

POPULATION VIABILITY ANALYSIS

Steven R. Beissinger and Dale R. McCullough, Editors

THE UNIVERSITY OF CHICAGO PRESS CHICAGO & LONDON

2002

16

Sensitivity Analysis to Evaluate the Consequences of Conservation Actions

L. Scott Mills and Mark S. Lindberg

ABSTRACT

Sensitivity analysis can be defined as the set of analytical and simulation-based tools that evaluates how changes in life-history attributes of a demographic model affect population growth or rate of extinction. We describe four approaches to sensitivity analysis: (1) manual perturbation of deterministic and stochastic models, (2) analytical elasticity analysis, (3) life-table response experiment (LTRE), and (4) life-stage simulation analysis (LSA). In a case study using data from snow geese, we address two emerging issues in sensitivity analysis. First, although sensitivity analysis has typically been applied to single populations, it has potential to clarify metapopulation processes by quantifying the importance of among- versus within-population dynamics; our example shows that, relative to other life-history attributes, connectivity among populations has a strong impact on population growth. Second, variation in vital rates has been identified as a critical component of sensitivity analysis, yet the variation usually obtained from field estimates contains sampling variation (variation inherent in estimating vital rates) in addition to the relevant process variation (arising from spatial and temporal variation). Using the snow goose data, we find that conservation inferences based on total variation (sampling + process variation) can differ from those based on process variation alone. Sensitivity analysis is an essential counterpart to population viability analysis, because it goes beyond identifying a problem and helps define the most effective solutions. Advances in both data collection and model evaluation must move forward in tandem to obtain the unique insights possible under sensitivity analysis.

INTRODUCTION

Sensitivity analysis can be defined as the set of analytical and simulation-based tools that facilitates evaluation of how past or future changes in

We thank S. Beissinger and D. McCullough for organizing the PVA conference and editing the book. E. Cooch provided snow goose data and helpful feedback. M. Burgman, J. Citta, K. Crooks, S. Hoekman, M. McCarthy, R. Rockwell, J. Rotella, B. Sandercock, and M. Wisdom provided insightful comments. LSM was supported by NSF grant DEB-9870654.

life-history attributes affect population growth or persistence. It arose from the realization that intuition alone is not enough to predict the effect that changes in individual life-history components will have on the likelihood of a population's reaching a predefined population threshold. In the language of deterministic demographic models, for example, different age- or stage-specific vital rates (i.e., birth, death, immigration, and emigration rates) do not have equal impacts on population growth rate (λ). Although this simple demographic fact has been known a long time (Cole 1954), formal sensitivity analysis has become well developed only recently with the introduction of new analytical and simulation-based techniques.

A frequently cited example of how sensitivity analysis showed intuition to be misleading is the work on declining loggerhead sea turtles (*Caretta caretta*). After years of management focused on the seemingly obvious notion that increasing hatchling survival alone should reverse population decline, sensitivity analysis showed that the most efficient way to reverse the decline of this species is to reduce mortality of the life stages that get killed in shrimp nets (Crouse et al. 1987; Crowder et al. 1994); egg protection programs will also be necessary in areas where egg mortality is high (Grand and Beissinger 1997). Thus, sensitivity analysis on sea turtles informed and even helped change fishery policy (Crowder et al. 1994; Grand and Beissinger 1997). Although population viability analysis (PVA) practitioners are often interested in how best to increase population growth rate for species at risk, sensitivity analysis can be equally valuable to identify ways to decrease population growth rate in introduced or pest species (Shea and Kelly 1998; Citta and Mills 1999) or provide insights into managing maximum sustained yield of a stable population (Caughley 1977).

In addition to its role in directing management, sensitivity analysis can give basic insight into population dynamics and can direct research. For example, a study that documents that "inbreeding affects litter size" or "forest fragmentation affects adult survival" or "acid rain affects hatch probability" can be placed in a more meaningful context with consideration of how the observed changes would be expected to affect population growth.

Sensitivity analysis for conservation decision making has become increasingly sophisticated with recent debate and discussion (Tuljapurkar and Caswell 1997; Akçakaya and Raphael 1998; Ehrlén and van Groenendael 1998; Wisdom et al. 2000), but several issues have yet to be addressed. For readers unfamiliar with sensitivity analysis, we first give a brief overview of the four main sensitivity-analysis approaches that have been used to prioritize conservation management. We then consider

two issues—forms of variation in vital rates and the use of field data to evaluate the role of connectivity—that have rarely been incorporated into applications of sensitivity analysis. We explore the effect of these factors on management inferences, using a field data set. These factors may or may not affect rankings of sensitivity analysis for any particular application, but the only way to find out is to incorporate these issues into the analyses.

OVERVIEW OF APPROACHES TO SENSITIVITY ANALYSIS

Manual Perturbation

We term as “manual perturbation” the oldest, and probably most common, approach to sensitivity analysis (a.k.a. “conventional sensitivity” in Cross and Beissinger 2001). With this approach vital rates are manually altered by an amount deemed relevant to the problem at hand. In deterministic applications, net reproductive rate, or annual population growth rate (λ), may be plotted against varying levels of survival or reproductive parameters for different age (or stage) classes. This approach has been used to rank the “importance” of different rates to population growth in a range of species including condors (Mertz 1971), elk (Nelson and Peek 1982), and elephants (Fowler and Smith 1973). The use of stochastic models expands the metrics of sensitivity analysis to include not only how different factors affect population growth, but also how they affect probability of extinction or quasi-extinction (i.e., the probability of reaching some threshold of concern). Although in conventional usage each rate is typically changed by the same proportion or amount (e.g., 10% of the mean values), there is nothing inherent in the method that limits changes to fixed proportional changes. Cross and Beissinger (2001) conducted sensitivity analyses that were scaled relative to the range of values each input variable could assume.

Sensitivity analysis using manual perturbations is not limited to investigating the importance of vital rates alone. Rather, it can include impacts of a range of factors including age structure, density dependence, inbreeding depression, and connectivity (Burgman et al. 1993; Mills et al. 1996; Beissinger and Westphal 1998). For example, sensitivity analysis using manual perturbations has been used in various ways to explore the relative importance of dispersal and other parameters to conclusions of spatially explicit population models (Conroy et al. 1995; Dunning et al. 1995; South 1999; Ruckelshaus et al. 1999).

Also, manual perturbation sensitivity analysis has the unique ability to easily incorporate different age or stage structures. Both deterministic and stochastic analyses can either assume a stable age distribution or input an observed age distribution from the field. In fact, sensitivity

analysis can quantify the effect of age structure on population growth or extinction probability (Citta et al. in review).

The strength of manual perturbation sensitivity analysis—that is, the different measures for evaluating “importance” and the myriad of factors that can be considered in unique ways for particular situations—is also its biggest weakness, because there is no standardized metric that can be compared across species or studies. For example, one study may evaluate how 10% changes in demographic rates affect the probability of reaching 20 individuals in 200 years, while another considers how 5% changes affect the probability of total extinction within 50 years. As a result, these approaches can be incredibly valuable for the organism that they target, but the lack of a standardized metric comparable across species or studies is problematic for life-history comparisons and for inferring best management actions by analogy with other species.

Manual perturbation approaches may also be time-consuming, with many simulations of many combinations required. However, McCarthy et al. (1995) have developed an innovative approach to stochastic sensitivity analysis that efficiently reduces the computational effort required to determine quasi-extinction risk for an exhaustive array of model parameters and their interactions. A systematic array of parameter combinations is analyzed via sets of PVA, and logistic regression is used to summarize the relationship between extinction risk and the model parameters. Variables may be ranked according to their importance in predicting extinction or quasi-extinction based on the standardized regression coefficient (Cross and Beissinger 2001). Drechsler (1998) derived a complementary approach to identify parameter combinations that behave in similar ways, effectively reducing the magnitude of the problem to a manageable size for analyses based on extinction or quasi-extinction risk.

Examples of sensitivity analysis based on manual perturbations are as varied as the method itself; some would include Beissinger’s analysis (1995) of snail kites (*Rostrhamus sociabilis*), Marmontel et al.’s analysis (1997) of conservation options for the Florida manatee (*Trichechus manatus latirostris*), and Akçakaya and Raphael’s study (1998) of management options for northern spotted owls (*Strix occidentalis*). Cross and Beissinger (2001) found that the most sensitive variables in a model of wild dog (*Lycaon pictus*) population dynamics differed when sensitivity was evaluated by manual perturbations of the mean and the range, and when it was evaluated by logistic regression.

Analytical Sensitivity and Elasticity Analysis

Analytical sensitivities and elasticities are calculus-based measures of how infinitesimal changes in individual vital rates will affect population

growth. In contrast to manual perturbation, these measures assess sensitivity solely by evaluating changes on λ , so effects on extinction or quasi-extinction cannot be assessed. Analytical sensitivities are calculated from the reproductive value and stable age (or stage) distribution vectors (left and right eigenvectors, respectively) and λ (the dominant eigenvalue) of the population matrix containing stage-specific vital rates (Goodman 1971; Caswell 1989b; de Kroon et al. 2000). Sensitivities measure the absolute change in λ , given an infinitesimal absolute change in a vital rate, while all other vital rates remain constant. Analytical elasticities rescale the sensitivity to account for the magnitude of both λ and the vital rate. Thus, elasticities are “proportional sensitivities” that measure the proportional change in λ given an infinitesimal one-at-a-time proportional change in a vital rate (de Kroon et al. 1986; Caswell 1989b), assuming the population is growing or decreasing at a constant rate and has a stable age distribution (SAD). Elasticities can be added together to predict the joint effect of changes in multiple rates if the changes in vital rates and λ are linearly related, and elasticities of all matrix elements sum to one (de Kroon et al. 1986; Mesterton-Gibbons 1993). Elasticities can be calculated for both matrix elements and “lower-level” components of vital rates that make up matrix elements, such as reproduction and survival components in each element in the top row of a projection matrix (Caswell 1989b; Doak et al. 1994). Elasticities of component vital rates (“lower-level elasticities”) do not add to one but can still be ranked. The straightforward interpretations and wide generality of elasticities provide an intuitive metric that assays the relative importance of life-cycle transitions both within and among studies and species (de Kroon et al. 2000).

Because they are operationally defined, easily applied, and comparable across studies, elasticities have been embraced in applied biology. Elasticities are usually calculated from a single population matrix constructed from average, or even “best guess,” vital rates. The vital rate in the mean matrix with the highest elasticities is recommended for highest management or research priority (e.g., Crowder et al. 1994; Heppell et al. 1994; Maguire et al. 1995; Olmsted and Alvarez-Buylla 1995). Unlike elasticity analysis assumptions, however, changes due to management actions or natural variation are not infinitesimal, nor do they occur one at a time.

Mills et al. (1999) investigated whether the conservation applications of elasticities are robust to violation of their mathematical definitions and came to three major conclusions. First, if the vital rates in a matrix or a population of interest were different than those of the mean matrix used to calculate elasticities, the rankings of the elasticities could change

(see Caswell 1996b). Although changes in rankings may not occur often (Benton and Grant 1996; Dixon et al. 1997; de Kroon et al. 2000), the cases where such shifts do occur may have important conservation consequences because the priorities of research or management may be misdirected (Wisdom et al. 2000). Second, Mills et al. (1999) found that elasticities were good qualitative and quantitative predictors of changes in population growth rate as long as all vital rates changed by the same proportional amount. Unfortunately, vital rates seldom change by equal amounts in nature, and Mills et al. (1999) found that, when different vital rates changed by different amounts, deterministic elasticities were often poor predictors of how population growth would change (see also Caswell 1996a; Ehrlén and Van Groenendael 1998; Wisdom et al. 2000). This last issue—the disconnect between “importance” as assayed by elasticities and “importance” as related to relative variation in a vital rate—is especially disconcerting because vital rates with high elasticity tend to have low levels of variation (Gaillard et al. 1998; Pfister 1998). This implies that basing management inferences solely on elasticities could lead to erroneous predictions about which rates most affect population growth under management.

In short, elasticities are a mathematically elegant metric that can be derived from relatively sparse data in the form of a single matrix of vital rates. However, elasticities alone do not account for how much vital rates have changed in the past, or might change in the future. Also, elasticities are calculated on infinitesimal, one-at-a-time changes, with multiple changes assumed to be additive, and effects of vital rate changes on growth rate assumed to be linear. The calculations rely on asymptotic matrix properties, so a SAD is assumed, although it is possible to calculate elasticities for periodic deterministic vital rates that cycle predictably (Caswell and Trevisan 1994), and from stochastic models (Tuljapurkar 1990; Benton and Grant 1996; Dixon et al. 1997; Grant and Benton 2000). Correlations among vital rates can be incorporated using an extension of elasticity analysis explained by van Tienderen (1995).

Life-Table Response Experiments

The life-table response experiment (LTRE) approach to sensitivity analysis is an extension of analytical sensitivity and elasticity analysis that incorporates vital rate-specific changes or variation. Caswell (1997) explained the approach for a simple, one-way, fixed-effect experimental design as follows. Imagine a “control” set of vital rates and a “treatment” set, perhaps arising from a human-caused perturbation. A population growth rate at SAD is characteristic of the population matrix made up

of each set of vital rates. The difference between the two growth rates is a function of how much different vital rates change under the treatment and the effect of changes in each rate on λ . LTRE decomposes the treatment effects on λ into contributions from individual vital rates by taking the product of the vital rate effect (i.e., change in a given rate due to the perturbation) and the analytical sensitivity of λ to changes in that rate (Caswell 1989a, 1997; Brault and Caswell 1993).

LTRE approaches are not limited to fixed "experiments," but rather have been generalized to comparative observations under natural conditions for a variety of matrix models; they can also include known correlation structures among rates (Horvitz et al. 1997). They therefore have become an elegant way of quantifying the fact that "a large effect on a vital rate to which λ is insensitive may contribute much less to variation in λ than a much smaller effect on a vital rate to which λ is more sensitive" (Caswell 1996a, 74).

For example, Levin et al. (1996) and Caswell (1996a) evaluated how different sources of estuarine pollution from sewage, oil, and algae from eutrophication enrichment affected a deposit-feeding polychaete (*Capitella* sp.). The presence of sewage substantially increased *Capitella* population growth from $\lambda = 1.79$ without sewage to $\lambda = 4.06$ with sewage. With the addition of sewage, fertility increased by almost fourfold, while age at maturity decreased by about one-half. LTRE analysis was used to show that the overall contribution of age at maturity to the substantial increase in λ was three times greater than that of fertility. Survival, which was actually reduced by the addition of sewage, contributed very little to the change in growth rate. Ehrlén and van Groenendael (1998) provided another interesting example of LTRE analysis; for a leguminous herb (*Lathyrus vernus*) with different levels of variance for different rates, vital rate elasticities calculated from the mean matrix were poor indicators of the overall impacts of individual rates on population growth.

LTRE-based approaches are important extensions of analytical sensitivity and elasticity analysis because they can incorporate information on the amount, form, and correlations of changes in different vital rates. However, the approach still incorporates some of the same assumptions of elasticities, including additivity of effects on different growth rates, linearity of the relationship between vital rate and growth rate changes, and asymptotic properties such as SAD. Mills et al. (1999) found that, although LTRE-type approaches led to predictions of population growth that were much better than elasticities alone, nonlinearities between growth rate and vital rate changes did lead to some, usually minor,

disparity between actual population growth and that predicted by changing different rates by specified amounts.

Life-Stage Simulation Analysis

Wisdom and Mills (1997) developed a simulation-based approach to sensitivity analysis that might be considered a hybrid of the previous three methods. The approach is called life-stage simulation analysis (LSA; Wisdom et al. 2000) because it uses simulations to evaluate the impact of changes in different vital rates on λ . For purposes of conservation decision making, the user inputs the mean and variation of vital rates observed in the past or those expected in the future under different scenarios of management (see "Discussion" for the need to distinguish past from future changes). Correlations among vital rates are specified from field data if possible, as are the distribution functions for each vital rate (i.e., uniform, lognormal, beta, etc.). A computer program constructs many replicate matrices with each rate in each matrix drawn from the specified distributions. Currently, each matrix is projected asymptotically to a SAD.

Output metrics in LSA include elasticity-based measures (e.g., the frequency of replicates having the same vital rate of highest elasticity, and the differences in elasticity values whenever the rankings of elasticities change across the replicates), as well as other metrics that avoid elasticity entirely (Wisdom and Mills 1997; Wisdom et al. 2000). For example, an LSA approach can calculate the percentage of replicates having positive population growth under different scenarios. Also, by regressing λ on each vital rate as other rates change simultaneously, one can derive the coefficient of determination (r^2), representing the proportion of the variation in the population growth rates over all simulations that is explained by variation in that vital rate. When all main effects and interactions are included, the r^2 values for all rates sum to one.

An intuitive understanding of r^2 for each vital rate can be derived by comparing it to analytical sensitivities and elasticities. When λ is a linear function of the vital rates, the slope of the line equals the analytical sensitivity, and r^2 is a function of both the slope (i.e., analytical sensitivity) and the proportionate variation in that vital rate, adjusted for covariance among vital rate. The same relationships hold for elasticity, if the regression is done on log-transformed data (Brault and Caswell 1993; Horvitz et al. 1997; Wisdom and Mills 1997). Therefore, the simulation-based LSA r^2 corresponds to analytical LTRE approaches, because it accounts for both infinitesimal sensitivity and range in variation of differ-

ent rates (Caswell 2000; Wisdom et al. 2000). The r^2 metric of LSA is also mathematically similar to the standardized regression coefficient used by McCarthy et al. (1995) in logistic regression of PVA (see “Manual Perturbation” above), because the standardized regression coefficient is equivalent to the square root of r^2 (Snedecor and Cochran 1980, 357).

LSA has been applied to several cases of conservation decision making. For example, Crooks et al. (1998) used LSA to show that adult survival has the greatest influence on cheetah (*Acinonyx jubatus*) population growth, a result that questions whether juvenile mortality alone is limiting growth in this endangered species. In a very different application, Citta and Mills (1999) used LSA to ask which of several potential management scenarios would be more likely to reduce population growth of brown-headed cowbirds (*Molothrus ater*), a brood parasite on many passerine birds of conservation concern. They found that egg survival has the greatest importance to population growth of cowbirds under most conditions, implying that egg removal would have the largest effect, and that decreasing adult survival on wintering ranges would have little effect. Because the age structure is skewed toward eggs, however, it is more difficult to initiate a given proportional change in egg survival compared to the same proportional change in adult survival. Collectively, this situation, where egg removal has the largest proportional effect but adult survival is easier to change, points to a more holistic management of land uses to disfavor cowbirds (Citta and Mills 1999).

Thus, LSA has some of the versatility of the stochastic manual perturbation methods, and relies on repeatable metrics (e.g., r^2 and average elasticity measures) that could be compared across species and studies. Like manual perturbation methods and LTRE, it accounts for variation in vital rates. As it has been used to date, however, it shares the disadvantages of both elasticity and LTRE in assuming asymptotic properties. Also, all sensitivity inferences are based on λ ; sensitivity measures such as probability of extinction or quasi-extinction cannot be considered using this approach. Although Caswell (2000) argued that LSA cannot be used to make predictions of the future because it incorporates variation in vital rates, we disagree on the grounds that both means and variation can be used to describe the past or to pose scenarios for the future (see “Discussion”).

EMERGING ISSUES IN CONSERVATION DECISION MAKING WITH SENSITIVITY ANALYSIS

Next we consider two issues—forms of variation and the role of connectivity—that have rarely been explored but that have strong implications

for applying sensitivity analysis to conservation decision making. We provide a case study using field data to demonstrate how these factors can impact conservation conclusions.

All Variation Is Not Created Equal

Three of the four methods (manual perturbation with stochastic models, LTRE, and LSA) are designed to account for how variation in vital rates could affect population growth. However, connections among field data, model input, and conservation applications are often unclear because the total variation in estimates of vital rates includes two forms of variation—process variation and sampling variation—that are distinctly different (White et al., chap. 9 in this volume).

Process variation is caused by spatial and temporal changes in vital rates (Thompson et al. 1998). Spatial variation arises from changes in community composition, habitat quality, and habitat heterogeneity over the landscape, which in turn may be related to environmental conditions such as aspect, slope, precipitation, and successional-stage differences. Temporal variation is the unpredictable change in the environment that impacts a given population through time (Burgman et al. 1993). Weather is often an important driver for temporal variation, but biotic factors such as competition, predation, disease, and human impacts may also be critical. Interactions among factors make it difficult to separate spatial and temporal variation (Burbidge and McKenzie 1989; Doak et al. 1994; Ringsby et al. 1999).

In contrast to process variation, which directly acts on organisms, sampling variation is the uncertainty in parameter estimates that arises from the fact that vital rates are estimates from an incomplete enumeration of individuals. When modeling population dynamics, sampling variation should be removed from total variation so that the focus of a population analysis is on only process variation (Burnham et al. 1987; Link and Nichols 1994; Thompson et al. 1998). Problems due to failure to separate sampling from process variation have recently been noted in the context of population stability (Link and Nichols 1994; Gould and Nichols 1998), monitoring (Caswell et al. 1998; Thompson et al. 1998), and PVA (Beissinger and Westphal 1998; Ludwig 1999). Gould and Nichols (1998) demonstrated that most of the total variation in survival probabilities of three species of birds was the result of sampling variation (see also Hitchcock and Gratto-Trevor 1997). Ludwig (1999) showed that ignoring sampling error, when it is present in the estimates used for PVA analysis, leads to estimates of extinction probability that are positively biased and have confidence intervals that are too small.

The stochastic manual perturbation sensitivity approach can explicitly

include both spatial and temporal components of process variation. It captures spatial variation by simulating many different possible populations, and temporal variation using Monte Carlo simulations and calculating probability of extinction (Burgman et al. 1993) or stochastic population growth rate (Tuljapurkar 1997). In application, however, most users do not separate temporal and spatial variation. The other approaches that account for variation in sensitivity analysis, LTRE and LSA, easily accommodate spatial variation, but reliance on asymptotic growth rate at SAD limits the inclusion of temporal variation. LSA could use stochastic projections to model temporal variation, but to date it has only been used to project replicate matrices to SAD. Likewise, numerical differentiation or a stochastic analytical approach can be used to calculate elasticities and LTRE measures under temporal variation (Tuljapurkar 1990; Benton and Grant 1996; Grant and Benton 2000). This approach has seldom been applied to conservation questions, but may have great potential (Dixon et al. 1997). The consequences of failing to separate sampling from process variation in sensitivity analysis has rarely been explored (Gaillard et al. 1998), despite the fact that virtually all sensitivity analyses that include variation have included total variation (i.e., process plus sampling) rather than process variation.

The Value of Connectivity: Among- versus Within-Population Vital Rates

An entire field, metapopulation analysis, is predicated on an overwhelming importance of among-population movement for the persistence of the metapopulation. As Harrison (1994, 177) noted: "It seems necessary to adopt a broader and vaguer view of metapopulations as sets of spatially distributed populations, among which dispersal and turnover are possible but do not necessarily occur . . . A possible way forward is to ask, in each specific case, 'what is the relative importance of among-population processes, versus within-population ones, in the viability and conservation of this species?'"

Sensitivity analysis should be an ideal approach to facilitate an operational definition of metapopulation, because effects of among- versus within-population vital rates on growth rate or extinction can be compared. However, sensitivity analysis has focused primarily on single-population dynamics. In some cases, these single-population analyses may include an asymmetric treatment of movement, where estimates of apparent survival (Lebreton et al. 1992) include the effects of emigration, but estimates of fecundity do not include immigration. Only a few studies have used sensitivity analysis to evaluate the relative importance of among- versus within-population processes for specific populations where relevant field data exists (see Burgman et al. 1993). Most of the

examples have used manual perturbation PVA approaches, such as Beier (1993) for cougars (*Puma concolor*), Akçakaya and Baur (1996) for land snails (*Arianta arbustorum*), Lefkovitch and Fahrig (1985) and Fahrig and Paloheimo (1988) for mice (*Peromyscus leucopus*), Pulliam et al. (1992) and Liu et al. (1995) for Bachman's sparrow (*Aimophila aestivalis*), and Lindenmayer and Lacy (1995) for arboreal marsupials (*Trichosurus caninus*, *Petauroides volans*, and *Gymnobelideus leadbeateri*). Wootton and Bell (1992) calculated deterministic elasticities of within-population vital rates and migration rates between peregrine falcon (*Falco peregrinus anatum*) populations using multiregional matrix models (see Caswell 1989b; Burgman et al. 1993).

ADDING SPECIFIC FORMS OF VARIATION AND CONNECTIVITY TO SENSITIVITY ANALYSIS: A CASE STUDY

The Model System: Lesser Snow Geese

Our objective is to examine how the results of sensitivity analysis might change if types of variation and connectivity were accounted for in an analysis with real data. The challenge, however, is that the data needed for such an analysis typically do not exist for rare or endangered species. Lack of data does not decrease the importance of considering these factors and may guide data collection efforts for the future; it does, however, limit the choice of taxa for our analysis. Therefore, we chose a species, the lesser snow goose (*Anser caerulescens caerulescens*), whose conservation importance comes not from having low and declining numbers, but from having large and increasing numbers. We hope that exploring these issues with this data set will help future data collection and interpretation in other taxa, including threatened ones.

Based on the midwinter index of abundance, the midcontinent population of lesser snow geese (hereafter snow geese) increased by 300% between 1969 and 1994 (Abraham and Jefferies 1997). This dramatic increase is believed to result from changes in agricultural practices on the wintering grounds, where snow geese exploit waste grains, and from increased availability of refuges on wintering and staging areas (Batt 1997). Through excessive feeding pressure, large numbers of snow geese have severely degraded Arctic and sub-Arctic habitats where they stage during migration and breed (Abraham and Jefferies 1997). In addition to direct damage to vegetation resulting from such high snow goose numbers, habitat degradation may also negatively impact other species that breed in these regions.

For these populations of snow geese, as for the brown-headed cowbird example discussed earlier, the question of interest is how best to decrease population growth. The final decision of the best course of

action will include not only biological expectations, but logistics and social and political feasibility. Sensitivity analysis can inform the biological expectations. Our analysis for snow geese does not consider specific management scenarios.

Rockwell et al. (1997) conducted an elasticity analysis to consider the practical question of what actions would most reduce snow goose population growth. In one of their analyses, they developed a five-stage population projection matrix, parameterized with vital rate estimates based on 12 years of data (1973–1984) from a 30-year study of snow geese breeding at La Pérouse Bay, Manitoba (Cooke et al. 1995). All losses were attributable to mortality; the Rockwell et al. (1997) model contained no connectivity in terms of immigration or emigration. Rockwell et al. (1997) conducted deterministic elasticity analysis for five potential sets of data that accounted for some of the uncertainties in life-history data. In all cases, adult survival contributed more to λ than did any other vital rate. From these results, they considered how much change in growth rate would be achieved under a number of scenarios involving reduced survival or reproductive output.

We analyzed the same 12 years of snow goose data (with some minor exceptions presented below) and used the same basic projection model as Rockwell et al. (1997), except that we included connectivity and specific forms of variation in vital rates. Although we used similar data, our analysis does not explore management options that were considered in Rockwell et al. (1997). The elements in the top row of the matrix are post-birth pulse, age-specific fertilities, incorporating both fecundity (number of eggs laid that survive to fledge) and survival of females that produce those offspring. Age in years is indicated by subscript i , and the projection interval is one year. Thus, fertility in each element of the top row of the matrix is

$$F_i = S_i^* R_i,$$

where S_i is age-specific survival probability and R_i is age-specific fecundity. S_1 is juvenile survival (from fledging to the first anniversary of fledging), and adult survival probability is assumed constant for age classes 2 through 5+. Rockwell et al. (1997) defined the fecundity term (R_i) as

$$R_i = BP_i * (TCL_i/2) * (1 - TNF_i) * P1_i * P2_i * (1 - TBF_i) * P3_i,$$

where BP is breeding propensity or the probability that a female of that age class will breed, TCL is total clutch size reduced by one-half to focus on females only, TNF is total nest failure, $P1$ is egg survival, $P2$ is hatching success, $P3$ is gosling survival from hatching to fledging given that

the brood is not totally lost, and TBF is total brood failure for the i th age class. Thus, fecundity represents the number of birds fledged. Although fecundity comprises a number of different components, some parts do not have reliable parameter estimates, so we do not evaluate importance of individual fecundity components, although it is computationally easy to do.

There are many ways to add connectivity to a matrix model (see Caswell 1989b; Burgman et al. 1993). For demonstration purposes we chose the simple approach of modeling connectivity by multiplying survival probability by the sum of immigration probability and one minus emigration probability [$S_i((1 - E_i) + I_i)$], where I_i is probability of immigration to the La Pérouse population for age class i , and E_i is probability of permanent emigration from the La Pérouse population for age class i . Because the field data that we used come from a single population (La Pérouse Bay), emigration can be interpreted as the probability of permanently leaving the La Pérouse population sampled during brood rearing (where snow geese were banded), and immigration represents the proportion of the population that enters La Pérouse from anywhere else. Using these parameters, our projection matrix was

$$\begin{bmatrix} [S_1((1 - E_1) + I_1)]R_1 & [S_2((1 - E_2) + I_2)]R_2 & [S_3((1 - E_3) + I_3)]R_3 & [S_4((1 - E_4) + I_4)]R_4 & [S_5((1 - E_5) + I_5)]R_5 \\ S_1((1 - E_1) + I_1) & 0 & 0 & 0 & 0 \\ 0 & S_2((1 - E_2) + I_2) & 0 & 0 & 0 \\ 0 & 0 & S_3((1 - E_3) + I_3) & 0 & 0 \\ 0 & 0 & 0 & S_4((1 - E_4) + I_4) & S_5((1 - E_5) + I_5) \end{bmatrix}$$

Methods for parameter estimation and associated variances are reported in Cooke et al. (1995) with the following exceptions. Evan Cooch (Cornell University) provided us with age-specific estimates of means and variances of reproduction and survival parameters when these values were not reported in the original publication, as well as with estimates of emigration probability and variance from capture-recapture models (Burnham 1993). Estimates of immigration probability do not exist, so we made the simplifying assumption of setting the mean and variance for immigration equal to those of emigration probability. This is based on the premise that emigration probabilities for all other populations of snow geese in the midcontinent region are equal to that of La Pérouse Bay, and that the probability of an emigrant immigrating to La Pérouse is equal to the proportional size of that population relative to the overall numbers of snow geese in the midcontinent region. While it is true that setting $I_i = E_i$ would cause these terms to “cancel out” in the matrix, sensitivity analysis using elasticities can be conducted

Table 16.1 Annual Age-Specific Vital Rates Used in Sensitivity Analysis for Lesser Snow Goose

Scenario	Age Class	R_i	S_i	$E_i = I_i$
Mean	1	0	0.4443	0.3543
	2	0.3305	0.8683	0.02567
	3	0.7761	0.8683	0.02567
	4	0.9822	0.8683	0.02567
	5	1.032	0.8683	0.02567
Low (total variation)	1	0	0.2016	0.0985
	2	0.0846	0.7455	0
	3	0.2946	0.7455	0
	4	0.3167	0.7455	0
	5	0.4979	0.7455	0
High (total variation)	1	0	0.6870	0.6102
	2	0.8480	0.9910	0.1032
	3	1.614	0.9910	0.1032
	4	2.1818	0.9910	0.1032
	5	1.8787	0.9910	0.1032
Low (process variation only)	1	0	0.2289	0.1663
	2	0.1039	0.8282	0
	3	0.3976	0.8282	0
	4	0.4094	0.8282	0
	5	0.6002	0.8282	0
High (process variation only)	1	0	0.6597	0.5424
	2	0.7713	0.9743	0.06566
	3	1.3506	0.9743	0.06566
	4	1.8967	0.9743	0.06566
	5	1.6574	0.9743	0.06566

Notes: The mean rate, as well as the low and high bounds calculated from total variation (process + sampling variation) and from process variation alone, are listed for each annual age class, for fecundity (R), survival (S), emigration (E), and immigration (I).

for I_i and E_i separately, and in the stochastic LSA-based approach immigration and emigration will be drawn as individual random variates for each matrix.

We used the averages of the point estimates for the 12 years of available data as the mean value of survival and emigration rates (table 16.1). Mean R_i (fecundity) values were calculated as the mean of the product of its components.

We estimated total variance (T^2) for the i th age-class mean of each parameter (\bar{X}_i) as

$$T_i^2 = \frac{1}{n-1} \sum_{j=1}^n (\hat{X}_{ij} - \hat{\bar{X}}_i)^2,$$

where n equals the number of years in the study (12 years) and \hat{X}_{ij} is the estimated parameter value for the i th age class in the j th year of

the study. We obtained process variance (in this case temporal variance, τ_i^2) by subtracting average sampling variance from our estimate of total variance (Link and Nichols 1994; White et al., chap. 9 in this volume). Sampling covariance among estimates for each parameter was set at zero because covariance estimates were not available for several parameters. In cases where temporal variance was estimated as a negative value (Gould and Nichols 1998), we assigned a value equal to the smallest positive value that we estimated (0.0004). Based on both total and temporal variance alone (i.e., process variance with sampling variation removed—see also White et al., chap. 9 in this volume), we established a range of vital rates (table 16.1) from which to sample in our sensitivity analysis. For total variance the maximum and minimum were equal to $\bar{X}_i \pm 2.0 T_i$, and for temporal variance (process alone) the range was equal to $\bar{X}_i \pm 2.0 \tau_i$. For all parameters we truncated the range of values at a minimum of 0.0, and for probabilities we truncated the maximum value at 1.0.

Sensitivity Analysis for the Snow Goose Model Incorporating Connectivity and Forms of Variation

The effects of connectivity and exact type of variation could readily be evaluated using stochastic manual perturbation approaches, LTRE, or LSA. Our goal here was not to perform a snow goose sensitivity analysis per se (Cooch et al. 2001), but rather to use these data to explore the general issues of how connectivity and type of variation affect sensitivity analysis. For the purposes of demonstration, we use the LSA approach. As described above, the LSA approach uses simulations to calculate traditional elasticities across a range of variation, as well as metrics that bypass elasticities entirely. For the sake of simplicity, in this example we provide elasticities for comparison to previous work and discuss them briefly, but we focus primarily on only one of the LSA sensitivity metrics, r^2 , as an index of vital rate “importance.” The r^2 metric indicates the proportion of variation in growth rate explained by changes in each vital rate with all other rates changing simultaneously. We let each rate vary independently, although LSA can readily incorporate covariation among vital rates (Hoekman et al. 2000; Wisdom et al. 2000). Moreover, we stress that obtaining information on covariation among rates from the field is highly important (Horvitz et al. 1997; Schmutz et al. 1997), but those data are not yet available.

Currently, the LSA approach can use uniform, beta, poisson, or log-normal distribution for vital rates (Hoekman et al. 2000; Wisdom et al. 2000). Again, to simplify our approach, we elected to use a uniform distribution for all rates. Note that by using the minimum and maximum

observed in the field data, we are performing a sensitivity analysis that includes both natural and human-induced variation observed in the past as well as sampling variation, although we shall see what happens when sampling variation is removed. This may be an appropriate starting point to project future changes, assuming that bounds of the past will apply to the future. Alternatively, we could easily relax this assumption of using the past variation to reflect the future and instead simulate specific future management scenarios, change the bounds of variation, or consider different distributions for vital rates (Citta and Mills 1999; Hoekman et al. 2000; Wisdom et al. 2000).

If we perform a deterministic, single population, analytical sensitivity analysis and consider just the mean vital rates and ignore immigration and emigration, our matrix model converges to that of Rockwell et al. (1997) with the same result: adult survival is most important. Based on component elasticities using mean vital rates, values are highest for adult survival (elasticities summed across ages 2 through 5 = 0.832), with much lower elasticity for juvenile survival (0.168) and fecundity (elasticities summed across ages 2 through 5 = 0.168).

How do conclusions change when the analysis accounts for emigration, immigration, and measured variation in vital rates? First we use the LSA approach with total variation, as done in virtually all sensitivity analyses to date that have incorporated variation in vital rates. That is, we followed the usual approach of setting the bounds of vital rates based on total variation including both process and sampling variation observed from field data. Sensitivity analysis using the r^2 metric and the model with connectivity identified juvenile survival as explaining the highest proportion of variation in growth rate, followed by juvenile movement (emigration and immigration), adult fecundity, adult survival, and adult movement (fig. 16.1A). We also performed the sensitivity analysis using total variation and the model without connectivity by using the same model as for calculating elasticities above. Juvenile survival again is ranked highest ($r^2 = 0.54$), with fecundity and adult survival considerably lower ($r^2 = 0.21$ and 0.21 , respectively). Therefore, we conclude that variation can lead to very different rankings of "importance" than deterministic elasticity analysis—in this case causing juvenile survival to replace adult survival as the highest-ranking rate—because overall change in population growth rate is a function of both the infinitesimal impact of vital rates on growth rate and the amount that a given vital rate can change (see Caswell 1997; Gaillard et al. 1998; Mills et al. 1999; Wisdom et al. 2000). Also, this example demonstrates that connectivity, or movement, is nontrivial in terms of its impact on λ for this population.

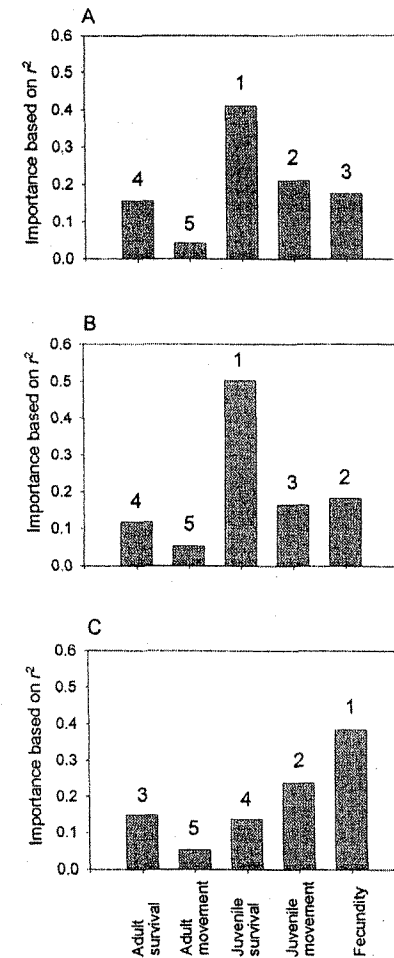


Fig. 16.1 Sensitivity analysis of snow goose data using life-stage simulation analysis (LSA). Relative "importance" of each vital rate to population growth rate is assayed by the proportion of the variance in population growth (r^2) accounted for by changes in each vital rate. Numbers above bars give importance rank, with one being the highest. "Movement" refers to connectivity, or immigration and emigration. The deterministic elasticity analysis ranked adult survival highest. However, LSA, including connectivity and forms of variation, led to different rankings: A, using total variation (process + sampling); B, using process variation only (sampling variation removed); and C, using process variation only, under the hypothetical scenario where juvenile survival had the same proportion of process to sampling variation as adult survival had.

How might removing sampling variation from our estimate of total variation alter our conclusions? The range of variation due only to real-world processes is less than total variation (table 16.1), with the decrease varying across vital rates according to the proportion of process variation versus sampling variation. Interestingly, in this case, differences in sensitivity rankings with total variation versus process variation were small (compare fig. 16.1B to 16.1A). Juvenile survival still accounted for the most variation in growth rate, and juvenile movement still had a nontrivial impact on λ . However, these small changes in sensitivity rankings using total versus process variation alone resulted from the fact that the rates with highest total variation tended to have the highest proportion of process to sampling variation. In particular, the highly variable juvenile survival rate was estimated to contain 79% process variation and 21% sampling variation, whereas adult survival had minimal total variation of which only 11% was process and 89% was sampling variation. Therefore, in this particular case, which may be unusual, removing sampling variation did little to change the impact of variation on overall importance.

Given that high total variation in other data sets could be made up of any ratio of process variation to sampling variation, we next consider a different scenario. Suppose that variation in juvenile survival had the same proportion of process to sampling variation as adult survival. In other words, suppose total variation remained unchanged but variation in juvenile survival comprised 11% process variation and 89% sampling variation. With this one hypothetical change, the rankings of importance of different vital rates changed drastically (compare fig. 16.1C to figs. 16.1A and 16.1B). Juvenile survival dropped from highest ranking to fourth, and fecundity went from third highest to first. In this case, conclusions based on sensitivity analysis using total variation (fig. 16.1A) were very different than those based on only process variation (fig. 16.1C). We stress that this last scenario is hypothetical. However, it shows that use of total variation in sensitivity analysis could cloud conclusions, because sampling variation can inflate the "importance" of certain rates. It will not be unusual for this to occur in real population data because some rates will be more difficult to estimate than others (e.g., juvenile survival in passerines).

Other Issues Related to Sensitivity Analysis

Our evaluation of how process variation and connectivity affect sensitivity analysis is not complete without further consideration of the link between the measurement and the modeling of these factors. Process variation can be estimated by subtracting the mean of the sampling vari-

ation from total variation if sampling variation is assumed constant (Skalski and Robson 1992; Link and Nichols 1994) or by more complex estimators if sampling variation is not constant (Burnham et al. 1987; Thompson et al. 1998). In either case, components of variance analysis require valid estimates of vital rates. It is difficult to separate sampling from process variation if indices are used instead of valid estimates (Link and Nichols 1994; White et al., chap. 9 in this volume). We think that capture-recapture methods provide some of the most robust approaches for parameter estimation (e.g., Lebreton et al. 1992). Recent advances in capture-recapture approaches have provided new opportunities for estimating movement parameters (e.g., Nichols 1996), which were difficult to estimate in the past. We suggest that more emphasis be placed on estimating vital rates needed to parameterize a matrix model, rather than rushing to conduct a matrix analysis that may provide misleading results. We recognize, however, that appropriately parameterizing a matrix model is a challenging task. Even in a data set as rich as that for the snow goose, some parameters were not rigorously estimated.

It is less clear how demographic stochasticity should be included in sensitivity analysis, especially if the analysis is performed on a different population than the one from which vital rates were estimated. If the population being analyzed is small, and expected to remain small, demographic stochasticity should probably be considered a form of process variation (Lande 1998). If the sampled population from which vital rates are estimated is much smaller than the target population to which modeling will be applied, however, demographic stochasticity in the small population should not be included as process variation in the large population, where demographic stochasticity is unlikely to manifest. Sæther et al. (1998) and Sæther and Engen (chap. 10 in this volume) describe a way to separate demographic from environmental stochasticity.

After process variation is estimated, it can be modeled in a sensitivity analysis. Asymptotic models that account for variation, including LTRE and LSA, properly model only spatial variability, not temporal variability, as process variation. In our snow goose example we used data from one population over 12 years, so that all of the process variation was attributable to temporal variation. By using an approach that depends on asymptotic properties, we must assume that changes in different rates would be constant long enough for the population to reach a SAD. This assumption is probably a stretch, but at least focuses on process variation alone, without being confounded by sampling variation. It remains to be seen how important the violation of this assumption is for the kinds of analyses explored in this work (Citta et al. n.d.).

Finally, our case study does not consider specific management

scenarios (Rockwell et al. 1997) nor does it directly address how easy it is, logistically or politically, to change certain rates. This becomes critical when evaluating management alternatives using sensitivity analysis, because we must evaluate not only how changes will affect population growth or persistence, but also how likely those changes are to occur. There is not yet a formal protocol for linking sensitivity analysis with the ability to change different rates, but certainly many investigators have performed sensitivity analyses with an eye toward management possibilities (see for example McKelvey et al. 1993; Lindenmayer and Possingham 1996; Silvertown et al. 1996; Akçakaya and Raphael 1998; Martien et al. 1999). There may be some utility in linking sensitivity analysis with formal decision analysis (Ralls and Starfield 1995). We did not consider management alternatives in our snow goose analysis, but we suggest that the issues we raise—type of variation and connectivity—should be considered in management scenarios evaluated with sensitivity analysis.

DISCUSSION

Sensitivity analysis is critical to understanding population dynamics. In the spirit of this volume of papers, it is an essential extension of PVA because it analyzes what particular actions are most likely to change the population trajectory of the species of interest. Sensitivity analysis is not limited to single-population studies, but can also give useful insights that go to the heart of metapopulation analysis: whether among- versus within-population vital rates are more important to persistence of the metapopulation (see also Wootton and Bell 1992; Hitchcock and Gratto-Trevor 1997). The scale of analysis, or which populations to include and which to properly apply inferences to, remains critically important (Doak et al. 1992; Donovan et al. 1995).

An array of sensitivity analysis approaches is now available, with a range of data requirements and assumptions. Deterministic manual perturbation analysis and analytical elasticities require the least data, but may be more limited for providing insights into future management options because they do not account for variation in vital rates. Stochastic or PVA-based manual perturbation analyses relax nearly all assumptions, but consequently require the estimation of many more parameters. For example, PVA-based approaches do not have to assume asymptotic properties, but if SAD is not assumed, an initial stage distribution must be determined (e.g., we did not have field-based stage distributions even for the well-studied La Pérouse snow goose population!). Of course, parameters that are unknown can and should themselves be considered the targets of sensitivity analysis, but at some point the uncertainty be-

comes overwhelming. In contrast to PVA-based approaches, LTRE and LSA are, respectively, analytical and simulation-based approaches that use changes in asymptotic population growth rate instead of changes in extinction or quasi-extinction probability. Again, the “best” sensitivity analysis technique will depend on what data are available and what are the most meaningful conservation scenarios.

Caswell (1997, 2000) and Horvitz et al. (1997) make the distinction between prospective and retrospective analysis. Under this artificial dichotomy, elasticities are considered prospective, because they quantify the expected change in growth rate given a specified infinitesimal change in mean vital rates or matrix elements; LTRE and LSA approaches are considered retrospective, because they embrace variation that has occurred in the past. Distinguishing between prospective and retrospective analysis would be useful if it were based on clarifying whether assumptions and inferences are based on potential future changes (i.e., prospective) versus changes that actually have occurred (i.e., retrospective). In strong contrast to the recommendations of Caswell (1997, 2000), however, we do not believe the distinction between retrospective and prospective should hinge purely on whether variation is included in the sensitivity analysis (see also Mills et al. 2001). Any projection into the future is based on both what we know about the past and what we expect in the future, in terms of mean rates, variances, and relationships among parameters. From a conservation decision-making perspective, such projections into the future, inherent in both applied sensitivity analyses and PVA, use information from the past coupled with the changes that are thought to be biologically, politically, and logistically possible under management in the future. These future changes may or may not be very different from changes in the past (Citta and Mills 1999). The LSA technique was developed specifically to avoid the dichotomy of prospective versus retrospective analyses (Wisdom et al. 2000). Instead of implying that mean rates are reliable measures of future dynamics while variances are not, a constructive way forward would be to make explicit whether variation is included in the sensitivity analysis, where the estimates of variation and mean rates are derived, and the rationale for potential future changes in vital rates (Mills et al. 2001).

Obtaining estimates of vital rates, interactions among rates, and variation within rates is not trivial and requires more attention. Indices as opposed to estimates of survival, reproduction, or connectivity are problematic because they may be biased, and because process and sampling variation of indices cannot easily be separated. Recent analytical approaches allow for rigorous estimation of both survival and movement rates that could be used to parameterize matrix models (Lebreton 1992;

Nichols et al. 1992; Brownie et al. 1993). If mark-recapture data are available, Nichols et al. (2000) propose a powerful approach for directly estimating both population growth and sensitivities of vital rates from the data, without assumptions of asymptotic population growth. We believe that this approach has much potential.

Sensitivity analysis is now at a pivotal point. The analytical equations and simulation models are in place to give profound insights to conservation practitioners, but analysis requires data on parameters that are challenging to estimate, especially in a fashion rigorous enough to remove sampling variation. Thus, sensitivity analysis provides an exciting juncture where field biology, biometry, and population analysis converge to provide new insights into populations of concern. A profitable next step would include adaptive management approaches that implement actions or field research based on predictions from sensitivity analysis, monitor the actual impacts, and use that information to refine the models.

LITERATURE CITED

- Abraham, K. F., and R. L. Jefferies. 1997. High goose populations: causes, impacts, and implications. Pages 7–72 in B. D. J. Batt, editor, *Arctic ecosystems in peril: report of the Arctic goose habitat working group*. Arctic Goose Joint Venture Special Publication. U.S. Fish and Wildlife Service, Washington, D.C.; Canadian Wildlife Service, Ottawa, Ontario.
- Akçakaya, H. R., and B. Baur. 1996. Effects of population subdivision and catastrophes on the persistence of a land snail metapopulation. *Oecologia* 105:475–483.
- Akçakaya, H. R., and M. G. Raphael. 1998. Assessing human impact despite uncertainty: viability of the northern spotted owl metapopulation in the northwestern USA. *Biodiversity and Conservation* 7:875–894.
- Batt, B. D. J., editor. 1997. *Arctic ecosystems in peril: report of the Arctic goose habitat working group*. Arctic Goose Joint Venture Special Publication. U.S. Fish and Wildlife Service, Washington, D.C.; Canadian Wildlife Service, Ottawa, Ontario.
- Beier, P. 1993. Determining minimum habitat areas and habitat corridors for cougars. *Conservation Biology* 7:94–108.
- Beissinger, S. R. 1995. Modeling extinction in periodic environments: Everglades water levels and snail kite population viability. *Ecological Applications* 5:618–631.
- Beissinger, S. R., and M. I. Westphal. 1998. On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management* 62:821–841.
- Benton, T. G., and A. Grant. 1996. How to keep fit in the real world: elasticity analyses and selection pressures on life histories in a variable environment. *American Naturalist* 147:115–139.
- Brault, S., and H. Caswell. 1993. Pod-specific demography of killer whales (*Orcinus orca*). *Ecology* 74:1444–1454.
- Brownie, C., J. E. Hines, J. D. Nichols, K. H. Pollock, and J. B. Hestbeck. 1993. Capture-recapture studies for multiple strata including non-Markovian transitions. *Biometrics* 49:1173–1187.
- Burbidge, A. A., and N. L. McKenzie. 1989. Patterns in the modern decline of western Australia's vertebrate fauna: causes and conservation implications. *Biological Conservation* 50:143–198.
- Burgman, M. A., S. Ferson, and H. R. Akçakaya. 1993. *Risk assessment in conservation biology*. Chapman and Hall, New York, New York.
- Burnham, K. P. 1993. A theory for combined analysis of ring recovery and recapture data. Pages 199–213 in J.-D. Lebreton and P. M. North, editors, *Marked individuals in the study of bird population*. Birkhäuser Verlag, Basel, Switzerland.
- Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and K. H. Pollock. 1987. Design and analysis methods for fish survival experiments based on release-recapture. American Fisheries Society Monograph no. 5. American Fisheries Society, Bethesda, Maryland.
- Caswell, H. 1989a. Analysis of life table response experiments: 1, decomposition of effects on population growth rate. *Ecological Modelling* 46:221–237.
- . 1989b. *Matrix population models*. Sinauer Associates, Sunderland, Massachusetts.
- . 1996a. Analysis of life table response experiments: 2, alternative parameterizations for size- and stage-structured models. *Ecological Modelling* 88:73–82.
- . 1996b. Second derivatives of population growth rate: calculation and applications. *Ecology* 77:870–879.
- . 1997. Matrix methods for population analysis. Pages 19–58 in S. Tuljapurkar and H. Caswell, editors, *Structured-population models in marine, terrestrial, and freshwater systems*. Chapman and Hall, New York, New York.
- . 2000. Prospective and retrospective perturbation analyses: their roles in conservation biology. *Ecology* 81:619–627.
- Caswell, H., S. Brault, A. J. Read, and T. D. Smith. 1998. Harbor porpoise and fisheries: an uncertainty analysis of incidental mortality. *Ecological Applications* 8:1226–1238.
- Caswell, H., and M. C. Trevisan. 1994. The sensitivity analysis of periodic matrix models. *Ecology* 75:1299–1303.
- Caughley, G. 1977. *Analysis of vertebrate populations*. John Wiley and Sons, New York, New York.
- Citta, J. J., and L. S. Mills. 1999. What do demographic sensitivity analyses tell us about controlling brown-headed cowbirds? *Studies in Avian Biology* 18:121–134.
- Citta, J., L. S. Mills, and M. Lindberg. N.d. An experimental field test of sensitivity analysis models. Manuscript.
- Cole, L. C. 1954. The population consequences of life history phenomena. *Quarterly Review of Biology* 29:103–137.
- Conroy, M. J., Y. Cohen, F. C. James, Y. G. Matsinos, and B. A. Maurer. 1995. Parameter estimation, reliability, and model improvement for spatially explicit models of animal populations. *Ecological Applications* 5:17–19.

- Cooch, E. G., R. F. Rockwell, and S. Brault. 2001. Retrospective analysis of demographic response to environmental change: an example in the lesser snow goose. *Ecological Monographs*. In press.
- Cooke, F., R. F. Rockwell, and D. B. Lank. 1995. *The snow geese of La Pérouse Bay: natural selection in the wild*. Oxford University Press, New York, New York.
- Crooks, K. R., M. A. Sanjayan, and D. F. Doak. 1998. New insights on cheetah conservation through demographic modeling. *Conservation Biology* 12:889–895.
- Cross, P. C., and S. R. Beissinger. 2001. Using logistic regression to analyze sensitivity of PVA models: a comparison of methods based on African wild dog models. *Conservation Biology* 15:1335–1346.
- Crouse, D. T., L. B. Crowder, and H. Caswell. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. *Ecology* 68:1412–1423.
- Crowder, L. B., D. T. Crouse, S. S. Heppell, and T. H. Martin. 1994. Predicting the impact of turtle excluder devices on loggerhead sea turtle populations. *Ecological Applications* 4:437–445.
- de Kroon, H., A. Plaisier, J. van Groenendael, and H. Caswell. 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. *Ecology* 67:1427–1431.
- de Kroon, H., J. van Groenendael, and J. Ehrlén. 2000. Elasticities: a review of methods and model limitations. *Ecology* 81:607–618.
- Dixon, P., N. Friday, P. Ang, S. Heppell, and M. Kshatriya. 1997. Sensitivity analysis of structured-population models for management and conservation. Pages 471–514 in S. Tuljapurkar and H. Caswell, editors, *Structured-population models in marine, terrestrial, and freshwater systems*. Chapman and Hall, New York, New York.
- Doak, D. F., P. M. Kareiva, and B. Klepetka. 1994. Modeling population viability for the desert tortoise in the western Mojave Desert. *Ecological Applications* 4:446–460.
- Doak, D. F., P. C. Marino, and P. M. Kareiva. 1992. Spatial scale mediates the influence of habitat fragmentation on dispersal success: implications for conservation. *Theoretical Population Biology* 41:315–336.
- Donovan, T. M., R. H. Lamberson, A. Kimber, F. R. Thompson III, and J. Faaborg. 1995. Modeling the effects of habitat fragmentation on source and sink demography of neotropical migrant birds. *Conservation Biology* 9:1396–1407.
- Drechsler, M. 1998. Sensitivity analysis of complex models. *Biological Conservation* 86:401–412.
- Dunning, J. B., Jr., D. J. Stewart, B. J. Danielson, B. R. Noon, T. L. Root, R. H. Lamberson, and E. E. Stevens. 1995. Spatially explicit population models: current forms and future uses. *Ecological Applications* 5:3–11.
- Ehrlén, J., and J. M. van Groenendael. 1998. Direct perturbation analysis for better conservation. *Conservation Biology* 12:470–474.
- Fahrig, L., and J. Paloheimo. 1988. Determinants of local population size in patchy habitats. *Theoretical Population Biology* 34:194–213.
- Fowler, C. W., and T. Smith. 1973. Characterizing stable populations: an application to the African elephant population. *Journal of Wildlife Management* 37:513–523.
- Gaillard, J.-M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology and Evolution* 13:58–63.
- Goodman, L. A. 1971. On the sensitivity of the intrinsic growth rate to changes in the age-specific birth and death rates. *Theoretical Population Biology* 2:339–354.
- Gould, W. R., and J. D. Nichols. 1998. Estimation of temporal variability of survival in animal populations. *Ecology* 79:2531–2538.
- Grand, J., and S. R. Beissinger. 1997. When relocation of loggerhead sea turtle (*Caretta caretta*) nests becomes a useful strategy. *Journal of Herpetology* 31:428–434.
- Grant, A., and T. G. Benton. 2000. Elasticity analysis for density dependent populations in stochastic environments. *Ecology* 81:680–693.
- Harrison, S. 1994. Metapopulations and conservation. Pages 111–128 in P. J. Edwards, R. M. May, and N. R. Webb, editors, *Large-scale ecology and conservation ecology*. Blackwell Scientific, Oxford, United Kingdom.
- Heppell, S. S., J. R. Walters, and L. R. Crowder. 1994. Evaluating management alternatives for red-cockaded woodpeckers: a modeling approach. *Journal of Wildlife Management* 58:479–487.
- Hitchcock, C. L., and C. Gratto-Trevor. 1997. Diagnosing a shorebird local population decline with a stage-structured population model. *Ecology* 78:522–534.
- Hoekman, S. T., L. S. Mills, D. W. Howerter, J. H. Devries, and I. J. Ball. 2000. Sensitivity analysis of the life cycle of mid-continent mallards. Manuscript.
- Horvitz, C. C., D. W. Schemske, and H. Caswell. 1997. The relative “importance” of life-history stages to population growth: prospective and retrospective approaches. Pages 247–272 in S. Tuljapurkar and H. Caswell, editors, *Structured-population models in marine, terrestrial, and freshwater systems*. Chapman and Hall, New York, New York.
- Lande, R. 1998. Demographic stochasticity and Allee effect on a scale with isotropic noise. *Oikos* 83:353–358.
- Lebreton, J.-D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67–118.
- Lefkovich, L. P., and L. Fahrig. 1985. Spatial characteristics of habitat patches and population survival. *Ecological Modelling* 30:297–308.
- Levin, L., H. Caswell, T. Bridges, C. DiBacco, D. Cabrera, and G. Plaia. 1996. Demographic responses of estuarine polychaetes to pollutants: life table response experiments. *Ecological Applications* 6:1295–1313.
- Lindenmayer, D. B., and R. C. Lacy. 1995. Metapopulation viability of arboreal marsupials in fragmented old-growth forests: comparison among species. *Ecological Applications* 5:183–199.
- Lindenmayer, D. B., and H. P. Possingham. 1996. Ranking conservation and timber management options for Leadbeater’s possum in southeastern Australia using population viability analysis. *Conservation Biology* 10:235–251.
- Link, W. A., and J. D. Nichols. 1994. On the importance of sampling variance to investigations of temporal variation in animal population size. *Oikos* 69:539–544.
- Liu, J., J. B. Dunning Jr., and H. R. Pulliam. 1995. Potential effects of a forest management plan on Bachman’s sparrows (*Aimophila aestivalis*): linking a spatially explicit model with GIS. *Conservation Biology* 9:62–75.

- Ludwig, D. 1999. Is it meaningful to estimate a probability of extinction? *Ecology* 80:298–310.
- Maguire, L. A., G. F. Wilhere, and Q. Dong. 1995. Population viability analysis for red-cockaded woodpeckers in the Georgia Piedmont. *Journal of Wildlife Management* 59:533–542.
- Marmontel, M., S. R. Humphrey, and T. J. O'Shea. 1997. Population viability analysis of the Florida manatee (*Trichechus manatus latirostris*), 1976–1991. *Conservation Biology* 11:467–481.
- Martien, K. K., B. L. Taylor, E. Slooten, and S. Dawson. 1999. A sensitivity analysis to guide research and management for Hector's dolphin. *Biological Conservation* 90:183–191.
- McCarthy, M. A., M. A. Burgman, and S. Ferson. 1995. Sensitivity analysis for models of population viability. *Biological Conservation* 73:93–100.
- McKelvey, K., B. R. Noon, and R. H. Lamberson. 1993. Conservation planning for species occupying fragmented landscapes: the case of the northern spotted owl. Pages 424–450 in P. M. Kareiva, J. G. Kingsolver, and R. B. Huey, editors, *Biotic interactions and global change*. Sinauer Associates, Sunderland, Massachusetts.
- Mertz, D. B. 1971. The mathematical demography of the California condor population. *American Naturalist* 105:437–453.
- Mesterton-Gibbons, M. 1993. Why demographic elasticities sum to one: a postscript to de Kroon et al. *Ecology* 74:2467–2468.
- Mills, L. S., D. F. Doak, and M. J. Wisdom. 1999. Reliability of conservation actions based on elasticity analysis of matrix models. *Conservation Biology* 13:815–829.
- . 2001. Elasticity analysis for conservation decision making: Reply to Ehrlén et al. *Conservation Biology* 15:281–283.
- Mills, L. S., S. G. Hayes, C. Baldwin, M. J. Wisdom, J. Citta, D. J. Mattson, and K. Murphy. 1996. Factors leading to different viability predictions for a grizzly bear data set. *Conservation Biology* 10:863–873.
- Nelson, L. J., and J. M. Peek. 1982. Effect of survival and fecundity on rate of increase of elk. *Journal of Wildlife Management* 46:535–540.
- Nichols, J. D. 1996. Sources of variation in migratory movements of animal populations: statistical inference and a selective review of empirical results for birds. Pages 147–197 in O. E. Rhodes Jr., R. K. Chesser, and M. H. Smith, editors, *Population dynamics in ecological space and time*. University of Chicago Press, Chicago, Illinois.
- Nichols, J. D., J. E. Hines, J.-D. Lebreton, and R. Pradel. 2000. Estimation of contributions to population growth: a reverse-time capture-recapture approach. *Ecology* 81:3362–3377.
- Nichols, J. D., J. R. Sauer, K. H. Pollock, and J. B. Hestbeck. 1992. Estimating transition probabilities for stage-based population projection matrices using capture-recapture data. *Ecology* 73:306–312.
- Olmsted, I., and E. R. Alvarez-Buylla. 1995. Sustainable harvesting of tropical trees: demography and matrix models of two palm species in Mexico. *Ecological Applications* 5:484–500.
- Pfister, C. A. 1998. Patterns of variance in stage-structured populations: evolutionary predictions and ecological implications. *Proceedings of the National Academy of Sciences (USA)* 95:213–218.
- Pulliam, H. R., J. B. Dunning Jr., and J. Liu. 1992. Population dynamics in complex landscapes: a case study. *Ecological Applications* 2:165–177.
- Ralls, K., and A. M. Starfield. 1995. Choosing a management strategy: two structured decision-making methods for evaluating the predictions of stochastic simulation models. *Conservation Biology* 9:175–181.
- Ringsby, T. H., B.-E. Sæther, R. Altwegg, and E. J. Solberg. 1999. Temporal and spatial variation in survival rates of a house sparrow, *Passer domesticus*, meta-population. *Oikos* 85:419–425.
- Rockwell, R. F., E. Cooch, and S. Brault. 1997. Dynamics of the mid-continent population of lesser snow geese: projected impacts of reduction in survival and fertility on population growth rates. Pages 73–100 in B. D. J. Batt, editor, *Arctic ecosystems in peril: report of the Arctic goose habitat working group*. Arctic Goose Joint Venture Special Publication. U.S. Fish and Wildlife Service, Washington, D.C.; Canadian Wildlife Service, Ottawa, Ontario.
- Ruckelshaus, M., C. Hartway, and P. Kareiva. 1999. Dispersal and landscape errors in spatially explicit population models: a reply. *Conservation Biology* 13:1223–1224.
- Sæther, B.-E., S. Engen, A. Islam, R. McCleery, and C. Perrins. 1998. Environmental stochasticity and extinction risk in a population of a small songbird, the great tit. *American Naturalist* 151:441–450.
- Schmutz, J. A., R. F. Rockwell, and M. R. Petersen. 1997. Relative effects of survival and reproduction on the population dynamics of emperor geese. *Journal of Wildlife Management* 61:191–201.
- Shea, K., and D. Kelly. 1998. Estimating biocontrol agent impact with matrix models: *Carduus nutans* in New Zealand. *Ecological Applications* 8:824–832.
- Silvertown, J., M. Franco, and E. Menges. 1996. Interpretation of elasticity matrices as an aid to the management of plant populations for conservation. *Conservation Biology* 10:591–597.
- Skalski, J. R., and Robson, D. S. 1992. *Techniques for wildlife investigations: design and analysis of capture data*. Academic Press, San Diego, California.
- Snedecor, G. W., and W. G. Cochran. 1980. *Statistical methods*. 7th edition. Iowa State University Press, Ames, Iowa.
- South, A. 1999. Dispersal in spatially explicit population models. *Conservation Biology* 13:1039–1046.
- Thompson, W. L., G. C. White, and C. Gowan. 1998. *Monitoring vertebrate populations*. Academic Press, San Diego, California.
- Tuljapurkar, S. 1990. *Population dynamics in variable environments*. Springer-Verlag, New York, New York.
- . 1997. Stochastic matrix models. Pages 59–88 in S. Tuljapurkar and H. Caswell, editors, *Structured-population models in marine, terrestrial, and freshwater systems*. Chapman and Hall, New York, New York.
- Tuljapurkar, S., and H. Caswell. 1997. *Structured-population models in marine, terrestrial, and freshwater systems*. Chapman and Hall, New York, New York.
- van Tienderen, P. H. 1995. Life cycle trade-offs in matrix population models. *Ecology* 76:2482–2489.
- Wisdom, M. J., and L. S. Mills. 1997. Sensitivity analysis to guide population recovery: prairie-chickens as an example. *Journal of Wildlife Management* 61:302–312.

- Wisdom, M. J., L. S. Mills, and D. F. Doak. 2000. Life-stage simulation analysis: estimating vital-rate effects on population growth for conservation. *Ecology* 81: 628–641.
- Wootton, J. T., and D. A. Bell. 1992. A metapopulation model for the peregrine falcon in California: viability and management strategies. *Ecological Applications* 2:307–321.