

Robust population management under uncertainty for structured population models

A. Deines¹, E. Peterson², D. Boeckner³, J. Boyle⁴
A. Keighley⁵, J. Kogut⁶, J. Lubben³, R. Rebarber³
R. Ryan⁷, B. Tenhumberg⁸, S. Townley⁹, A.J. Tyre⁸ *

¹ *Department of Mathematics, Kansas State University,
Manhattan, KS 66506 U.S.A.*

² *Department of Mathematics, Wittenberg University,
Springfield, OH 45501 U.S.A.*

³ *Department of Mathematics, University of Nebraska-Lincoln,
Lincoln, NE, U.S.A.*

⁴ *Department of Mathematics, University of Notre Dame,
Notre Dame, IN 46556 U.S.A.*

⁵ *Department of Mathematical Sciences, Rensselaer Polytechnic Institute,
Troy, NY 12180 U.S.A.*

⁶ *Department of Mathematics, Simmons College,
Boston, MA 02115 U.S.A.*

⁷ *Department of Mathematics, University of Rhode Island,
Kingston, RI 02881 U.S.A.*

⁸ *School of Natural Resources, University of Nebraska-Lincoln,
Lincoln, NE, U.S.A.*

⁹ *Department of Mathematical Sciences,
University of Exeter, Exeter, EX4 4QE, U.K.*

*Corresponding author, atyre2@unl.edu

1 **Abstract**

2 Structured population models are increasingly used in decision making, but typically
3 have many entries that are unknown or highly uncertain. We present an approach for the
4 systematic analysis of the effect of uncertainties on long-term population growth or decay.
5 Many decisions for threatened and endangered species are made with poor or no information.
6 We can still make decisions under these circumstances in a manner that is highly defensible,
7 even without making assumptions about the distribution of uncertainty, or limiting ourselves
8 to discussions of single, infinitesimally small changes in the parameters. Suppose that the
9 model (determined by the data) for the population in question predicts long-term growth.
10 Our goal is to determine how uncertain the data can be before the model loses this property.
11 Some uncertainties will maintain long-term growth, and some will lead to long-term decay.
12 The uncertainties are typically structured, and can be described by several parameters. We
13 show how to determine which parameters maintain long-term growth. We illustrate the
14 advantages of the method by applying it to a peregrine falcon population. The US Fish
15 and Wildlife Service recently decided to allow minimal harvesting of peregrine falcons after
16 their recent removal from the Endangered Species List. Based on published demographic
17 rates, we find that an asymptotic growth rate $\lambda > 1$ is guaranteed with 5% harvest rate up

18 to 3% error in adult survival if no two year olds breed, and up to 11% error if all two year
19 olds breed. If a population growth rate of 3% or greater is desired, the acceptable error in
20 adult survival decreases to between 1 and 6% depending of the proportion of two year olds
21 that breed. These results clearly show the interactions between uncertainties in different
22 parameters, and suggest that a harvest decision at this stage may be premature without
23 solid data on adult survival and the frequency of breeding by young adults.

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

25 Running Head: Population management under uncertainty

26 **Introduction**

27 Decision making under uncertainty is a pervasive characteristic of conservation biology. Some-
28 times, the scientific uncertainty can be so severe that it paralyzes decision making, or causes deci-
29 sions to be made solely on social grounds, without being informed by science. Current quantitative
30 approaches to decision making usually rely on being able to construct models or scenarios that illu-
31 minate the consequences of decisions for various stakeholders. Managers of wildlife populations use
32 population projection matrices (Caswell 2001) to assess decisions with increasing frequency, but pa-
33 rameters in these matrices are inherently uncertain. Unfortunately, the standard tools for assessing

34 the effects of parameter uncertainty on matrix models require better data than is typically available
35 in the management of threatened or endangered species. The method of sensitivity and elasticity
36 analyses is predicated on analyzing perturbed behaviors resulting from small deviations away from
37 some assumed nominal behavior. In fact, this approach can be misleading for large perturbations
38 (see Hodgson and Townley 2004, Mills, *et. al.* 1999). Another standard approach is to use Monte
39 Carlo simulations, where the data is assumed to be substantial enough to determine parameter
40 estimates of the distributional form of random variables. In the management of threatened or en-
41 dangered species, where information can be extremely scarce, it is unlikely that the perturbations
42 are small, and in many cases there is not enough information available to know the distribution
43 of uncertainties. Scarcity of data particularly impacts estimates of the variance, possibly leading
44 to underestimates of the probability of extreme values. Even when empirical variance estimates or
45 bounds on parameters are available, and accepted by all parties, correlations between parameters
46 are certainly present and usually unknown. In this paper we present an alternate approach for the
47 systematic analysis of the effect of uncertainties on long-term population growth or decay. This
48 approach does not require the perturbations to be small, can handle simultaneous uncertainty in
49 several parameters, and does not require strong distributional assumptions.

50 Suppose that the model (determined by the data) for the population in question predicts long-
51 term growth. Our focus is to determine how uncertain the data can be before the model loses this

52 property. Roughly speaking, the *robustness* of a desired property (such as long-term population
53 growth) to uncertainty or perturbation of data is a measure of how much the data can be changed
54 before the desired property is destroyed. A general framework of robustness analysis, which has
55 been developed in the field of control theory, has been adapted for population dynamics in ecology
56 by Hodgson and Townley (2004). The robustness approach adopts a different viewpoint to that
57 typified by sensitivity/elasticity analysis: the latter is microscopic, perturbing away from a nominal
58 model and focusing in on the infinitesimal dependence of a specific dynamical property on the
59 perturbation; the latter is essentially macroscopic and focuses in on perturbation as a function of
60 required dynamical property. Hodgson and Townley (2004) tabulates a clear comparison between
61 these micro. vs. macro-scopic approaches.

62 Whilst we build on the approach in Hodgson and Townley (2004), our approach differs from
63 theirs in several ways. Most importantly our focus is on robustness of population growth (at least
64 one eigenvalue greater than one in modulus), which is more delicate than their simpler problem of
65 robustness of population decline (all eigenvalues less than one in modulus). In addition, we describe
66 *all* acceptable uncertainties, while they give the answer in terms of the stability radius, which gives
67 a distance that the data can be changed before causing the desired property to be lost.

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

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

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

83 In July 2005 controversy arose over the number of falcons currently being harvested in Oregon.
84 The Audubon Societies of Portland and Denver, the Center for Biological Diversity, and the New
85 Mexico Audubon Council questioned the decision of the US Fish and Wildlife Service allowing
86 harvesting of the peregrine falcon population. In particular, the plaintiffs claimed that the US Fish
87 and Wildlife Service's calculations of the margin of error misrepresented the data, and consequently

88 harvesting exposed peregrine falcon populations to unnecessary risk of decline. These concerns were
89 dismissed and 5% of the population are still allowed to be harvested (*Audubon Society of Portland*
90 *v. United States Fish and Wildlife Service* 2005). The key issue on which this case hinged was
91 whether or not the incorporation of uncertainty into the calculations of the allowable harvest rate
92 was done appropriately.

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

99 **Methods**

100 **General Method for Classifying Perturbations**

101 Begin by assuming that \mathbf{A} is a time-invariant population projection matrix for the population in
102 question. The leading eigenvalue of \mathbf{A} , which we denote by $\lambda(\mathbf{A})$, satisfies $\lambda(\mathbf{A}) > 1$, which implies
103 that the population is increasing if \mathbf{A} accurately models the population dynamics. The parameters

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

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

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

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

119 If the dimension of the population vector is n , then the matrices \mathbf{A} , $\tilde{\mathbf{A}}$ and \mathbf{P} have n^2 entries.
120 The uncertainties are typically *structured*, and can be described by m parameters (p_1, p_2, \dots, p_m) ,
121 where $m \leq n^2$. The smaller the number of parameters we consider, the more tractable the analysis
122 will be, so this approach will be easier if we consider only the most significant parameters, for
123 instance, the parameters which affect λ the most, or the most uncertain parameters. We say that
124 (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
125 set of admissible (p_1, p_2, \dots, p_m) ; for example, it will be typical to restrict the perturbations so
126 that the sum of the survival probabilities are always between 0 and 1. We can denote the explicit
127 dependence of $\tilde{\mathbf{A}}$ and λ on (p_1, p_2, \dots, p_m) by writing

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

128 Now consider the subset of S given by

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

129 This is the set of (p_1, p_2, \dots, p_m) which lead to a leading eigenvalue of 1. Mathematically, this set is
130 a *hypersurface*. If we are considering two uncertain parameters, then $m = 2$ and C is a curve; this

131 is the case which is illustrated in this paper. If we are considering three uncertain parameters, then
 132 $m = 3$ and C is an ordinary surface (that is, a two dimensional object in three dimensions). When
 133 $m = 2$ 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
 134 of C . For hypersurfaces in dimensions higher than 3, it is sometimes not possible to define the
 135 notion of the “side” of the hypersurface. However, for the surfaces described by (??), the notion
 136 of the side of C can be made precise mathematically, using Proposition A.1 in Appendix A. Since
 137 we are assuming that the unperturbed matrix \mathbf{A} has $\lambda(\mathbf{A}) = \lambda(0, 0, \dots, 0) > 1$, the “population
 138 growth” side of C is the one containing $(0, 0, \dots, 0)$. Hence we consider all “good” perturbations
 139 to be those which are on the population growth side of C . Since the nominal model corresponds
 140 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
 141 the case where $m = 2$ or 3 , we get stronger results, since we get a graphical representation showing
 142 exactly which combinations of uncertainties maintain and destroy population growth.

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

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

145 Furthermore, it should be pointed out that for some applications we will be interested in maintaining
 146 population decay, in which case the good perturbations will be on the side of C which guarantees

147 that $\lambda(p_1, p_2, \dots, p_m) < 1$.

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

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

150 For the peregrine falcon model, in Appendix B we determine Γ manually, and we show that Γ
151 is the same curve as C by using an analytical argument based on the Peron-Frobenius Theorem
152 (Seneta 1981). The manual computations would be arduous for larger matrices or multidimensional
153 perturbations, so in the electronic Supplement we provide MATLAB code demonstrating how to
154 apply this method to a larger matrix and more complex perturbations. For all matrices we have
155 tried so far, it is easy to confirm numerically that Γ is the same curve as C . A thorough theoretical
156 study of when $C = \Gamma$ is forthcoming (D. Boeckner *et al.* unpublished manuscript). Even if Γ is
157 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)
158 on Γ , the eigenvalue of largest modulus $\lambda(p_1, p_2, \dots, p_m)$ must be greater than or equal to 1, since
159 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
160 contains $(0, 0, \dots, 0)$, it is guaranteed that $\lambda(p_1, p_2, \dots, p_m) > 1$; however, it is not guaranteed that
161 on the other side of Γ we have $\lambda(p_1, p_2, \dots, p_m) < 1$.

162 Falcon Population Model

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

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

169 S

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

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

172 where \mathbf{A} is the population projection matrix. The nominal population projection matrix we
173 use is a correction of the post-breeding model derived in Craig *et al.* (2004); the published
174 matrix incorrectly includes an additional juvenile age class, although the reported model
175 results are from the correct model (Gary C. White, personal correspondence). The model
176 parameters are: S_0 , the survivorship from birth to age one; S_1 , the survivorship from age one
177 to age two; S_2 , the yearly survivorship for all older birds. The fecundity F is assumed to be

178 the same for all breeding pairs. Birds under 2 years old may or may not breed. We quantify
 179 this by letting B represent the proportion of birds in the second age class that breed. R
 180 denotes the proportion of birds that are female. In terms of these parameters, the nominal
 181 population projection matrix is

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

182 We use parameter values estimated from the peregrine falcons in Colorado, USA (Table
 183 1; Craig *et. al.* 2004). We need to incorporate harvesting into the population projection
 184 matrix. We introduce the variable h , which represents the proportion of nestlings harvested,
 185 so the term $(1 - h)$, denoting the proportion of nestlings remaining in the wild population,
 186 is included in the matrix \mathbf{A} by multiplying this term by the fecundities (Caswell 2001). The
 187 amount of harvesting is assumed to be the same in both age classes since for many birds the
 188 age cannot be determined. This also assumes that the two age classes are equally vulnerable
 189 to harvesting. Let

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

190 Harvesting can effect the nesting habits of the parents and the survivorship of the re-
 191 maining nestlings. Peregrine falcons are known to re-nest (lay another clutch) if a clutch is

192 lost early (Ratcliffe 1993). However, by US Fish and Wildlife Service regulations, nestlings
193 may not be harvested prior to 10 days of age (U.S. Fish and Wildlife Service 2001); thus
194 removing nestlings will not cause the parents to re-nest. Removing a nestling could increase
195 the survivorship of remaining nestlings due to less work for the parents. However, removing
196 nestlings only minimally improves the survivorship of the remaining young (Thomas Cade,
197 The Peregrine Fund, personal correspondence), thus, in modeling the worst case we may
198 ignore this.

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

203 **Data Uncertainties**

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

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

213 In Figure 1, we see how λ is affected by changes in each of the parameters. When
214 determining the effect of a parameter on λ , we can think of λ as a function of each parameter
215 while the other parameters stay fixed at the nominal values. Figure 1 gives $\lambda(p)$ for each
216 parameter. The value of p (shown on the x -axis) represents the proportional change in the
217 parameter from the nominal value (e.g. $p = -.1$ represents a 10% decrease in the parameter).
218 The y axis gives the value of λ obtained when that entry is changed and other entries are not
219 changed. These curves are obtained using (A.2) in Appendix A. From these graphs we see
220 that changes in S_2 are more important to λ than changes in S_1 or S_0 . Since the long-term
221 growth rate λ is most sensitive to S_2 , and B is the most uncertain parameter, we look at how
222 λ is affected by simultaneous changes in B and S_2 . In particular, we will determine what
223 changes can be tolerated in B and S_2 without destroying the conservation property $\lambda > 1$.

224 The traditional approach to analyzing the affect of a change of p to a parameter a on

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

229 We now analyze the effect of simultaneous changes in both B and S_2 . We parameterize
 230 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
 231 a relative change. In particular, we want the perturbed matrix to be

$$\tilde{\mathbf{A}} = \mathbf{A} + \mathbf{P}_1 + \mathbf{P}_2 = \begin{pmatrix} 0 & FRS_1 p_1 & FRS_2(1 + p_2) \\ S_0 & 0 & 0 \\ 0 & S_1 & S_2(1 + p_2) \end{pmatrix}. \quad (6)$$

232 As in Appendix A, we write

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

233 where

$$\mathbf{D}_1 = \begin{pmatrix} FRS_1 \\ 0 \\ 0 \end{pmatrix}, \quad \mathbf{E}_1 = (0 \ 1 \ 0) \quad (7)$$

234 and

$$\mathbf{D}_2 = \begin{pmatrix} FRS_2 \\ 0 \\ S_2 \end{pmatrix}, \quad \mathbf{E}_2 = (0 \ 0 \ 1). \quad (8)$$

235 The admissible range of p_1 is 0 to 1, where $p_1 = 1$ implies all 2 year old females breed.
 236 The admissible range of p_2 is constrained so that the term $S_2(1 + p_2)$, which is a probability,
 237 is between 0 and 1, so p_2 ranges from -1 to 0.25 . Thus the set of admissible perturbations

238 is described by

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

239 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
240 (p_1, p_2) plane on which some eigenvalue (*not* necessarily the largest eigenvalue λ) is equal
241 to one. Hence on this curve λ must be greater than or equal to 1. If we can prove that on
242 this curve $\lambda = 1$, then the curve breaks up the set S of admissible perturbations into two
243 regions, one of which corresponds to $\lambda > 1$, while the other region corresponds to $\lambda < 1$. In
244 Appendix B we find the equation of the curve using a method which *guarantees* that $\lambda = 1$
245 for (p_1, p_2) on this curve. The curve is shown in Figure 2, on a coordinate system with p_1 on
246 the horizontal axis and p_2 on the vertical axis. The nominal values of (B, S_2) are represented
247 by $(p_1, p_2) = (0, 0)$. The shaded area in Figure 2 represents those (p_1, p_2) which correspond
248 to $\lambda > 1$.

249 Figure 2 shows us how much error is acceptable in B and S_2 , and more importantly
250 shows the interplay between uncertainties in the two variables. For instance, for any value
251 of B , S_2 can tolerate a negative error of 4% (or, of course, any positive error). If $B = 1$,
252 S_2 can tolerate a negative error of 13% or less. This illustrates an important principle -

253 new information about one parameter often changes the robustness to uncertainty in other
254 parameters.

255 Now suppose that we wish to identify all (p_1, p_2) which guarantee a long term growth rate
256 of at least 3%. Then we simply replace 1 in our computations with 1.03. This yields a new
257 curve (Figure 2) that is shifted upwards relative to the previous curve; because $\lambda = 1.0287$
258 at the nominal values, this new curve runs through the nominal point. The region above
259 that curve gives the values of (p_1, p_2) for which $\lambda > 1.03$ for \mathbf{A} .

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

268 The effect of harvesting on long-term growth

269 We now examine the effect of harvesting on the largest eigenvalue λ of the modified
270 population projection matrix \mathbf{A}_h (see (??)). As a simple example, let \mathbf{A}_h use the nominal
271 values of B and S_2 ; we find that the smallest value of h which gives an eigenvalue of 1 is
272 .1714. Therefore, since λ varies continuously with h and the nominal matrix \mathbf{A} with $h = 0$
273 has largest eigenvalue 1.0288, any value of h less than .1714 gives a largest eigenvalue of A_h
274 greater than 1. Thus even with no 2-year old falcons breeding, if there is no uncertainty,
275 then 17.41% may be harvested while maintaining a growth rate of $\lambda = 1$.

276 However, this does not take into account uncertainties in B and S_2 . Hence we again
277 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
278 subsection ?? of the Appendix, for several values of h we find curves in the (p_1, p_2) plane
279 on which the largest eigenvalue λ for \mathbf{A}_h is 1. For $h = 0, .05, .1, .15, .1714$ and $.2$, these
280 curves are shown in Figure 3. The region above each curve gives the values of (p_1, p_2) for
281 which $\lambda > 1$ for \mathbf{A}_h . If $B = 1$ and 17.41% are harvested, S_2 can tolerate uncertainties of
282 up to -6% . The US Fish and Wildlife Service suggests that 5% can be harvested. Reading
283 from the $h = .05$ graph in Figure 3, we see that if $B = 0$, this allows an uncertainty of 3%

284 in S_1 , and if $B = 1$, this allows an uncertainty of 11% in S_1 .

285 If our objective is to maintain 3% population growth even with harvesting, then we can
286 recalculate our curves as we did for the no harvesting model (Figure 2). Although we do
287 not show the figure it is straightforward to calculate that 3% population growth cannot be
288 maintained with 5% harvesting, unless our nominal value of S_2 is an underestimate, or at
289 least 20% of 2 year old birds breed. If more than 20% of two year old birds breed, then
290 uncertainties of up to 6% in adult survival can be tolerated when $B = 1$.

291 Discussion

292 The difficulty of incorporating the effects of uncertainty in matrix parameters into popu-
293 lation management decisions is possibly one of the largest problems preventing widespread
294 adoption of models in decision making. One of the best examples of thoroughly incor-
295 porating uncertainty in the assessment of management is Heppell *et al.*'s (1994) work on
296 Red-cockaded woodpeckers, which relied on simulation to explore the effects of simultaneous
297 uncertainties, as well as linear approximations using elasticities. This approach of using
298 linear approximations from elasticities in one dimension, and Monte Carlo simulations in

299 multiple dimensions is widely used (e.g. Ferriere *et al.* 1996, Caswell *et al.* 1998 among
300 many others). Although it is possible to explore multidimensional parameter uncertainty
301 reasonably easily in this fashion, the exact results obtained by simulation depend heavily
302 on the details of how perturbations are selected. This is especially true when considering
303 the possibility of constraints or correlations among life history traits; information on such
304 correlations is generally unavailable (Wisdom *et al.* 2000). Caswell *et al.* (1998) incorpo-
305 rated constraints on life history traits by sampling survival curves from a group of related
306 species. However, if a different set of species had been selected, the results would differ by
307 an unknown amount, and this still does not answer the problem of correlated environmental
308 variation. The method we introduce here gives an analytical result for all possible pertur-
309 bations, and is straightforward to implement in readily available software (e.g. Symbolic
310 Toolbox in MATLAB, see electronic supplement).

311 It is widely reported that predictions of the perturbations needed to effect a given change
312 in λ using sensitivities or elasticities are accurate to relative changes of $\pm 50\%$ (e.g. de Kroon
313 *et al.* 2000). However, careful inspection of the numerical examples used to support this
314 claim show that they typically involve perturbations of single vital rates or matrix entries. As
315 shown in Figure 2 this is true for our matrix as well. However, once multiple parameters are

316 perturbed the linear approximation breaks down. Some examples for multiple perturbations
317 are provided in Caswell (2001; Chapter 18), and these demonstrate increasing approximation
318 errors with both the dimension and size of the perturbation. Tenhumberg *et al.* (manuscript
319 in review) conducted a Monte Carlo analysis of a large matrix with simultaneous uncertainty
320 in 19 parameters, and found that when parameters varied simultaneously the local and linear
321 elasticities were poor predictors of which parameters have a large influence on λ . Our method
322 makes all of these predictions easily and without approximation errors.

323 The notion of using direct perturbations of the life cycle to improve decision making in
324 conservation biology was put forward for empirical perturbations by Ehrlén and van Groe-
325 nendael (1998). They suggested that the tools of “Life Table Response Experiments” (sensu
326 Caswell 2001) should be used to analyze multiple years of data as perturbations of an under-
327 lying matrix. A key improvement of this idea over using elasticities alone is the incorporation
328 of the differential variability of each matrix entry (de Kroon et al. 2000), arising because of
329 differential variability in life history traits. However, small observed variation in a vital rate
330 does not necessarily mean it is a poor target for management (Caswell 2001, pg 619), and
331 similarly large observed variation does not automatically lead to a good management target.
332 We have not addressed this issue in the present example, but it would be straightforward to

333 rescale the perturbations (p_1, p_2) by the relative amount of variability in the parameters they
334 are affecting, if estimates of this variability are available. A better, prospective approach
335 would rescale the perturbations by their relative cost (ease of manipulation); an excellent
336 example of how to do this using sensitivity analysis is given by Baxter *et al.* (2006).

337 A general, but underappreciated, problem with using models to assess the effects of
338 management options is uncertainty in the connection between management and population
339 vital rates. For example, when considering the effects of river flows on fish populations,
340 it may not be at all clear what relationship exists between flow and spawning frequency.
341 This type of uncertainty could be included in the methodology we present here by careful
342 parameterization of the perturbations, although this will increase the number of dimensions
343 in the perturbation, making interpretation more difficult. In the falcon harvesting example
344 we ignored the issue of how many nestlings a harvest rate of 5% actually represents. There
345 is substantial uncertainty in estimates of numbers of breeding pairs, and consequently in
346 the number of nestlings that can be taken. However, if detectability of breeding pairs is
347 less than 1, then the actual number of identified nests will be an underestimate. As long
348 as the actual, observed number of nests is used to calculate the number of nestlings that
349 can be taken, the actual harvest rate will be less than 5%. This cannot be guaranteed if

350 the permitted take is based on an estimated number of breeding pairs. In that case, if the
351 breeding population is over-estimated then the nominal 5% harvest rate would in fact be
352 larger, and consequently there is a greater risk that the population growth targets would
353 not be maintained. The robust, conservative decision is to use the actual observed number
354 of nests. This harvest level could be increased, but this is only safe when the accuracy of
355 breeding population estimates can be carefully defined.

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

365 Robustness approaches are a relatively new idea in ecology and conservation biology,
366 although they find wide application in many other fields (e.g. Ben-Haim 2001). In addition to

367 applications in conservation biology (e.g. Hodgson and Townley 2004, Hodgson et al. 2006),
368 the concept was recently applied to foraging theory to examine the possibility that foragers
369 seek to guarantee minimum returns rather than maximize returns (Carmel and Ben-Haim
370 2005). The key difference from a decision-making perspective is the shift from maximizing a
371 performance criterion to guaranteeing some minimum level of that criterion. Although our
372 current work focuses on the asymptotic growth rate of a structured population, the general
373 notion of guaranteeing performance could be applied to any measure of how well a population
374 is doing. For example, a minimum probability of quasi-extinction over T years could be
375 specified, and then simulations carried out to determine the largest parameter perturbation
376 that has that as a worst case performance. By restricting our focus to asymptotic population
377 growth rates we enable the use of a powerful set of analytical results rather than having to
378 rely on simulations.

379 This new approach may make setting objectives for decision making much easier in
380 conservation biology. For example, when comparing two or more management decisions for
381 their effect on the risk of extinction, we may choose the strategy that provides the lowest
382 risk of extinction (Regan *et al.* 2005). However, if the costs of these decisions differ, we are
383 then forced into making arguments about how much a species is “worth” in order to justify

384 a greater expense. In contrast, if we specify some minimum performance that we wish to
385 guarantee, we can use robustness methods to compare decisions based on how much error
386 each can tolerate and still guarantee the minimum. Differing costs then purchase different
387 levels of robustness, relieving us of the need to value each species. We still have to value the
388 robustness, but this would appear to be easier to do than argue about the value of a species.

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

396 **Acknowledgements**

397 This work was supported by NSF REU Site Grant 0354008. RR was supported in part by
398 NSF Grant 0206951. ST Supported in part by a Leverhulme Trust Research Fellowship.

399 **References**

400 *Audubon Society of Portland v. United States Fish and Wildlife Service*, No. 04-670-KI (D.
401 Oregon July 21, 2005).

402 Baxter, P. W. J., M. A. McCarthy, H. P. Possingham, P. W. Menkhorst, and N. McLean.
403 2006. Accounting for management costs in sensitivity analyses of matrix population
404 models. *Conservation Biology* **20**:893-905.

405 Bermon, A. and R. J. Plemmons. 1994. *Non-negative matrices in the mathematical sciences*.
406 SIAM, Philadelphia

407 Ben-Haim, Y. 2001. *Information-gap decision theory: decisions under severe uncertainty*.
408 Academic Press, London.

409

410 Carmel, Y. and Y. Ben-Haim. 2005. Info-gap robust-satisficing model of foraging behavior:
411 Do foragers optimize or satisfice? *American Naturalist* **166**: 633-641.

412 Caswell, H., S. Brault, A.J. Read, T.D. Smith. 1998. Harbor Porpoise and Fisheries: An
413 Uncertainty Analysis of Incidental Mortality. *Ecological Applications* 8:1226-1238.

- 414 Caswell, H. 2001. Matrix Population Models: Construction, Analysis, and Interpretation.
415 Second Edition. Sinauer Associates, Inc. Publishers, Sunderland, Massachusetts, USA.
- 416 Craig, G. R., G. C. White, and J. H. Enderson. 2004. Survival, Recruitment, and Rate of
417 Population Change of the Peregrine Falcon Population in Colorado. *Journal of Wildlife*
418 *Management* **68**, 1032-1038.
- 419 de Kroon, H., J. Van Groenendael, and J. Ehrlen. 2000. Elasticities: a review of methods
420 and model limitations. *Ecology* **81**:607-618.
- 421 Ehrlen, J., and J. Van Groenendael. 1998. Direct perturbation analysis for better conserva-
422 tion. *Conservation Biology* **12**:470-474.
- 423 Ferriere, R. G., F. Sarrazin, S. Legendre, and J. Baron. 1996. Matrix population models
424 applied to viability analysis and conservation: theory and practice using the ULM
425 software. *Acta Oecologica* **17**:629-656.
- 426 Heppell, S. S., J. Walters, and L. B. Crowder. 1994. Evaluating management alternatives
427 for red-cockaded woodpeckers: a modeling approach. *Journal of Wildlife Management*
428 **58**:479-487.

- 429 Hodgson, D. J. and S. Townley. 2004. Linking management changes to population dynamic
430 responses: the transfer function of a projection matrix perturbation. *Journal of Ap-*
431 *plied Ecology* **41**:1155-1161.
- 432 Hodgson, D., S. Townley, and D. McCarthy. 2006. Robustness: Predicting the effects of life
433 history perturbations on stage-structured population dynamics. *Theoretical Popula-*
434 *tion Biology* **70**:214-224.
- 435 Hunt, W. G. 1988. The natural regulation of peregrine falcon populations. In: *Peregrine falcon*
436 *populations: their management and recovery*. Editors: Cade, T. J., J. H. Enderson,
437 C. G. Thelander, and C. M. White. The Peregrine Fund, Inc, Boise.
- 438
- 439 Mills, L. S., D. F. Doak, M. J. Wisdom 1999. Reliability of conservation actions based on
440 elasticity analysis of matrix, models. *Conservation Biology* **13**:815-829.
- 441 Ratcliffe, D. 1993. *The Peregrine Falcon*. 2nd Ed. T & A D Poyser, London.
- 442 Regan, Helen M., Yakov Ben-Haim, Bill Langford, William G. Wilson, Per Lundberg, Sandy J.
443 Andelman, Mark A. Burgman. 2005. Robust decision-making under severe uncertainty

444 for conservation management. *Ecological Applications* **15**:1471-1477.

445 Seneta, E., 1981. *Non-negative Matrices and Markov Chains*. Second Edition. Springer-
446 Verlag, New York, New York, USA., 3-7.

447 Tuljapurkar, S., and C. V. Haridas. 2006. Temporal autocorrelation and stochastic population
448 growth. *Ecology Letters* **9**:324-334.

449 U.S. Fish and Wildlife Service, 2001. *Falconry Take of Nestling American Peregrine Falcons*
450 *in the Contiguous United States and Alaska*. U.S. Fish and Wildlife Service, Arlington,
451 Virginia, USA.

452 U.S. Fish and Wildlife Service. 2003. *Monitoring Plan for the American Peregrine Falcon, A*
453 *Species Recovered Under the Endangered Species Act*. U.S. Fish and Wildlife Service,
454 Divisions of Endangered Species and Migratory Birds and State Programs, Pacific
455 Region, Portland, OR. 53 pp.

456 Wisdom M. J., Mills, L. S., D. F. Doak. 2000. Life stage simulation analysis: estimating
457 vital-rate effects on population growth for conservation. *Ecology* **81**:628-641.

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 ≥ 2	0.800	0.8901	0.6922
B	Proportion of 2 year old birds that breed	0	0.0453	0

458 **Figure Captions**

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

460 **Figure 2** The boundary curve represents all pairs of perturbations (p_1, p_2) for which $\lambda(p_1, p_2) =$

461 1. The shaded area represents all pairs of perturbations (p_1, p_2) for which $\lambda(p_1, p_2) > 1$. The

462 dashed line is $\lambda(p_1, p_2) = 1.0287$, the growth rate of the unperturbed matrix. The dotted

463 line shows the linear approximation to these curves obtained from direct use of sensitivity

464 to predict the effects of perturbations.

465 **Figure 3** The effect of the harvesting fraction h on the $\lambda(p_1, p_2) = 1$ curves. The bold line

466 is $h = 0.1714$, the amount of harvesting that yields $\lambda(p_1, p_2) = 1$ with no uncertainty for the

467 nominal values.