevant graphs are given in Figure 3. From these graphs we can read off how much uncertainty the data can have and still guarantee long-term growth. For instance, when S_2 is larger than or equal to the nominal value .8, up to 17.41% of the nestlings may be harvested without destroying long-term growth, no matter what B is. If $B = 1$ and 17.41% are harvested, S_2 can tolerate uncertainties of up to -6% . The US Fish and Wildlife Service suggests that 5% can be harvested. Reading from the $h = .05$ graph in Figure 1, we see that if $B = 0$, this allows an uncertainty of 3% in S_1 , and if $B = 1$, this allows an uncertainty of 11% in S_1 . If we are trying to maintain 3% population growth, then we look at Figure 4. We see, for instance, that 3% population growth cannot be maintained with 5% harvesting, unless our nominal value of S_2 is an underestimate, or at least 20% of 2 year old birds breed. If more than 20% of two year old birds breed, then uncertainties of up to 6% in adult survival when $B = 1$ can be tolerated.

We have ignored the issue of how many nestlings a harvest rate of 5% actually represents.

There is substantial uncertainty in estimates of numbers of breeding pairs, and consequently in the number of nestlings that can be taken. However, if detectability of breeding pairs is less than 1, then the actual number of identified nests will be an underestimate. As long as the actual, observed number of nests is used to calculate the number of nestlings that can be taken, the actual harvest rate will be less than 5%. This cannot be guaranteed if the permitted take is based on an estimated number of breeding pairs. In that case, if the breeding population is over-estimated then the nominal 5% harvest rate would in fact be larger, and consequently there is a greater risk that the population growth targets would not be maintained. The robust, conservative decision is to use the actual observed number of nests. This harvest level could be increased, but this is only safe when the accuracy of breeding population estimates can be carefully defined.

Robustness approaches are a relatively new idea in ecology and conservation biology, although they find wide application in many other fields (e.g. Ben-Haim 2001). In addition to applications in conservation biology (e.g. Hodgson *et al.* 2004, 2005), the concept was recently applied to foraging theory to examine the possibility that foragers seek to guarantee minimum returns rather than maximize returns (Carmel and Ben-Haim 2005). The key difference from a decision making perspective is the shift from maximizing a performance criterion to guaranteeing some minimum level of that criterion.

This new approach may make setting objectives for decision making much easier in conservation biology. For example, when comparing two or more management decisions for their effect on the risk of extinction, we may choose the strategy that provides the lowest risk of extinction (Regan *et al.* 2005). However, if the costs of these decisions differ, we are then forced into making arguments about how much a species is "worth" in order to justify a greater expense. In contrast, if we specify some minimum performance that we wish to guarantee, we can use robustness methods to compare decisions based on how much error each can tolerate and still guarantee the minimum. Differing costs then purchase different levels of robustness, relieving us of the need to value each species. We still have to value the robustness, but this would appear to be easier to do than argue about the value of a species.

In conclusion, the approach we have outlined here provides a powerful set of tools for examining the effect of decisions in the face of unbounded and poorly characterized uncertainty in population projection matrices. Many decisions for threatened and endangered species are made with poor or no information. We can still make decisions under these circumstances in a manner that is highly defensible, even without making assumptions about the distribution of uncertainty or limiting ourselves to discussions of single, infinitesimally small changes in the parameters.

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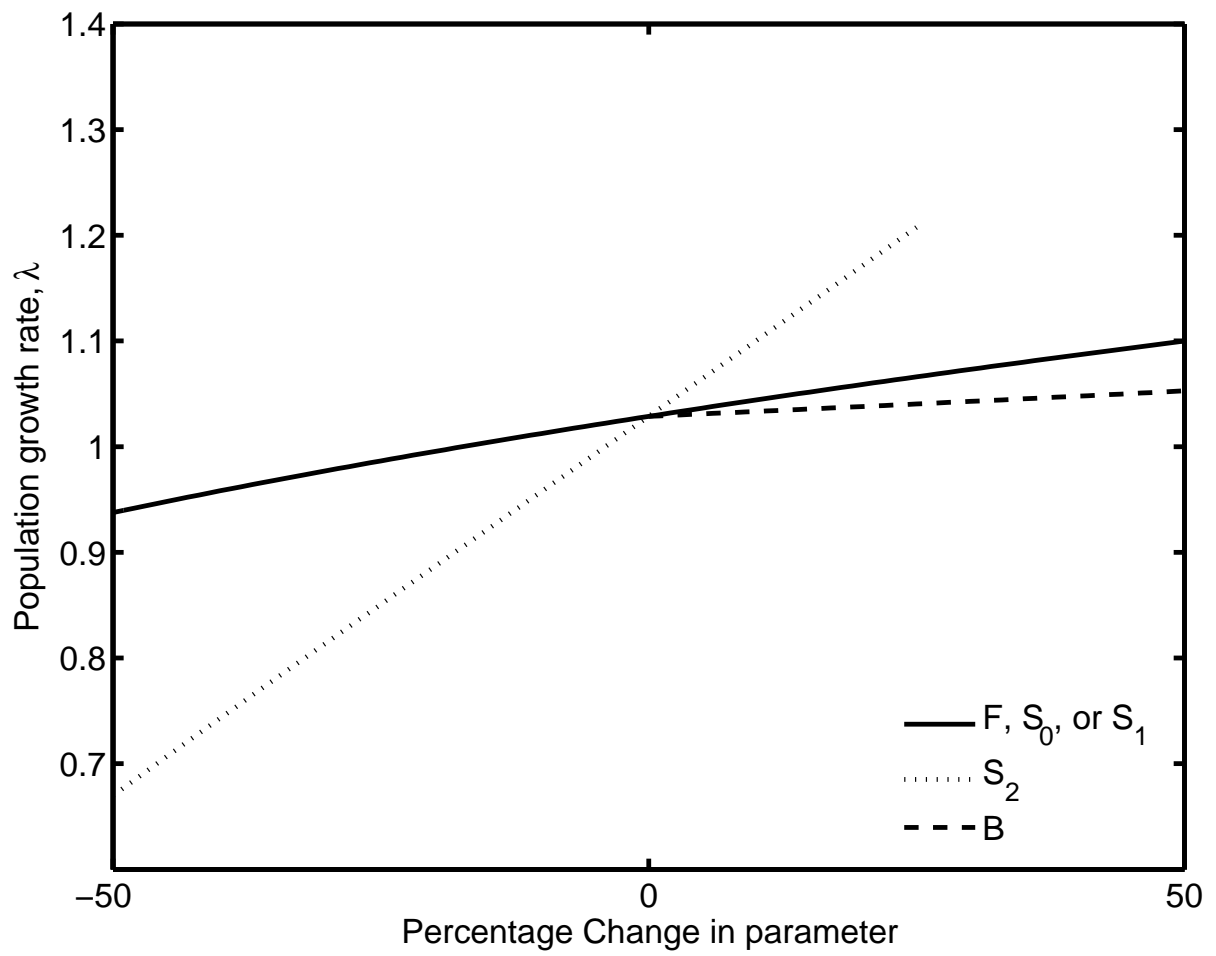


Figure 1: λ vs. percentage change in parameters

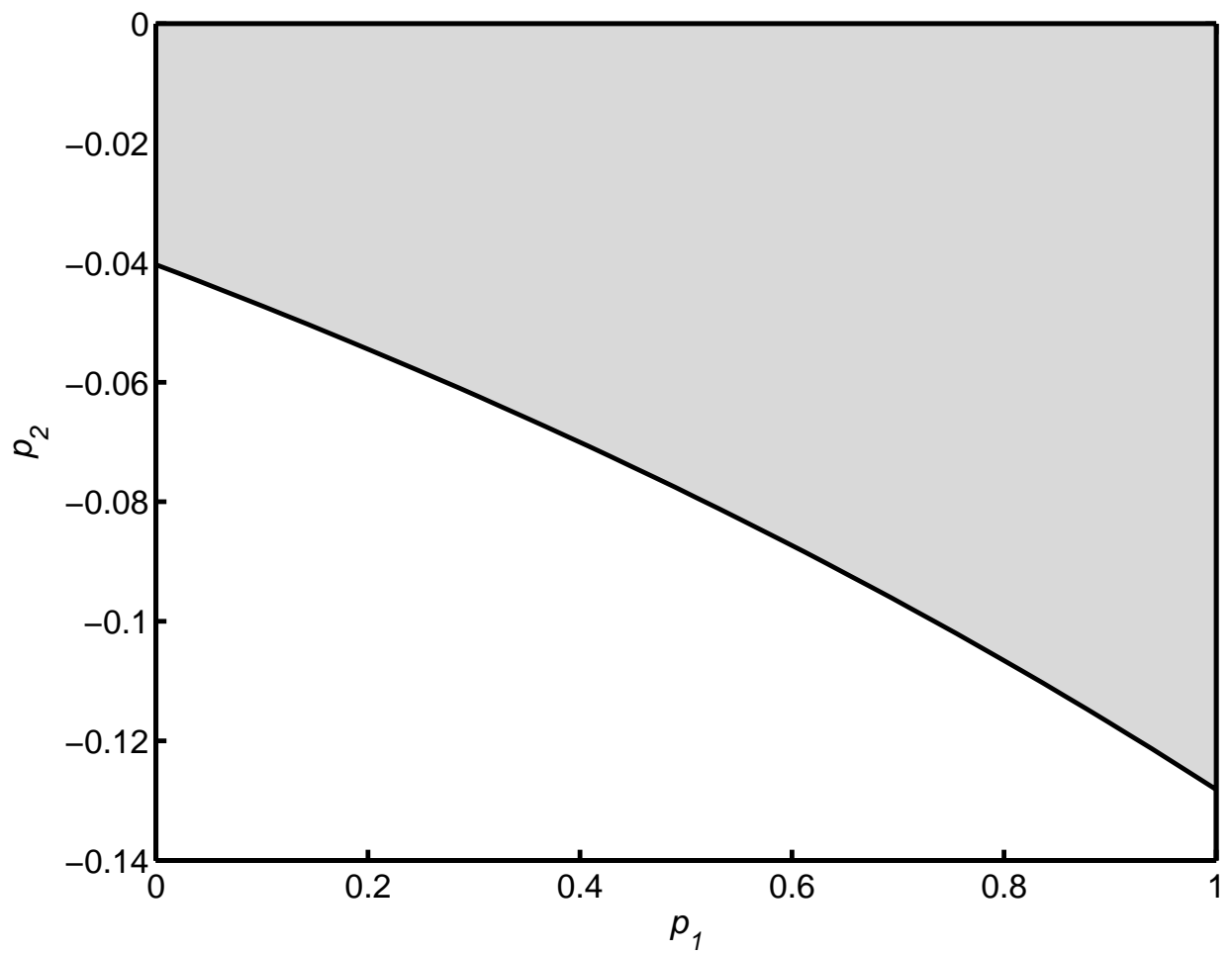


Figure 2: The boundary curve represents all pairs of perturbations (p_1, p_2) for which $\lambda = 1$. The shaded area represents all pairs of perturbations (p_1, p_2) for which $\lambda > 1$.

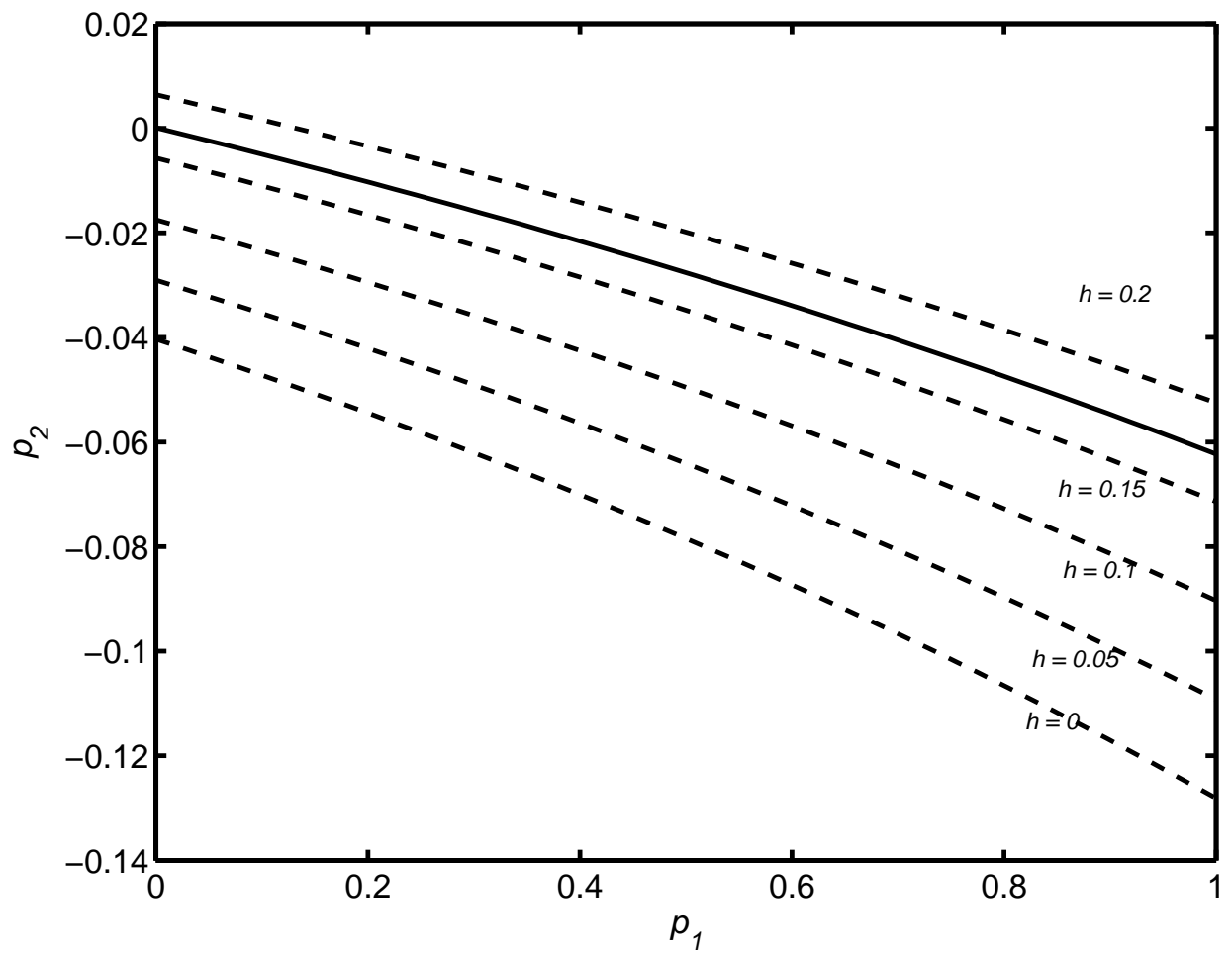


Figure 3: The effect of harvesting on the $\lambda = 1$ curves. The bold line is $h = 0.1714$, the amount of harvesting that yields $\lambda = 1$ with no uncertainty for the nominal values.

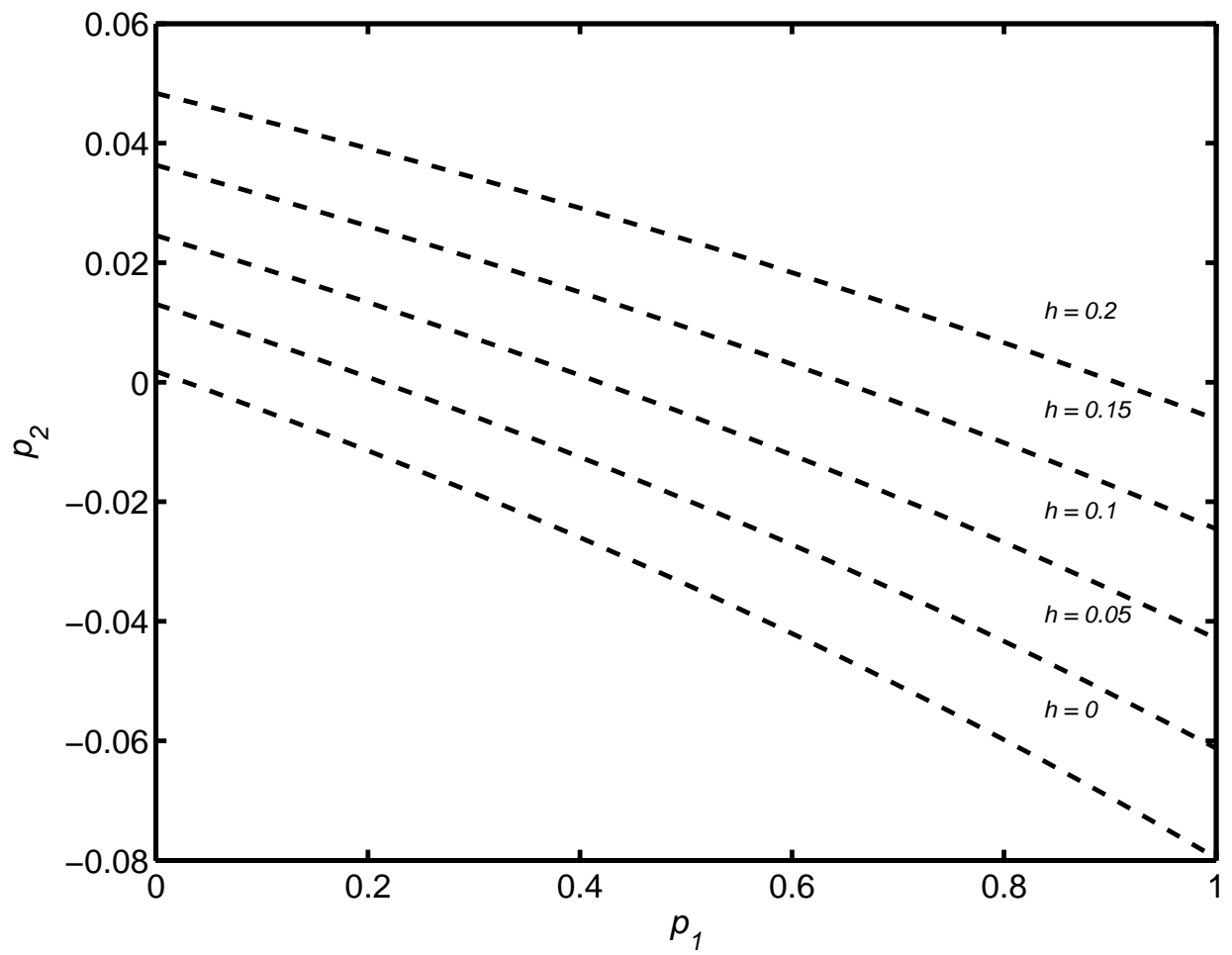


Figure 4: The effect of harvesting on the $\lambda = 1.03$ curves.

A. Appendix

A.1 Eigenvalues and population growth

For a matrix \mathbf{M} , we write $\mathbf{M} \geq 0$ if all of its entries are nonnegative, and we write $\mathbf{M} > 0$ if all of its entries are positive. For matrices \mathbf{M}_1 and \mathbf{M}_2 , we write $\mathbf{M}_1 \geq \mathbf{M}_2$ if $\mathbf{M}_1 - \mathbf{M}_2 \geq 0$. Population projection matrices are *primitive* matrices; a primitive matrix is a square matrix $\mathbf{A} \geq 0$ for which there exists k such that $\mathbf{A}^k > 0$. It is easy to check that any matrix of the form (2.4) is primitive, since $A^4 > 0$. From the Peron-Frobenius Theorem, for all primitive matrices λ (the eigenvalue of largest modulus) is real and of geometric and algebraic multiplicity 1 (Seneta 1981). This simplifies the analysis of such matrices considerably, since any physically reasonable uncertainties in the matrix will not change the fact that \mathbf{A} is primitive, so when analyzing long term growth rate, we only need to concern ourselves with real eigenvalues. If $\lambda > 1$ the total population represented by \mathbf{x} is (denoting the dimension of the system by n)

$$\|\mathbf{x}\| := x_1 + x_2 + \dots + x_n,$$

the ℓ^1 norm of \mathbf{x} . The population increases geometrically, i.e. there exists $m > 0, \rho > 1$ such that

$$\|\mathbf{x}_k\| \geq m\rho^k, \quad k = 0, 1, \dots$$

If $\lambda < 1$, the total population decreases geometrically, i.e. there exists $M \geq 1, \rho < 1$ such that

$$\|\mathbf{x}_k\| \leq M\rho^k, \quad k = 0, 1, \dots$$

If $\lambda = 1$, the total population is asymptotically constant, i.e.

$$\lim_{k \rightarrow \infty} \mathbf{x}_k = \mathbf{x},$$

where \mathbf{x} is the eigenvector of \mathbf{A} associated with an eigenvalue 1. We also note, for future reference, that the Peron-Frobenius Theorem states that the eigenvector associated with the largest eigenvalue has all positive entries, and that this is the only eigenvector with this property.

For population projection matrices, it is reasonable that if the survival rates or fecundity increases, then $\lambda(\mathbf{A})$ will also increase. In the following simple but useful Proposition we generalize this idea to primitive matrices.

Proposition A.1. *If \mathbf{A} is primitive and $\mathbf{P} \geq 0$, then $\mathbf{A} + \mathbf{P}$ is primitive and $\lambda(\mathbf{A}) \leq \lambda(\mathbf{A} + \mathbf{P})$.*

Proof. Suppose \mathbf{A} is primitive, so there exists $m \in \mathbb{N}$ such that $\mathbf{A}^m > 0$, and suppose $\mathbf{P} \geq 0$. Expanding $(\mathbf{A} + \mathbf{P})^m$ by the binomial theorem, we see that for any $k \in \mathbb{N}$,

$$(\mathbf{A} + \mathbf{P})^k = \mathbf{A}^k + \mathbf{M}_k$$

for some $\mathbf{M}_k \geq 0$. Hence $(\mathbf{A} + \mathbf{P})^m \geq \mathbf{A}^m$, so $\mathbf{A} + \mathbf{P}$ is primitive.

For the remainder of the proof we will use the well-known formula (see Kato 1980) for the modulus of $\lambda(\mathbf{A})$:

$$\lambda(A) = \lim_{k \rightarrow \infty} \|\mathbf{A}^k\|^{\frac{1}{k}}, \tag{A.1}$$

where the norm $\|\mathbf{M}\|$ is defined by

$$\|\mathbf{M}\| = \sup_{\|\mathbf{x}\|=1} \|\mathbf{M}\mathbf{x}\|.$$

Since $\mathbf{A}^k > 0$ for large enough $k \in \mathbb{N}$, we see that

$$\|\mathbf{A}^k\| = \sup_{\|\mathbf{x}\|=1} \|\mathbf{A}^k \mathbf{x}\|$$

is taken on for a vector \mathbf{x} which has nonnegative entries. For \mathbf{x} which maximizes this last expression,

$$\|(\mathbf{A} + \mathbf{P})^k\| \geq \|(\mathbf{A} + \mathbf{P})^k \mathbf{x}\| \geq \|\mathbf{A}^k \mathbf{x}\| = \|\mathbf{A}^k\|.$$

Therefore

$$\|\mathbf{A}^k\|^{\frac{1}{k}} \leq \|(\mathbf{A} + \mathbf{P})^k\|^{\frac{1}{k}}. \quad (\text{A.2})$$

Hence, taking limits in (A.2) as $k \rightarrow \infty$ and using (A.1),

$$\lambda(\mathbf{A}) \leq \lambda(\mathbf{A} + \mathbf{P}).$$

□

A.2 Simple perturbations and transfer functions

In some cases the perturbation matrix \mathbf{P} can be factored in a way which will ultimately simplify our computations, see Hodgson, *et al.* 2004, 2005 for many examples of this. As a simple example, suppose the only uncertain term which affects λ is the fecundity of the second age group. Then \mathbf{P} is of the form

$$\mathbf{P} = \delta \begin{pmatrix} 0 & 0 & 1 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix},$$

where δ is the magnitude of the perturbation. This \mathbf{P} can be written as

$$\mathbf{P} = \mathbf{D}\delta\mathbf{E},$$

where

$$\mathbf{D} = \begin{pmatrix} 1 \\ 0 \\ 0 \end{pmatrix} \quad \text{and} \quad \mathbf{E} = (0 \ 0 \ 1).$$

When \mathbf{P} is of the form $\mathbf{P} = \mathbf{D}\delta\mathbf{E}$ for some column vector \mathbf{D} and row vector \mathbf{E} , it is very easy to find the relationship between δ and the eigenvalues of the perturbed matrix $\tilde{\mathbf{A}} = \mathbf{A} + \mathbf{P}$. We define

the *transfer function*

$$\mathbf{G}(s) = \mathbf{E}(s\mathbf{I} - \mathbf{A})^{-1}\mathbf{D},$$

where \mathbf{I} is the identity matrix. Hodgson and Townley 2004 showed that a value μ which is not an eigenvalue of \mathbf{A} , is an eigenvalue of the perturbed matrix $\tilde{\mathbf{A}}$ if and only if

$$\delta = \frac{1}{\mathbf{G}(\mu)}. \tag{A.3}$$

This means that we can define the magnitude δ that will generate a given eigenvalue. Thus, if

$$\delta > \frac{1}{\mathbf{G}(1)},$$

then some eigenvalue of $\tilde{\mathbf{A}}$ is greater than 1, hence $\lambda > 1$ (since λ is the largest eigenvalue) and the actual system has long-term population growth. For the matrix \mathbf{A} in (2.4) and the example perturbation described above, $1/\mathbf{G}(1) = -0.115$, so the matrix $\tilde{\mathbf{A}}$ with the fertility of the second age class reduced by -0.115 has an eigenvalue of 1. Any change in the fertility of the second age class which is larger than -0.115 is guaranteed to lead to population growth.

A.3 The $\lambda = 1$ curve for two perturbations

Suppose λ (the eigenvalue of $\tilde{\mathbf{A}}$ of largest modulus) is considered to be a function of (p_1, p_2) , as in Sections 2.2 and 2.3. Suppose further that the curves shown in Figures 2 and 3 are indeed the $\lambda = 1$ curves. Then Proposition A.1, along with the fact that λ is a continuous function of (p_1, p_2) , shows that the curve $\lambda = 1$ separates the admissible part of the (p_1, p_2) plane into two regions: those (p_1, p_2) above the curve give $\lambda > 1$, and (p_1, p_2) below the curve give $\lambda < 1$.

It is easy to verify that the curve in Figure 2 can be obtained by the formula in (2.2). However, this formula does not help us prove that $\Gamma = C$, so we take a different approach. The curves in Figures 3 and 4 can be analyzed in exactly the same way.

Let λ have associated eigenvector \mathbf{v} . The Perron-Frobenius theorem states that \mathbf{v} has positive

entries, and that it is the only eigenvector with this property. Let \mathbf{D}_1 , \mathbf{D}_2 , \mathbf{E}_1 and \mathbf{E}_2 be as in (2.7) and (2.8). The condition that \mathbf{v} is an eigenvector of the perturbed matrix $\tilde{\mathbf{A}}$ with associated eigenvalue λ can then be written as

$$(\mathbf{A} + \mathbf{D}_1 p_1 \mathbf{E}_1 + \mathbf{D}_2 p_2 \mathbf{E}_2) \mathbf{v} = \lambda \mathbf{v},$$

or

$$(\mathbf{D}_1 p_1 \mathbf{E}_1 + \mathbf{D}_2 p_2 \mathbf{E}_2) \mathbf{v} = (\lambda \mathbf{I} - \mathbf{A}) \mathbf{v}.$$

This implies that

$$(\lambda \mathbf{I} - \mathbf{A})^{-1} \mathbf{D}_1 p_1 \mathbf{E}_1 \mathbf{v} + (\lambda \mathbf{I} - \mathbf{A})^{-1} \mathbf{D}_2 p_2 \mathbf{E}_2 \mathbf{v} = \mathbf{v}. \quad (\text{A.4})$$

We are trying to find the curve $\lambda = 1$ in the (p_1, p_2) plane. Plugging $\lambda = 1$ into (A.4) we see that this curve is given by

$$(\mathbf{I} - \mathbf{A})^{-1} \mathbf{D}_1 p_1 \mathbf{E}_1 \mathbf{v} + (\mathbf{I} - \mathbf{A})^{-1} \mathbf{D}_2 p_2 \mathbf{E}_2 \mathbf{v} = \mathbf{v}, \quad (\text{A.5})$$

provided that

$$\mathbf{v} = \begin{bmatrix} v_1 \\ v_2 \\ v_3 \end{bmatrix}$$

has all positive entries. We normalize \mathbf{v} by multiplying it by $1/v_3$, and plug in the values of \mathbf{D}_1 , \mathbf{D}_2 , \mathbf{E}_1 and \mathbf{E}_2 from (2.7) and (2.8), to obtain

$$(\mathbf{I} - \mathbf{A})^{-1} \begin{bmatrix} FRS_1 \\ 0 \\ 0 \end{bmatrix} p_1 \begin{bmatrix} 0 & 1 & 0 \end{bmatrix} \begin{bmatrix} v_1 \\ v_2 \\ 1 \end{bmatrix} + (\mathbf{I} - \mathbf{A})^{-1} \begin{bmatrix} FRS_2 \\ 0 \\ S_2 \end{bmatrix} p_2 \begin{bmatrix} 0 & 0 & 1 \end{bmatrix} \begin{bmatrix} v_1 \\ v_2 \\ 1 \end{bmatrix} = \begin{bmatrix} v_1 \\ v_2 \\ 1 \end{bmatrix},$$

where v_1 and v_2 must be positive. Substituting in numerical values for F, R, S_1 , and S_2 leads to the three equations

$$-2.6396 p_1 v_2 - 15.7588 p_2 = v_1 \quad (\text{A.6})$$

$$-1.4359p_1v_2 - 8.5728p_2 = v_2 \quad (\text{A.7})$$

$$-4.8104p_1v_2 - 24.7189p_2 = 1. \quad (\text{A.8})$$

Solving for v_1 and v_2 ,

$$v_1 = \frac{-15.7588p_2}{1 + 1.4359p_1}, \quad v_2 = \frac{-8.5728p_2}{1 + 1.4359p_1}. \quad (\text{A.9})$$

Substituting v_2 into (A.8) and solving for p_2 in terms of p_1 gives

$$p_2 = \frac{1 + 1.4359p_1}{5.7447p_1 - 24.7189} =: f(p_1). \quad (\text{A.10})$$

This is the equation for the curve we claim corresponds to $\lambda = 1$. We note that for f given in (A.9), $f(0) = -.0405$ and $f(1) = -.1284$. Furthermore

$$f'(p_1) = \frac{-41.2386}{(5.7447p_1 - 24.7189)^2} < 0$$

for all p_1 , so the curve is decreasing for all p_1 . Thus, if we wish to find *all* (p_1, p_2) in the admissible range $\{0 < p_1 < 1, -1 < p_1 < .25\}$ such that some eigenvalue is 1, it is that part of the curve (A.10) between $(0, -.0405)$ and $(1, -.1284)$. This is shown in Figure 2. We note that this means that on the on the curve,

$$0 < p_1 < 1, \quad -.1284 < p_2 < -.0405. \quad (\text{A.11})$$

We need to show that for (p_1, p_2) on this part of the curve, 1 is in fact the largest eigenvalue of $\tilde{\mathbf{A}}$. We do this by showing that for (p_1, p_2) on the curve, the associated eigenvector is positive, i.e. $v_1 > 0$ and $v_2 > 0$. However, this is clear from (A.9) and (A.11), since $p_2 < 0$ and $p_1 > 0$ on the curve. This completes the proof that curve in Figure 1 is indeed the curve of perturbations of B and S_2 which gives $\lambda = 1$.