

A Vital Rate Sensitivity Analysis for Nonstable Age Distributions and Short-Term Planning

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Abstract

There are multiple approaches to sensitivity analysis used to identify the age- (or stage-) specific rate of reproduction or survival that most affects population growth—all of which involve evaluating effects on λ , the dominant eigenvalue of the Leslie matrix. Management recommendations generated by these approaches can be difficult to determine, in part because results are valid only for populations with stable age distributions (i.e., the age structure is constant across years). Although these analytical approaches can identify the quickest way to increase population size to carrying capacity, they cannot identify best management options for short-term goals such as increasing population size above some critical value. We present a perturbation analysis—Vital Rate Sensitivity Analysis (VRSA)—to identify the vital rate that most limits population growth over any specified period by determining which vital rate has the greatest effect on population growth. The VRSA is effective for stable and nonstable age distributions, differentiates optimal short- and long-term management options, can incorporate stochasticity in vital rates, and can differentiate efficacy of alternative management strategies. In addition to being able to compare effects of incremental or specific changes in vital rates, VRSA can be used to compare specific management alternatives that affect single or multiple vital rates. We illustrate use of VRSA for a variety of management alternatives and hypothetical age-structures using demographic data from the literature for greater prairie-chickens (*Tympanuchus cupido*) and red-cockaded woodpeckers (*Picoides borealis*). We also present a method, using Monte Carlo simulation, for measuring robustness of VRSA results. Under all of our management scenarios for greater prairie-chickens, we found juvenile survival to be the most sensitive vital rate for the specific comparisons made. For red-cockaded woodpeckers, the most sensitive vital rate differed by management scenario and confidence was higher for larger populations. Results for both species might change given other conditions and/or age structures. The VRSA should be an effective tool for wildlife managers who want to compare alternative management strategies to increase population size. A downloadable Excel spread sheet for calculating VRSA for a life-table is available at <http://ase.tufts.edu/biology/faculty/reed/software.html>. (JOURNAL OF WILDLIFE MANAGEMENT 70(3):649–656; 2006)

Key words

elasticity, endangered species, greater prairie-chicken, Monte Carlo simulation, nonstable age distribution, Picoides borealis, population dynamics, population viability, population viability analyses, red-cockaded woodpecker, Tympanuchus cupido, wildlife management.

An important quantitative tool in population viability analysis is evaluating demographic sensitivity; i.e., identifying which vital rate (age- or stage-specific rate of reproduction or survival) most affects population growth (e.g., Caswell 2000, de Kroon et al. 2000, Reed et al. 2002). Methods of sensitivity analysis for evaluation within a population include 1) risk-based or perturbation analysis, which involves changing each variable by a biologically reasonable amount to determine effects on net reproductive rate or annual population growth (Akçakaya 2000, Mills and Lindberg 2002, Regan et al. 2003); 2) analytical sensitivity and elasticity analyses, which are calculus-based measures of the proportional effects on population growth rate of infinitesimally small changes in each parameter (Goodman 1971, Caswell 1989, Mills et al. 1999); and 3) life-stage simulation analysis, which uses simulations to evaluate the relative effects of each vital rate on population growth through elasticity and other measures (Wisdom and Mills 1997, Wisdom et al. 2000). Comparisons among real populations or hypothetical alternative populations can be done using life-table response experiments, which contrast populations by determining the vital-rate-specific contributions to the differences between populations in growth rates (Levin et al. 1987, Caswell 1997). Sensitivity analysis methods are reviewed by Mills and Lindberg (2002). These analytical tools are intended for use primarily to determine

which vital rate most affects the rate of population growth, with the implication that managing for the most sensitive or elastic parameter would be the most effective way to increase growth rate (e.g., Heppell et al. 1994, Schemske et al. 1994, Caswell 1996, Silvertown et al. 1996, Benton and Grant 1999, Norris and Stillman 2002). Recent papers discussing sensitivity analyses, however, have warned against simple interpretation of the so-called most sensitive or most elastic parameter for making management recommendations. De Kroon et al. (2000) summarized some concerns, including 1) the assumption that matrix values remain stable over time, 2) not all vital rates can be altered by similar degrees by management, and 3) that vital rates vary with population size and growth rate (also see Silvertown et al. 1996, Beissinger and Westphal 1998, de Kroon et al. 2000, Mills and Lindberg 2002, Norris and McCulloch 2003).

The details of how sensitivity, elasticity, and life-stage simulation analyses should be interpreted with respect to manipulating population growth rate are not readily transparent. One potential source of confusion is that some sensitivity analyses determine the sensitivity or elasticity of λ (the dominant eigenvalue associated with the Leslie Matrix) to alteration of the matrix elements rather than to the vital rates themselves. Because the top row of a Leslie matrix is a composite of vital rates, it is not clear what a resource manager should manipulate if one of these elements was determined to be the most sensitive. Wisdom and Mills (1997) recognized this problem and showed one way to

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calculate sensitivity of λ to vital rates rather than to the matrix values using partial derivatives (also see Citta and Mills 1999, Mills et al. 1999).

Another potential limitation with current sensitivity and elasticity analyses is that by focusing on maximizing λ , their solutions are valid only for populations with stable age distributions (i.e., the age structure is constant across years [Caughley and Sinclair 1994:46]; e.g., Mills and Lindberg 2002, cf. Caughley 1977). Although the dominant eigenvalue (λ) can be determined for any Leslie matrix, when the age distribution is not stable λ no longer represents the growth rate of the population (Williams et al. 2002:148). Although it has been suggested that elasticity analyses might be robust to violation of some assumptions (Benton and Grant 1999), age distribution stability is not one of those assumptions. Consequently, the standard protocol is to project the Leslie matrix until the age distribution is stable and determine sensitivity/elasticity using that matrix (e.g., Citta and Mills 1999). There is no reason, however, to think that the age distribution of a real population will be stable, particularly if the population is declining because of environmental stressors or exploitation. If sensitivity or elasticity results for the population with an existing age distribution are different from those of the projected population with a stable age distribution, the management recommendation from current analytical methods could be suboptimal. Consequently, a method for vital rate sensitivity analysis that does not depend on stable age distributions would be useful.

Finally, when using matrix sensitivity analyses, long-term solutions to increasing population size are revealed. That is, the analysis identifies which matrix or vital rate element should be increased to achieve the largest population growth rate over a long period. It could be valuable, in contrast, to have an analytical method that identifies the vital rate element that, when increased, most quickly increases population size over a short period (e.g., 3–10 years). One reason this would be valuable is because funding, social, or personnel constraints might allow planning for only a few years into the future, and one might be interested in the management activities that maximize short-term population growth. In addition, the management goal might be to increase population size above some critical minimum population size as quickly as possible, even if over the long term the population reaches carrying capacity more slowly. This might be particularly important for managing small populations because demographic and environmental stochasticity has a greater effect on persistence of small populations than it does for larger populations (Lande 1993), even after density-dependent effects are accounted for (Sæther and Engen 2002).

We present a new approach, Vital Rate Sensitivity Analysis (VRSA), for identifying the vital rate on which management activities would have the greatest effect on population growth. The VRSA is effective for nonstable (as well as stable) age distributions, and it allows differentiation of short-term and long-term population management activities. The VRSA determines which vital rate has the greatest effect on population size increase, so its interpretation is completely transparent. Another distinction between VRSA and traditional sensitivity/elasticity methods is that results from current sensitivity and elasticity are independent of initial population size because population size is not a model parameter. This is not true for VRSA, where results can vary with

initial population size. This makes sense biologically because the potential effects of vital rate stochasticity on population growth are greater for small populations (e.g., Lande 1993). In addition, we present a method to estimate the robustness of VRSA results, and, consequently, the suggested management alternative. Although we present this robustness estimation method as an integral part of our analysis, it could be applied separately to analyze the robustness of any estimation of comparative population growth that incorporates stochasticity.

We illustrate use of VRSA for a variety of management alternatives and hypothetical age structures using demographic data from the literature for greater prairie-chickens (*Tympanuchus cupido*) and red-cockaded woodpeckers (*Picoides borealis*), and we compare results to matrix elasticity and Wisdom and Mills' (1997) modified elasticity analysis (decomposed to evaluate individual vital elasticity rather than matrix value elasticity). We selected example species because of widespread management interests. The greater-prairie chicken is a gallinaceous bird that includes extinct and endangered subspecies, as well as many at-risk populations (Schroeder Robb 1993). The red-cockaded woodpecker is an endangered species inhabiting old-growth pine-savannah habitat in the southeastern United States. (Jackson 1994). From our analyses, we conclude that VRSA provides a robust approach for evaluating management options for population growth.

Methods

The VRSA quantifies effects of changes in vital rates on projected changes in population size, and it does not rely on λ or have the requirement of a stable age distribution. We compared predictions of how to maximize population growth among 3 methods (matrix elasticity, modified elasticity analysis, VRSA) for l_x - m_x tables (tables presenting age-specific cumulative survival and reproductive rates, respectively) for greater prairie-chickens and red-cockaded woodpeckers, hereafter Original life tables (Table 1). The VRSA is expected to give the same result as traditional

Table 1. Vital rates for greater prairie-chicken (from data in Schroeder & Robb 1993) and red-cockaded woodpecker (from data for unbanded birds in Maguire et al. [1995], with a maximum age from Jackson [1994]).

Age	Greater prairie-chicken			Red-cockaded woodpecker		
	m_x^a	P_x^b	l_x^c	m_x	P_x	l_x
0	0.0000	0.3403	1.0000	0	0.4010	1.0000
1	3.1640	0.4900	0.3403	0.1260	0.7340	0.4010
2	3.1640	0.4900	0.1667	1.0230	0.9610	0.2943
3	3.1640	0.4900	0.0817	1.1290	0.4560	0.2829
4	3.1640	0.4900	0.0400	1.5040	0.6670	0.1290
5	3.1640	0.4900	0.0196	1.5040	0.6670	0.0860
6	3.1640	0.0000	0.0096	1.5040	0.6670	0.0574
7				1.5040	0.6670	0.0383
8				1.5040	0.6670	0.0255
9				1.5040	0.6670	0.0170
10				1.5040	0.6670	0.0114
11				1.5040	0.6670	0.0076
12				1.5040	0.0000	0.0051

^a m_x denotes the average expected number of female offspring produced during age x .

^b P_x denotes the cumulative probability of surviving from birth/hatching through age x .

^c l_x denotes the probability of surviving age x , given the individual has already survived until age x .

Table 2. Percent of population in each age class for greater prairie-chickens in the stable age distribution projected from the Original life table in Table 1 (Stable Original), as well as the percents in each age class after 2 different simulated 1-time catastrophes: severe hatch-year loss (Distribution 1) and severe adult loss (Distribution 2). For both altered distributions, the Original P_x and m_x values from Table 1 apply in years after the catastrophe.

Age	Stable original	Distribution 1	Distribution 2
0	0.7598	0.0081	0.8000
1	0.1652	0.0017	0.1230
2	0.0517	0.0001	0.0300
3	0.0162	0.0198	0.0200
4	0.0051	0.0629	0.0100
5	0.0016	0.2053	0.0090
6	0.0005	0.7021	0.0080

elasticity analysis over a long time because the age structure becomes stable. Since one benefit of VRSA is its validity over short periods, we evaluated alternative management scenarios over 3 and 10 years. Although life-history data for these species are available by age, we find it unlikely that, for example, survival of age-5 adults could be managed independently of age-6 adults, and we therefore did stage-based analyses. For the greater prairie-chicken we used 2 stages corresponding to the 2 different P_x values reported in Table 1. For the red-cockaded woodpecker, we ran analyses for a 2-stage model (hatch-year vs. older) and for a 4-stage model (hatch year, age 1, ages 2 and 3 combined, and older) created by aggregating P_x (age- or stage-specific survival; Table 1).

To determine the effects of small errors in vital rate parameter estimates, we incorporated stochasticity into each entry of the life table using a normal distribution with a mean of the Original vital rate value and a standard deviation of 0.001 for l_x (survival) values and 0.05 for m_x (reproduction) values. Using the Leslie matrix generated using the “Original” life table and these variances, we computed the stable stage distribution ($D = 0$) for this population (the eigenvector associated with the unique positive eigenvalue of the Leslie matrix; Stable Original values; Tables 2 and 3) using the software package Poptools Version 2.6.2 (<http://sunsite.univie.ac.at/Spreadsite/poptools/>).

We also artificially generated 2 nonstable stage distributions for our populations, each designed to simulate a 1-time catastrophic event: 1 intended to mimic severe infant mortality and 1 intended to mimic severe adult depletion ($D = 1$ and $D = 2$, respectively; referred to as Distribution 1 and Distribution 2 in Tables 2 and 3). Note that the age structures for Distributions 1 and 2 should not be used to calculate vital rates (l_x values) because they no longer depict typical vital rates for the population. We then defined $S_{D,i}^0$ = the initial ($t = 0$) percentage of the total population of age i for the given age distribution D ; note that $\sum_{i=0}^{\max \text{age}} S_{D,i}^0 = 1$ by definition, for $\max \text{age}$ = the reported maximum natural age for the species. Consequently, the initial population size (N_0), regardless of age (or stage) structure can be represented by $\sum_{i=0}^{\max \text{age}} N_0 S_{D,i}^0$. We projected this sum over time in the following way: the expected reproduction for each age class $S_{D,i}^t$ was exactly m_i from our l_x - m_x table, so $m_i N_t S_{D,i}^t$ was the expected number of offspring produced by all of the individuals in age class i from the initial age distribution D during year t . Therefore, the percent of the population in age zero at year $t+1$ is $S_{D,0}^{t+1} = \sum_{i=0}^{\max \text{age}} m_i S_{D,i}^t$. Additionally, for $i > 0$, $S_{D,i}^{t+1} = P_{i-1} S_{D,i-1}^t$, where P_i was age- (or

Table 3. Percent of population in each age class for red-cockaded woodpeckers in the stable age distribution projected from the Original life table in Table 1 (Stable original), as well as the percents in each age class after 2 different simulated 1-time catastrophes: severe hatch-year loss (Distribution 1) and severe adult loss (Distribution 2). For both altered distributions, the Original P_x and m_x values from Table 1 apply in years after the catastrophe.

Age	Stable original	Distribution 1	Distribution 2
0	0.4638	0.0009	0.7300
1	0.1759	0.0010	0.1900
2	0.1220	0.0036	0.0500
3	0.1109	0.0099	0.0080
4	0.0478	0.0170	0.0030
5	0.0302	0.0490	0.0030
6	0.0190	0.0600	0.0030
7	0.0120	0.0900	0.0030
8	0.0076	0.1050	0.0020
9	0.0048	0.1200	0.0020
10	0.0030	0.1256	0.0020
11	0.0019	0.2080	0.0020
12	0.0012	0.2100	0.0020

stage-) specific survival for age i . We assumed each catastrophe affected the age distribution but not the vital rates. In this way, we iteratively defined the population size for each year in succession as $\sum_{i=0}^{\max \text{age}} N_t S_{D,i}^t$ so that our projection was based on 4 things: initial population size, vital rates from a life table, an initial demographic distribution of the population $S_{D,i}^0$, and our management timeframe (i.e., the number of years into the future we wish to examine).

In a real management situation, one would then make a list of alternative management actions and their expected effects on vital rates (e.g., increase infant survival by X%, or increase reproduction by Y%). For our examples, we compared the strategy of increasing age-specific adult survival by 1% with the alternative strategies first of increasing age-specific juvenile survival by 1% (i.e., for both, we added 0.01 to each survival rate) and second of increasing reproductive success by 1% of the original vital rate. For each alternative management option, we recomputed the projected population size for both 3 and 10 years after management was initiated, and we compared ΔN , the resulting ($N_t - N_0$) at each time t (3 and 10 years, respectively). The best management alternative at each time was the one with the largest ΔN . For each scenario, we ran models with starting populations of 100, and we ran them again with starting populations of 1,000 individuals. We then ran a variety of subsequent comparisons where alternative management scenarios ranged from increasing reproductive success and adult survival from 1 to 3% and increasing juvenile survival 1 to 5%.

We then measured relative efficacy of alternative management strategies by comparing ΔN , the change in population size, achieved by the different management strategies. A potential alternative measure that can be derived from VRSA is cumulative annual growth rate. However, cumulative annual growth rate is referred to in the literature as λ (or λ^t , where t = number of years), and this λ is not equivalent to the dominant eigenvalue associated with the Leslie matrix except when the age structure is stable. So, to avoid confusion, we measured ΔN and used λ to refer only to the dominant eigenvalue of the Leslie matrix and not to cumulative annual growth rate.

Table 4. Sensitivity analyses of stage-structured populations for greater prairie-chicken life tables and a variety of age distributions. The Vital Rate Sensitivity Analysis (VRSA) results are based on the specific management alternatives of increasing reproduction, juvenile survival, or adult survival by 1%.

Method ^a	Age structure ^b	Time frame (yrs)	Initial population size	Vital rate ^c						Management recommendation is to increase:	
				Reproduction		Juvenile survival		Adult survival			
Elasticity ^d	Any age distribution	Any	Any	0.6897		0.2154		0.0949		Reproduction	
Modified elasticity	Any age distribution	Any	Any	0.6897		0.6897		0.9915		Adult survival	
VRSA	Original stable	3	100	2	100%	1	100%	2	100%	Juvenile survival	
			1,000	3	100%	1	100%	2	100%	Juvenile survival	
			100	3	100%	1	100%	2	100%	Juvenile survival	
		Distribution 1	3	100	2	100%	1	100%	3	100%	Juvenile survival
				1,000	2	100%	1	100%	3	100%	Juvenile survival
			100	2	100%	1	100%	3	100%	Juvenile survival	
	Distribution 2	3	100	2	100%	1	100%	2	100%	Juvenile survival	
			1,000	2	100%	1	100%	2	100%	Juvenile survival	
			100	3	100%	1	100%	2	100%	Juvenile survival	
		10	100	3	100%	1	100%	2	100%	Juvenile survival	
				1,000	3	100%	1	100%	2	100%	Juvenile survival
			100	3	100%	1	100%	2	100%	Juvenile survival	

^a Modified elasticity is from Wisdom and Mills (1997), modified to get elasticity of vital rates.

^b Vital rates come from Table 1, age structures from Table 2.

^c Values are the output from the various sensitivity measures. Elasticity values add to 1, modified elasticities and VRSA do not. For VRSA numbers are ranks from most sensitive (=1) to least sensitive (=3) based on ΔN values; certainty of ranks and management recommendation based on Monte Carlo simulation is listed as a percentage immediately to the right. See Methods for an explanation of ranks and interpreting Monte Carlo results.

^d Values given under vital rates: for juvenile survival is the matrix elasticity associated with P_0 ; for adult survival it is the sum of the matrix elasticity values for P_1 – P_{max} ; for reproduction it is the sum of the matrix elasticity values for $P_x m_x$.

Confidence Assessment

Because we incorporated stochasticity into our vital rates, we iterated projections of the populations under each management strategy and the comparison of their resulting ΔN s 1,000 times in a Monte Carlo simulation using the PopTools extension to Excel to produce the likelihood that the same strategy would yield the largest population size at time t , which allowed us to evaluate the likelihood that these analyses gave consistent management recommendations. Because results from our VRSA varied due to the stochasticity we introduced, we presented results of the VRSA by showing the rank order from the most- to least-sensitive parameter across all runs. That is, the management alternative that most often results in the best ΔN in the simulations was ranked 1, the alternative that most often resulted in the second best ΔN was ranked 2, etc. We present certainty in the ranks as the percentage of times that this management option had a higher rank than the option with the next lower rank. Certainty for the lowest-ranked management option indicates how often it resulted in an increase in ΔN over the null of not altering management practices. Monte Carlo simulations traditionally have been used in estimating extinction risks to provide probabilistic parameter values for models (e.g., Dreschler et al. 2003); measures of the probability of extinction (e.g., Legendre et al. 1999); or to identify a range, distribution, or maximum or minimum of a value, predicted by a model over iterations (e.g. McCarthy and Thompson 2001). We used the method to evaluate the robustness of the ranks assigned the different strategies. If stochasticity was not included in the model, ranks should be set based on the best ΔN . Finally, for each of our species examples, we reported a management recommendation based on the ranks, and our certainty was the frequency of the runs in which the order of all 3 parameters agreed with the final ranks.

Results

Elasticity analysis identified reproductive success as the most-sensitive matrix element for the greater prairie-chicken life table, while the modified elasticity analysis identified adult survival as the most-sensitive vital rate (Table 4). Because of the way these analyses are done, these results would not vary by timeframe, initial population size, or initial age structure. In contrast, VRSA identified juvenile survival as the most-sensitive vital rate for the specified alternative management options compared (increasing by 1%: reproduction vs. juvenile survival vs. adult survival). This result was consistent across the range of timeframes, initial population sizes, and initial age structures evaluated (Table 4). However, the vital rate to which ΔN was second most sensitive was not consistent. Reproduction was ranked exclusively the second-most-sensitive vital rate in 4 scenarios, and adult survival was ranked exclusively the second most sensitive in 5 scenarios; in 3 scenarios, the 2 vital rates were tied. There was no obvious pattern based on timeframe, initial population size, or initial age structure. All ranks were 100% robust based on Monte Carlo simulation.

For red-cockaded woodpeckers, both elasticity and modified elasticity analyses identified adult survival as the most-sensitive parameter affecting λ , while VRSA identified reproduction as the most-sensitive parameter affecting ΔN (Table 5). Unlike results from the greater prairie-chicken, however, this conclusion was 100% robust—based on Monte Carlo simulation—in only 8 of the 12 scenarios. For the other scenarios, the confidence in reproduction being the top-ranked vital rate ranged from 33 to 96%. Vital rates ranked as second most effective at altering ΔN also often had confidence levels below 100% (Table 5). For this suite of management alternatives, confidence in our ranks and recommendations were consistently higher for larger initial

Table 5. Sensitivity analyses of stage-structured populations for red-cockaded woodpecker life tables with a variety of age distributions. The The Vital Rate Sensitivity Analysis (VRSA) results are based on the specific management alternatives of increasing reproduction, juvenile survival, or adult survival by 1%.

Method ^a	Age structure ^b	Time frame (yrs)	Initial population size	Vital rate ^c						Management recommendation is to increase	
				Reproduction		Juvenile survival		Adult survival			
Elasticity ^d	Any age distribution	Any	Any	0.2707		0.2578		0.4715		Adult survival	
Modified elasticity	Any age distribution	Any	Any	0.2707		0.2707		0.7120		Adult survival	
VRSA	Original Stable	3	100	1	73%	2	75%	3	9%	Reproduction	
			1,000	1	100%	2	100%	3	67%	Reproduction	
		10	100	1	94%	2	93%	3	10%	Reproduction	
			1,000	1	100%	2	100%	3	94%	Reproduction	
		Distribution 1	3	100	1	100%	2	89%	3	15%	Reproduction
				1,000	1	100%	2	100%	3	68%	Reproduction
	10	100	1	100%	2	97%	3	26%	Reproduction		
		1,000	1	100%	2	100%	3	99%	Reproduction		
	Distribution 2	3	100	1	81%	2	91%	3	5%	Reproduction	
			1,000	1	100%	2	100%	3	58%	Reproduction	
		10	100	1	96%	2	96%	3	14%	Reproduction	
			1,000	1	100%	2	100%	3	88%	Reproduction	

^a Modified elasticity is from Wisdom and Mills (1997), modified to get elasticity of vital rates.

^b Vital rates come from Table 1, age structures from Table 3.

^c Values are the output from the various sensitivity measures. Elasticity values add to 1, modified elasticities and VRSA do not. For VRSA numbers are ranks from most sensitive (=1) to least sensitive (=3) based on ΔN values; certainty of ranks and management recommendation based on Monte Carlo simulation is listed as a percentage immediately to the right. See Methods for an explanation of ranks and interpreting Monte Carlo results.

^d Values given under vital rates: for juvenile survival is the matrix elasticity associated with P_0 ; for adult survival it is the sum of the matrix elasticity values for $P_1 - P_{max}$; for reproduction it is the sum of the matrix elasticity values for P_{xM_x} .

population size, for longer timeframes, but confidence was lower for the stable age distribution than for the nonstable age distributions. Recall that our recommendations are based only on the a-priori-specified management alternatives, and they might change with other alternatives.

In the 4-stage VRSA for red-cockaded woodpeckers, results differed by the scenario we ran. In the short-term (3-year) scenario for our specific management alternatives with the Original Stable age distribution, the most-sensitive parameter when $N_0 = 100$, was survival of adults over age 4; reproductive success was the second-most-sensitive parameter (Table 6). For the larger initial

population size ($N_0 = 1,000$) the most-sensitive parameter was reproductive success. Over the longer timeframe (10 years), reproductive success was the most-sensitive parameter when $N_0 = 100$, but it was one of the least-sensitive parameters when $N_0 = 1,000$ (Table 6). Finally, we found that for the catastrophically altered initial age structures, one of the survival rates was always the most-sensitive parameter, although which age class was the most sensitive differed by the specific scenario (Table 6).

When we contrasted other suites of management scenarios, the greater prairie-chicken consistently showed reproductive success to be the most-sensitive parameter (Table 7). We note, however,

Table 6. Four-stage The Vital Rate Sensitivity Analysis (VRSA) analyses for red-cockaded woodpecker life tables and a variety of age distributions. Results are based on the specific management alternatives of increasing reproduction, juvenile survival, or adult survival by 1%.

Age structure ^a	Time-frame (yrs)	Initial population size	Vital rate ^b										Management recommendation is to increase	
			Survival stage											
			Reproduction	Hatch year		Age 1	Ages 2 and 3		Age 4+					
Original stable	3	100	2	43%	5	1%	3	27%	4	1%	1	43%	Age 4+ survival	
		1,000	1	86%	5	1%	3	67%	2	70%	4	99%		Reproduction
	10	100	1	44%	5	1%	2	50%	4	1%	3	40%	Reproduction	
		1,000	4	99%	5	1%	2	60%	1	54%	3	91%	Ages 2 and 3 survival	
	Distribution 1	3	100	3	73%	5	1%	1	58%	4	1%	2	41%	Age 1 survival
			1,000	3	97%	5	1%	2	70%	4	1%	1	73%	Age 4+ survival
10	100	2	56%	5	1%	1	56%	4	69%	3	43%	Age 1 survival		
	1,000	4	99%	5	1%	1	1%	3	97%	2	81%	Age 1 survival		
Distribution 2	3	100	2	32%	5	1%	3	55%	1	57%	4	1%	Ages 2 & 3 survival	
		1,000	3	99%	5	1%	2	90%	1	57%	4	1%	Ages 2 & 3 survival	
	10	100	3	48%	5	1%	2	55%	1	62%	4	41%	Ages 2 & 3 survival	
		1,000	4	99%	5	1%	2	60%	1	61%	3	91%	Ages 2 & 3 survival	

^a Vital rates come from Table 1, age structures from Table 3.

^b Numbers are ranks from most sensitive (=1) to least sensitive (=5) based on ΔN values; certainty of ranks and management recommendation based on Monte Carlo simulation is listed as a percentage immediately to the right. See Methods for an explanation of ranks and interpreting Monte Carlo results.

Table 7. Comparing The Vital Rate Sensitivity Analysis (VRSA) sensitivity results for 5 sets of alternative management scenarios using the 2-stage models for both the greater prairie-chicken and the red-cockaded woodpecker, and the situation of initial $N = 100$ individuals being evaluated for a 3-year time horizon.

	Increase reproduction (% of original m_x added)	Increase juvenile survival by (% added)	Increase adult survival by (% added)	Recommendation is to increase: ^a	
Greater prairie-chicken	1	1	1	Juvenile	100%
	1	3	2	Juvenile	100%
	2	3	2	Juvenile	100%
	2	5	3	Juvenile	100%
Red-cockaded woodpecker	3	5	3	Juvenile	100%
	1	1	1	Reproduction	100%
	1	3	2	Juvenile	79%
	2	3	2	Reproduction	75%
	2	5	3	Juvenile	85%
	3	5	3	Reproduction	70%

^a Confidence reported here is different from that reported in Tables 4–6. Here, the confidence value reported to the right refers to the probability that vital rate recommended for increase always had a greater positive effect on growth rate than did the other vital rates in the analysis.

that this result might not hold for other (possibly more realistic) management scenarios. For the 2-stage woodpecker evaluation, the most-sensitive parameter differed with the suite of management scenarios being evaluated (Table 7). Confidence in our ranks and recommendations still were consistently higher for larger initial population size, but confidence was not consistent based on management timeframe.

Discussion

Our goal was to create an analytical tool to identify which vital rate most affects population growth. We developed a vital rate sensitivity analysis (VRSA) that focuses on the sensitivity of vital rates affecting ΔN . The VRSA offers multiple advantages over other methods of evaluating sensitivity: 1) Results of VRSA are readily interpretable as the effects of specific management alternatives on population growth, as long as estimates are available for how the alternatives are expected to affect vital rates. As new management alternatives become available, reanalysis might show that management should change. This cannot occur with the other methods. 2) The VRSA can be applied to nonstable age distributions, and management recommendations might differ based on local differences in age structure. 3) The VRSA allows for stochasticity, which is inherent in all vital rates, and by using Monte Carlo simulation one can determine confidence in sensitivity results and management recommendations. 4) Finally, VRSA has flexibility not available in other approaches, including being sensitive to initial population size and to the timeframe across which species are to be managed. The VRSA does not focus only on maximizing the long-term population growth. Rather, it can be used to evaluate short-term changes in population size, and it can be used to determine the fastest way to increase population size beyond some critical minimum even if it does not reach carrying capacity in the fewest number of years. By incorporating both stochasticity and dependence on population size into the evaluation of management strategies, VRSA examines the

probability of falling below any such critical minimum as part of its estimation of robustness of intervention strategy ranking. This is especially important when examining options for managing small populations, which face greater threats from stochastic events due solely to their small size (Lande 1993).

This approach solves specific concerns about current alternatives approaches for evaluating sensitivity and confusion over appropriate application of the traditional methods to population management (e.g., Mills et al. 1999, 2001; Caswell 2000; Ehrlén et al. 2001; Mills and Lindberg 2002). We believe that most current concerns are caused because of using methods that focus on maximizing λ and the restrictions associated with this demographic parameter. In particular, sensitivity, elasticity, and related analyses evaluating λ require a stable age distribution. Because real populations—particularly declining ones—might not be stable, it is not always clear what analyses of stable age distributions might reveal about their population management. The VRSA does not require a stable age distribution, so results of its vital rate sensitivity apply directly to the population in question. Wisdom and Mills (1997) showed how elasticity analysis could be modified to evaluate sensitivity of λ to vital rates rather than to matrix elements. However, doing their calculations can be time-consuming, and interpretation of the results is not always obvious. For example, if we run Wisdom and Mills' (1997) modified elasticity analysis on our life tables, the vital rate elasticity value for pre-reproductive survival is always equal to that for total reproduction (Tables 4, 5). This result is difficult to interpret biologically, and the requirement of a stable age distribution for analysis remains.

Results from our VRSA for our species examples differed from some previous analyses. Using modified elasticity analysis combined with LSA, Wisdom and Mills (1997) concluded that the most-sensitive vital rate for greater prairie-chickens was juvenile survival (age zero to 1). Elasticity analysis results suggested that reproduction was the most-sensitive vital rate, and modified elasticity (without LSA) concluded adult survival was the most sensitive (Table 1). The VRSA concurred with Wisdom and Mills' (1991) conclusion that juvenile survival is the most-sensitive parameter.

There have been multiple population viability analyses (PVAs) of red-cockaded woodpeckers that provided sensitivity analyses. For example, Reed et al. (1993) used a model focusing on maintaining a minimum effective population size rather than maximizing population growth. Using perturbation analysis, they concluded that adult survival was the most-sensitive parameter to decreasing loss of genetic variation. The PVAs done by Heppell et al. (1994) and Maguire et al. (1995) used stochastic simulations from demographic data to determine the probability of population persistence. Both used elasticity analysis, but Heppell et al. (1994) found λ most sensitive to reproduction, while Maguire et al. (1995) found juvenile survival rate to be the most-sensitive parameter. This difference is probably due both to differences in population model structure and differences in vital rates. We used stage-based models rather than age-based models because we believed it was unlikely for management of this species to improve, for example, survival of age-3 adults independently from survival of age-4 adults. Using VRSA to analyze alternative management strategies, we found a more complicated story. For a model using 2

age classes, under our management alternatives, increasing reproductive success had the greatest impact on population growth for initial populations of 100 and 1,000 individuals, and for timeframes of 3 and 10 years. However, our confidence that increasing reproduction was the best management strategy (of the 3 we compared) was higher for larger populations and for the longer period. When we used a model with 4 age classes, the most-sensitive parameter changed by scenario. In some scenarios, population growth was most sensitive to reproductive output, and in some scenarios, it was more sensitive to increasing survival at a given stage, but it was never most sensitive to first year (hatch year) survival.

Our results are for the specified management strategies (only adult and juvenile survival and reproduction in each stage), management options (increasing each vital rate by 1–5%), timeframes, initial population sizes, and suite of age structures. When we ran VRSA using a 4-stage age structure rather than using 2-stages, and when we evaluated different suites of management alternatives, our results changed significantly (Tables 6, 7). From this we conclude that the results from VRSA might be sensitive to stage classes as defined, and that accurate data are required for constructing life tables for sensitivity analysis. We suspect this result holds for all methods of sensitivity analysis. In addition, even though our examples involved comparing simple management alternatives, management that affects multiple vital rates also can be compared.

The procedure for VRSA is familiar to population modelers, as it is the same one used for stochastic demographic population projections in population viability analysis (e.g., Beissinger and Westphal 1998, Akçakaya 2000), particularly to matrix-based projections such as the RAMAS programs (e.g., Akçakaya et al. 2003). The primary difference between VRSA and PVA is that PVA allows the computation of a probability of a population persisting in the long-term, whereas we are interested in causing the greatest increase in population size over a specified period. Although the methods are nearly identical, the focus is altered to give a different insight from the same information. In this sense, VRSA is closer in approach to Thompson's (1993) simulations to evaluate the effects of alternative forest management options on forest birds. The use of this type of population projection, however, has not previously been recognized as an approach to evaluate vital rate sensitivity.

The VRSA does not get around any problems caused if vital rates change with population density (Watkinson and Sutherland 1995, Beissinger and Westphal 1998). However, as with PVA, if

one knows the relationships between vital rates and population density, the VRSA equations can be modified to incorporate density dependence.

Management Implications

Because of its flexibility and simple interpretation of output, VRSA makes an excellent tool for comparing alternative management strategies for short- and long-term population planning. It avoids most problems with currently used sensitivity methods, and its results are readily interpretable with regards to which management alternative is best and the degree of confidence in this conclusion. Additionally, by incorporating stochasticity in vital rates, we can determine and evaluate resulting ranks of relative management effectiveness using iteration. This method shows not only the relative benefits gained from implementing each method, but it also determines the robustness of the ranks. This stochastic approach also could be used with perturbation and elasticity analyses to determine robustness from these methods as well. However, if long-term resources for management are uncertain; if populations do not have a stable age distribution; or if environmental stochasticity affecting vital rates, age structure, or sex ratio is high, VRSA provides a robust approach for vital rate sensitivity analysis.

One potential concern in managing for short-term population growth might be the possibility of compromising long-term recovery. This is a potential concern, although we do not know how likely it is in real circumstances. This could occur in a number of ways. As an extreme example, if you have a small population that because of catastrophe resulted in a population where all individuals were of pre-reproductive age, VRSA would recommend increasing juvenile survival if give a short projection timeframe. However, if the management timeframe is longer, VRSA might show that population growth rate is maximized by managing for increasing reproductive success. Consequently, if a manager continues to focus on juvenile survival even after some individuals have attained reproductive age, long-term persistence might be compromised. Therefore, we recommend re-running VRSA in years subsequent to the initiation of management to determine if the management focus should change. This is consistent with the concepts of adaptive management.

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