Robust population management 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 an asymptotic growth rate $\lambda > 1$ 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.

Keywords: matrix sensitivity; elasticity; robustness; structured population models;

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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 parameters 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 analyses is predicated on analyzing perturbed behaviors resulting from small deviations away from some assumed nominal behavior. In fact, this approach can be misleading for large perturbations (see Hodgson and Townley 2004, Mills, *et. al.* 1999). 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, and in many cases there is not 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. Even when empirical variance estimates or bounds on parameters are available, and accepted by all parties, correlations between parameters are certainly present and usually unknown. 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 focus 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. A general framework of robustness analysis, which has been developed in the field of control theory, has been adapted for population dynamics in ecology by Hodgson and Townley (2004). The robustness approach adopts a different viewpoint to that typified by sensitivity/elasticity analysis: the latter is microscopic, perturbing away from a nominal model and focusing in on the infinitessimal dependence of a specific dynamical property on the perturbation; the latter is essentially macroscopic and focuses in on perturbation as a function of required dynamical property. Hodgson and Townley (2004) tabulates a clear comparison between these micro. vs. macro-scopic approaches.

Whilst we build on the approach in Hodgson and Townley (2004), our approach differs from theirs in several ways. Most importantly our focus is on robustness of population growth (at least one eigenvalue greater than one in modulus), which is more delicate than their simpler problem of robustness of population decline (all eigenvalues less than one in modulus). 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 (*Falco peregrinus anatum*) 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, *et. al.* 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.

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.

Methods

General Method for Classifying Perturbations

Begin by assuming that $\mathbf{A}$ is a time-invariant population projection matrix for the population in question. The leading eigenvalue of $\mathbf{A}$, which we denote by $\lambda(\mathbf{A})$, satisfies $\lambda(\mathbf{A}) > 1$, which implies that the population is increasing 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 Appendix A. 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), then 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 $(p_1, p_2, \ldots, p_m)$, 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 $(p_1, p_2, \ldots, p_m)$ is *admissible* if $\mathbf{A} + \mathbf{P}$ is an acceptable projection matrix, and we let S be the set of admissible $(p_1, p_2, \ldots, p_m)$; for example, it will be typical to restrict the perturbations so that the sum of the survival probabilities are always between 0 and 1. We can denote the explicit dependence of $\tilde{\mathbf{A}}$ and λ on $(p_1, p_2, \ldots, p_m)$ by writing

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

Now consider the subset of S given by

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

This is the set of $(p_1, p_2, \ldots, p_m)$ 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;

this is the case which is illustrated in this paper. 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). When $m = 2$ or 3, it is clear what it means for a particular $(p_1, p_2, \ldots, p_m)$ to be on one side or another of C. For hypersurfaces in dimensions higher than 3, it is sometimes not possible to define the notion of the "side" of the hypersurface. However, for the surfaces described by (1), the notion of the side of C can be made precise mathematically, using Proposition A.1 in Appendix A. Since we are assuming that the unperturbed matrix $\mathbf{A}$ has $\lambda(\mathbf{A}) = \lambda(0, 0, \ldots, 0) > 1$, the "population growth" side of C is the one containing $(0, 0, \ldots, 0)$. Hence we consider all "good" perturbations to be those which are on the population growth side of C. Since the nominal model corresponds to $(p_1, p_2, \ldots, p_m) = (0, 0, \ldots, 0)$, one measure of robustness is how far $(0, 0, \ldots, 0)$ 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

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

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 $\lambda(p_1, p_2, \ldots, p_m) < 1$.

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

$$\Gamma := \{(p_1, p_2, \ldots, p_m) \in S \mid \det(I - \mathbf{A}(p_1, p_2, \ldots, p_m)) = 0\}. \quad (2)$$

For the peregrine falcon model, in Appendix B we determine Γ manually, and we show that Γ is the same curve as C by using an analytical argument based on the Peron-Frobenius Theorem (Seneta 1981). The manual computations would be arduous for larger matrices or multidimensional perturbations, so in the electronic Supplement we provide MATLAB code demonstrating how to apply this method to a larger matrix and more complex perturbations. For all matrices we have tried so far, it is easy to confirm numerically that Γ is the same curve as C. A thorough theoretical study of when $C = \Gamma$ is forthcoming (D. Boeckner *et al.* unpublished manuscript). Even if Γ is not the same as C (or cannot be proved to be the same as C), it is still useful. For $(p_1, p_2, \ldots, p_m)$ on Γ, the eigenvalue of largest modulus $\lambda(p_1, p_2, \ldots, p_m)$ must be greater than or equal to 1, since some eigenvalue of $\tilde{\mathbf{A}}((p_1, p_2, \ldots, p_m)$ is equal to 1. Hence for $(p_1, p_2, \ldots, p_m)$ on side of Γ which contains $(0, 0, \ldots, 0)$, it is guaranteed that $\lambda(p_1, p_2, \ldots, p_m) > 1$; however, it is not guaranteed that on the other side of Γ we have $\lambda(p_1, p_2, \ldots, p_m) < 1$.

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 the population of birds in each of these three classes as x_1, x_2 and x_3, respectively, and the population vector is

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

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

$$\mathbf{x}_{k+1} = \mathbf{A}\mathbf{x}_k, \tag{3}$$

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 *et al.* (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

$$\mathbf{A} = \begin{pmatrix} 0 & FRBS_1 & FRS_2 \\ S_0 & 0 & 0 \\ 0 & S_1 & S_2 \end{pmatrix}. \tag{4}$$

We use parameter values estimated from the peregrine falcons in Colorado, USA (Table 1; Craig *et. al.* 2004). 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. This also assumes that the two age classes are equally vulnerable to harvesting. Let

$$\mathbf{A}_h = \begin{pmatrix} 0 & (1-h)FRBS_1 & (1-h)FRS_2 \\ S_0 & 0 & 0 \\ 0 & S_1 & S_2 \end{pmatrix}. \tag{5}$$

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.

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 percentage 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 (A.2) in Appendix A. 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 **??**). 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

$$\tilde{\mathbf{A}} = \mathbf{A} + \mathbf{P}_1 + \mathbf{P}_2 = \begin{pmatrix} 0 & FRS_1p_1 & FRS_2(1+p_2) \\ S_0 & 0 & 0 \\ 0 & S_1 & S_2(1+p_2) \end{pmatrix}. \tag{6}$$

As in Appendix A, we write

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

where

$$\mathbf{D}_1 = \begin{pmatrix} FRS_1 \\ 0 \\ 0 \end{pmatrix}, \qquad \mathbf{E}_1 = \begin{pmatrix} 0 & 1 & 0 \end{pmatrix} \tag{7}$$

and

$$\mathbf{D}_2 = \begin{pmatrix} FRS_2 \\ 0 \\ S_2 \end{pmatrix}, \qquad \mathbf{E}_2 = \begin{pmatrix} 0 & 0 & 1 \end{pmatrix}. \tag{8}$$

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

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

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 Appendix B 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.

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. This yields a new curve (Figure 2) that is shifted upwards relative to the previous curve; because $\lambda = 1.0287$ at the nominal values, this new curve runs through the nominal point. The region above that curve gives the values of (p_1, p_2) for which $\lambda > 1.03$ for $\mathbf{A}$.

It is possible to approximate the effect of multiple large perturbations using sensitivities alone by assuming that $\lambda(p_1, p_2)$ is linear (pg. 224, Caswell 2001; Figure 2). When uncertainty in S_2 is considered alone (i.e. along the y-axis of the figure) the approximation is very close because the nonlinearity of λ with respect to S_2 is not great (Figure 1). However, when uncertainty in two parameters is considered simultaneously the linear approximation underestimates how much uncertainty is allowed in S_2 as B increases. For larger matrices or more complex perturbations the non-linearity, and hence the inadequacy of the linear approximation, could easily be more severe.

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 (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, then 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 **??** 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 $\mathbf{A}_h$. 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 3, 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 our objective is to maintain 3% population growth even with harvesting, then we can recalculate our curves as we did for the no harvesting model (Figure 2). Although we do not show the figure it is straightforward to calculate 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 can be tolerated when $B = 1$.

Discussion

The difficulty of incorporating the effects of uncertainty in matrix parameters into population management decisions is possibly one of the largest problems preventing widespread adoption of models in decision making. One of the best examples of thoroughly incorporating uncertainty in the assessment of management is Heppell *et al.'s* (1994) work on Red-cockaded woodpeckers, which relied on simulation to explore the effects of simultaneous uncertainties, as well as linear approximations using elasticities. This approach of using linear approximations from elasticities in one dimension, and Monte Carlo simulations in multiple dimensions is widely used (e.g. Ferriere *et al.* 1996, Caswell *et al.* 1998 among many others). Although it is possible to explore multidimensional parameter uncertainty reasonably easily in this fashion, the exact results obtained by simulation depend heavily on the details of how perturbations are selected. This is especially true when considering the possibility of constraints or correlations among life history traits; information on such correlations is generally unavailable (Wisdom *et al.* 2000). Caswell *et al.* (1998) incorporated constraints on life history traits by sampling survival curves from a group of related species. However, if a different set of species had been selected, the results would differ by an unknown amount, and this still does not answer the problem of correlated environmental variation. The method we introduce here gives an analytical result for all possible perturbations, and is straightforward to implement in readily available software (e.g. Symbolic Toolbox in MATLAB, see electronic supplement).

It is widely reported that predictions of the perturbations needed to effect a given change in λ using sensitivities or elasticities are accurate to relative changes of $\pm50\%$ (e.g. de Kroon *et al.* 2000). However, careful inspection of the numerical examples used to support this claim show that they typically involve perturbations of single vital rates or matrix entries. As shown in Figure 2 this is true for our matrix as well. However, once multiple parameters are perturbed the linear approximation breaks down. Some examples for multiple perturbations are provided in Caswell (2001; Chapter 18), and these demonstrate increasing approximation errors with both the dimension and size of the perturbation. Tenhumberg *et al.* (manuscript in review) conducted a Monte Carlo analysis of a large matrix with simultaneous uncertainty in 19 parameters, and found that when parameters varied simultaneously the local and linear elasticities were poor predictors of which parameters have a large influence on λ. Our method makes all of these predictions easily and without approximation errors.

The notion of using direct perturbations of the life cycle to improve decision making in conservation biology was put forward for empirical perturbations by Ehrlen and van Groenendael (1998). They suggested that the tools of "Life Table Response Experiments" (sensu Caswell 2001) should be used to analyze multiple years of data as perturbations of an underlying matrix. A key improvement of this idea over using elasticities alone is the incorporation of the differential variability of each matrix entry (de Kroon et al. 2000), arising because of differential variability in life history traits. However, small observed variation in a vital rate does not necessarily mean it is a poor target for management (Caswell 2001, pg 619), and similarly large observed variation does not automatically lead to a good management target. We have not addressed this issue in the present example, but it would be straightforward to rescale the perturbations (p_1, p_2) by the relative amount of variability in the parameters they are affecting, if estimates of this variability are available. A better, prospective approach would rescale the perturbations by their relative cost (ease of manipulation); an excellent example of how to do this using sensitivity analysis is given by Baxter *et al.* (2006).

A general, but underappreciated, problem with using models to assess the effects of management options is uncertainty in the connection between management and population vital rates. For example, when considering the effects of river flows on fish populations, it may not be at all clear what relationship exists between flow and spawning frequency. This type of uncertainty could be included in the methodology we present here by careful parameterization of the perturbations, although this will increase the number of dimensions in the perturbation, making interpretation more difficult. In the falcon harvesting example we 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.

We have approached the problem of uncertainty using perturbations in a time-invariant matrix model. Vital rates vary through time and space in natural populations, and ignoring these stochastic effects leads to predictable biases in the long term population growth rates (e.g. Tuljapurkar and Haridas 2006). When comparing management alternatives, the leading eigenvalue of a time invariant matrix works well in the relative sense, because it is a performance measure that integrates across the entire life history (Caswell 2001, pg. 615), so for that purpose our approach should work well. Nonetheless it would be an interesting exercise to formally compare the perturbation approach with stochastic population dynamics, and see if they can be combined or reconciled.

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 and Townley 2004, Hodgson et al. 2006), 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. Although our current work focuses on the asymptotic growth rate of a structured population, the general notion of guaranteeing performance could be applied to any measure of how well a population is doing. For example, a minimum probability of quasi-extinction over T years could be specified, and then simulations carried out to determine the largest parameter perturbation that has that as a worst case performance. By restricting our focus to asymptotic population growth rates we enable the use of a powerful set of analytical results rather than having to rely on simulations.

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 large 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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Table 1: Nominal, or unperturbed, matrix parameters for the Falcon model, sensitivities and elasticities. Note these are "lower level" sensitivities, so the corresponding elasticities do not add to one.

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	0.0453	0

Figure Captions

Figure 1 The largest eigenvalue λ vs. percentage change in the falcon life history parameters.

Figure 2 The boundary curve represents all pairs of perturbations (p_1, p_2) for which $\lambda(p_1, p_2) = 1$. The shaded area represents all pairs of perturbations (p_1, p_2) for which $\lambda(p_1, p_2) > 1$. The dashed line is $\lambda(p_1, p_2) = 1.0287$, the growth rate of the unperturbed matrix. The dotted line shows the linear approximation to these curves obtained from direct use of sensitivity to predict the effects of perturbations.

Figure 3 The effect of the harvesting fraction h on the $\lambda(p_1, p_2) = 1$ curves. The bold line is $h = 0.1714$, the amount of harvesting that yields $\lambda(p_1, p_2) = 1$ with no uncertainty for the nominal values.