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PROSPECTIVE AND RETROSPECTIVE PERTURBATION ANALYSES: THEIR ROLES IN CONSERVATION BIOLOGY

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Abstract. Demographic perturbation analysis explores how population statistics (especially population growth rate λ) respond to changes in the vital rates (survival, growth, development, reproduction, and so on). Perturbation analysis is used in two logically distinct ways. *Prospective* analyses (sensitivity and elasticity) explore the functional dependence of λ on the vital rates. They predict the changes in λ that would result from any specified change in the vital rates and are independent of previous patterns of variability of the vital rates. *Retrospective* analyses (life table response experiment [LTRE] methods and other kinds of variance decomposition) express observed variation in λ as a function of observed (co)variation in the vital rates. Their results are specific to the observed pattern of variation. Sensitivity and elasticity analysis can be used to identify potential management targets because changes in vital rates with high sensitivity or elasticity will produce large changes in λ. Sometimes that potential may not be realized because it is difficult or impossible to change those vital rates. Retrospective analyses cannot identify potential management targets because they compare the contributions of past changes in vital rates, not the effects of future changes. Just as the results of heritability analysis say nothing about the efficacy of clinical treatments, so the results of retrospective analysis say nothing about the efficacy of potential management tactics. Perturbation analysis is a powerful tool with important implications for conservation. It is important that perturbation analyses be applied properly.

Key words: conservation biology; elasticity analysis; life table response experiments; matrix population models; population growth rate; sensitivity analysis.

SPECIAL FEATURE

INTRODUCTION

Demographic perturbation analysis asks how population statistics respond to changes in the vital rates (a collective term for rates of survival, growth, development, reproduction, and so on; some vital rates appear as projection matrix entries, others as lower level parameters that determine matrix entries [Caswell 1989*a*]). One of the most important of these statistics is the asymptotic population growth rate λ (or $r = \log \lambda$). If the vital rates are incorporated into a population projection matrix $\mathbf{A}$, then λ is the dominant eigenvalue of $\mathbf{A}$. Twenty years ago a simple formula was presented for the sensitivity of λ to changes in the stage-specific vital rates (Caswell 1978). Since then, many new analytical developments have appeared, including life-cycle graph analyses (Hubbell and Werner 1979, Caswell 1982), eigenvector sensitivities (Caswell 1980, 1989*a*), transient sensitivities (Caswell 1989*a*), elasticities (Caswell et al. 1984, de Kroon et al. 1986, Mesterton-Gibbons 1993), second derivatives of λ (Caswell 1996*a*), and loop analysis (van Groenendael et al. 1994, Wardle 1998). Perturbation analyses have been extended to periodic models (Caswell and Trevisan 1994), stochastic models (Tuljapurkar 1990, Benton and Grant 1996, Dixon et al. 1997, Caswell 2000), and density-dependent models (Takada and Nakajima 1992, 1996, 1998, Grant 1997, Grant and Benton 2000).

As a result, perturbation analysis is now a standard tool in demography. It has been widely applied to evolutionary life history theory (Roff 1992, Stearns 1992), to quantifying uncertainty in parameter estimates, to comparing the effects of potential management strategies, and to figuring out why λ changes in response to environmental factors.

Perturbation analysis is used in two logically distinct ways. They employ different methods, require different interpretations, and are useful in different contexts. But the distinction between them is subtle, and has been overlooked in some of the recent literature. In an attempt to clarify the situation, I introduced the terms "prospective" and "retrospective" to distinguish the two approaches (Caswell 1997, Horvitz et al. 1997). My goal here is to explore this distinction and show why it is important in conservation biology. I will focus on linear deterministic models, and on λ as a demographic statistic, but my conclusions also apply to other dependent variables, and to stochastic and density-dependent models.

PROSPECTIVE AND RETROSPECTIVE ANALYSIS

Population growth rate λ is a function of the vital rates. *Prospective analyses* explore this functional dependence. They look, as it were, forward, and ask how much λ would change in response to specified changes

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in one or more of the vital rates. The functional dependence of λ on the vital rates is a property of the life history, and is independent of any actual variation in those rates. Indeed, it can be used to calculate accurately the consequences of impossible changes (if pigs had wings; see Horvitz et al. 1997). Prospective analyses tell nothing about how the vital rates have varied in the past, are varying now, or might vary in the future, and knowledge of how the rates actually vary contributes nothing to prospective analyses.

Because prospective analyses project the consequences of future changes in the vital rates, they have become an important tool in life history theory (where the changes might result from natural selection) and conservation biology (where the changes might result from implementation of management tactics).

In contrast, *retrospective analyses* are not concerned with the functional dependence of λ on the vital rates. They express *variation in* λ as a function of *variation in* the vital rates. They look backwards, as it were, at observed variation in the vital rates, and ask how that variation expressed itself as variation in λ. If a vital rate did not vary, it can have made no contribution to the observed variation in λ, no matter what the functional dependence of λ on that rate. The results of a retrospective analysis are specific to the observed variation in the vital rates, and can be extrapolated to other situations only with great care.

Prospective and retrospective analyses rely on different kinds of data: the former on a single matrix from which λ can be calculated, the latter on a set of matrices from which the variance in λ can be calculated. (The fact that all demographic analyses begin with data, from which λ and everything else is computed, is not relevant. The distinction between prospective and retrospective analyses is not whether they depend on the values of the vital rates, but whether they depend on variability in those values.)

Tools for Prospective Analysis

Powerful tools exist for both prospective and retrospective analysis (reviewed in Caswell [2000]). The population growth rate λ is given by the dominant eigenvalue of $\mathbf{A}$, and the stable stage distribution $\mathbf{w}$ and reproductive value vector $\mathbf{v}$ are the corresponding right and left eigenvectors. Without loss of generality, I will assume that the scalar product $\mathbf{v}^{\mathrm{T}}\mathbf{w} = 1$, where $\mathbf{v}^{\mathrm{T}}$ is the transpose of $\mathbf{v}$.

Suppose that the matrix $\mathbf{A}$ is perturbed to a new matrix $\mathbf{A} + d\mathbf{A}$, where $d\mathbf{A}$ is a matrix of perturbations (with no restriction on how many of the a_{ij} are perturbed). The effect on λ is the differential

$$d\lambda = \mathbf{v}^{\mathrm{T}}(d\mathbf{A})\mathbf{w}. \tag{1}$$

If only one entry, say a_{ij}, changes, the result is the sensitivity:

$$\frac{\partial\lambda}{\partial a_{ij}} = v_i w_j \tag{2}$$

(Caswell 1978, 1989*a*).

Imagine λ plotted as a multidimensional surface as a function of the a_{ij}. The sensitivity (Eq. 2) is the slope of this surface in the direction of changing a_{ij}, holding all the other entries constant. Sensitivity is a derivative, and is thus a local analysis, focusing on the neighborhood of the point in parameter space where $\mathbf{A}$ is evaluated. Since λ is not a linear function of the a_{ij}, the slope changes from one point on the surface to another.

If more than one rate is changed simultaneously, Eq. 1 shows how to compute the resulting change in λ; when written out, it says

$$d\lambda = \sum_{ij} v_i w_j da_{ij} \tag{3}$$

$$= \sum_{ij} \frac{\partial\lambda}{\partial a_{ij}} da_{ij}. \tag{4}$$

If some factor x affects many of the a_{ij} (e.g., temperature might affect growth rate of all size classes), then the total derivative of λ is

$$\frac{d\lambda}{dx} = \sum_{ij} \frac{\partial\lambda}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial x}. \tag{5}$$

Thus sensitivities can be used to compute the change in λ resulting from simultaneous changes in many of the vital rates.

The elasticity, or proportional sensitivity (Caswell et al. 1984, de Kroon et al. 1986) of λ is given by

$$e_{ij} = \frac{\partial \log\lambda}{\partial \log a_{ij}} \tag{6}$$

$$= \frac{a_{ij}}{\lambda} \frac{\partial\lambda}{\partial a_{ij}}. \tag{7}$$

Imagine a multidimensional surface plotting $\log\lambda$ as a function of the $\log a_{ij}$. The elasticity is the slope of this surface, in the direction of varying $\log a_{ij}$, holding all other variables fixed. It is also a local analysis.

Equal intervals on a logarithmic scale correspond to equal proportions on an arithmetic scale. Thus the elasticity gives the proportional change in λ caused by a proportional change in a_{ij}. This makes elasticity a popular way to compare the effects of changes in vital rates that are measured on different scales (e.g., survival, which is bounded by zero and one, and fertility, which may be arbitrarily large). However, sensitivities can equally be used for such comparisons. Elasticity analysis is often used to identify attractive targets for management interventions. This use is supported by the following simple argument. A management strategy is designed to change the vital rates. If it changes a rate to which the elasticity of λ is large, it will have a bigger impact on λ than if it changes, by the same proportion, a rate to which the elasticity of λ is small.

The most famous application is to the loggerhead sea turtle (Crouse et al. 1987, Crowder et al. 1994; see also Doak et al. [1994] and Heppell et al. [1994]).

Both sensitivities and elasticities are derivatives; their predictions of changes in λ become more accurate as the changes in the a_{ij} become smaller. Because λ is a nonlinear function of the a_{ij}, these derivatives cannot be expected to give accurate predictions of the result of large perturbations. In practice, however, λ is often close to linear (Caswell 1996*a*), and the elasticities and sensitivities do a remarkably good job of predicting the results of even moderately large perturbations. But, if one wants to avoid difficulties with large perturbations, numerical simulations are a valuable tool. One simply changes the entries in **A**, following a rule that tells how the different entries vary, and evaluates the resulting value of λ.

The calculation of sensitivities and elasticities depends only on **A**. The observed variability in the vital rates appears nowhere in Eqs. 1 or 7, so it has no influence on sensitivity or elasticity. The total derivatives, as in Eqs. 1 or 5, depend on the functional dependence of λ on all the a_{ij}, and on the local functional relationships among the a_{ij}. Van Tienderen (1995) calls these integrated sensitivities, although he emphasizes that only the name, and not the concept, is new. Covariances appear in his formulae, but only as estimates of slopes of functional relationships (i.e., as ratios of covariances to variances). As such, they are independent of observed variation, and van Tienderen quite rightly points out that the relationships can be estimated in other ways as well.

Tools for Retrospective Analysis

Retrospective analysis looks back at an observed pattern of variation in the vital rates and asks how that pattern has affected variation in λ. The factors causing the variation in the vital rates can be thought of, in very general terms, as "treatments" in an "experiment" (even if they are observational rather than manipulative). Powerful methods are available for such life table response experiments (LTREs; Levin et al. 1987, 1996, Caswell 1989*a*, *b*, 1996*b*, *c*, 1997, 2000, Silva et al. 1991, Walls et al. 1991, Brault and Caswell 1993, Horvitz et al. 1997). These papers contain methods specific to a variety of experimental designs (see especially Caswell 1996*b*), but here I will focus on a simple approach to variance decompositions in a random design (Brault and Caswell 1993; H. Caswell and P. Dixon, *unpublished results*).

Suppose that matrices $\mathbf{A}_1, \mathbf{A}_2, \ldots, \mathbf{A}_N$, have been observed under N different conditions (e.g., different locations, or different years, or different subpopulations). They yield a set of growth rates $\lambda_1, \lambda_2, \ldots, \lambda_N$. The variability in λ generated by this set of vital rates is characterized by the variance:

$$V(\lambda) = \frac{1}{N-1}\left[\sum_i \lambda_i^2 - \frac{(\Sigma_i \lambda_i)^2}{N}\right].$$

The goal of the analysis is to decompose $V(\lambda)$ into contributions from the variability in the vital rates. This is done by writing, to first order,

$$V(\lambda) \approx \sum_{i,j}\sum_{k,l} \mathrm{cov}(a_{ij}, a_{kl}) \frac{\partial\lambda}{\partial a_{ij}} \frac{\partial\lambda}{\partial a_{kl}} \tag{8}$$

$$= \sum_{ij} V(a_{ij}) \left(\frac{\partial\lambda}{\partial a_{ij}}\right)^2 + \sum_{ij\neq kl} \mathrm{cov}(a_{ij}, a_{kl}) \frac{\partial\lambda}{\partial a_{ij}} \frac{\partial\lambda}{\partial a_{kl}} \tag{9}$$

where cov denotes the covariance. Each of the terms in the summation is a contribution of the covariance between a pair of the vital rates to the variance in λ.

Some recent approaches to variance decomposition have left out the covariance terms and written

$$V(\lambda) \approx \sum_{ij} V(a_{ij}) \left(\frac{\partial\lambda}{\partial a_{ij}}\right)^2 \tag{10}$$

(Wisdom and Mills 1997, Ehrlén and van Groenendael 1998, Pfister 1998). This formula is incorrect unless the vital rates vary independently. In theoretical calculations it is sometimes necessary to assume independence for lack of a reasonable hypothesis about covariation (Caswell et al. 1998), but such assumptions should be made only when necessary and stated clearly. As far as data are concerned, every case examined to date includes prominent covariances among the vital rates, and in two of the three cases those covariances make large contributions to $V(\lambda)$ (Brault and Caswell 1993, Horvitz et al. 1997, and the examples shown below). Moreover, on strictly biological grounds, there is every reason to expect covariance among the vital rates. Positive covariances are expected when the vital rates of different stages are determined by the same biological mechanisms (e.g., a good location for growth of small plants is probably a good location for the growth of large plants). Negative covariances are expected when different stages are adapted to different conditions. Thus, in analyzing demographic data sets, in which the covariances are readily available, they should be incorporated into the variance decomposition. (Computational convenience is no reason to ignore covariances; given a set of matrices and a sensitivity matrix, it takes only three MATLAB commands to obtain the complete covariance and contribution matrices.)

Taking the square root of Eqs. 9 or 10 gives the standard deviation of λ. However, if we use Eq. 10 for simplicity, note that

$$\mathrm{SD}(\lambda) = \sqrt{\sum_{ij} V(a_{ij}) \left(\frac{\partial\lambda}{\partial a_{ij}}\right)^2} \tag{11}$$

$$\neq \sum_{ij} \mathrm{SD}(a_{ij}) \frac{\partial\lambda}{\partial a_{ij}}. \tag{12}$$

Ehrlén and van Groenendael (1998) propose a formula equivalent to Eq. 12 as a way to decompose the "variation" in λ into contributions. They do not say if they are thinking of variation in terms of $V(\lambda)$ or SD(λ), but clearly Eq. 12 gives neither.

The contributions to $V(\lambda)$ are made by *pairs* of matrix entries. Horvitz et al. (1997) suggested defining a summed contribution of each matrix entry as

$$\chi_{ij} = \sum_{k,l} \mathrm{cov}(a_{ij}, a_{kl}) \frac{\partial \lambda}{\partial a_{ij}} \frac{\partial \lambda}{\partial a_{kl}}. \quad (13)$$

This index sums the contributions of the variance in a_{ij} and all the covariances involving a_{ij}; half of the contribution of $\mathrm{cov}(a_{ij}, a_{kl})$ is allocated to $_{ij}$ and half to $_{kl}$. The value of $_{ij}$ may be positive or negative. If it is negative, it says that the observed pattern of variability involving a_{ij} acted to reduce $V(\lambda)$.

Retrospective Analysis Applied to Prospective Questions

The decomposition of variance is a retrospective analysis. The covariance terms in Eqs. 9 and 13 depend on a specific, observed, pattern of covariation in the vital rates. They show how $V(\lambda)$ was produced by that set of environments, but do not predict how λ will respond to future changes in the vital rates. Sensitivities and elasticities do make such predictions, because they describe the functional dependence of λ on the a_{ij}, regardless of how, or whether, a_{ij} varied in the past.

Recently a number of workers have tried to use retrospective analysis to answer the prospective question, "What will happen if we change the vital rates in this or that way?" An example is the recent study by Wisdom and Mills (1997) of the Prairie Chicken (*Tympanuchus cupido pinnatus*). Concerned with the recovery of the species, they wanted to know whether increasing nest success and brood survival were good management tactics.

To answer this question, they constructed an age-classified model, and obtained minimum and maximum estimates for each of the parameters from the literature. These ranges included both spatiotemporal variability and measurement uncertainty. They generated a large set of matrices by drawing each parameter independently from a uniform distribution over its minimum-to-maximum range. They regressed λ against each parameter individually, and calculated the coefficient of determination R^2 (i.e., the proportion of variance in λ explained by variation in that parameter).

So far, this is a somewhat laborious way to estimate the relationship in Eq. 9, with the covariances assumed to be zero and the sensitivities replaced by the slope of the regression line. However, when they found that the R^2 values for each parameter were only weakly correlated with the sum of all the elasticities involving that parameter, they concluded that elasticities are not a reliable guide to the effects of changes in the vital rates and that R^2 is a better indication of its potential value to management (Wisdom and Mills 1997: 310):

> *Thus if management relied exclusively on elasticity calculations to prioritize recovery efforts, one might assume that increasing the vital rates having the second or third highest elasticity would yield positive non-linear changes in λ (Caswell 1989[a]). This was not true when variance in the vital rates was considered . . . . [A] modeling process like that used here could help prioritize management or modeling efforts. This could be done by identifying those vital rates or life stages that presumably have greatest effect on λ . . . .*

But since the elasticities are independent of the particular pattern of variation in the vital rates, there is no reason to expect them to correlate with the contributions to variance generated by one particular pattern. Nor does an observed pattern of variation say anything about the effect of future changes in the vital rates. Thus, the contributions to $V(\lambda)$ will not in general identify management tactics that will yield large positive changes in λ. The effect of increasing a vital rate depends only on the functional relationship between that rate and λ, not on how that vital rate has varied in the past. Contrary to Wisdom and Mills' (1997) claim, increasing the vital rate with the second highest elasticity would indeed have yielded positive changes in λ. Retrospective analysis of past vital rate variation cannot predict the impact of future changes in the vital rates.

Two Examples

To demonstrate the difference between prospective and retrospective analyses, I will compare the patterns of elasticity and of contribution to $V(\lambda)$ in two plant populations. I will show that elasticity, and *not* the contribution to variance, successfully predicts the effects of changing vital rates.

The first example uses a set of 16 stage-classified matrices (seeds, seedlings, juveniles, pre-reproductives, and small, medium, large, and extra-large flowering plants) for *Calathea ovandensis,* a forest understory herb in Mexico. The matrices were obtained at four sites over four years by Horvitz and Schemske (1995). Perturbation analyses, both prospective and retrospective, can be found in Horvitz et al. (1997).

The second example is based on 17 stage-classified matrices for another perennial forest herb, *Lathyrus vernus* (Ehrlén 1995). Individuals were classified as seeds, dormant seeds, seedlings, very small, small, intermediate, or large plants. The 17 matrices were obtained at six sites, over three years, in Sweden. In each population, the environmental variability generated considerable variation in λ, as shown in Fig. 1.

Figs. 2 and 3 show the covariances among the a_{ij}, and the contributions of those covariances to $V(\lambda)$, for each population. There are large covariances among the vital rates. The most conspicuous aspect of the

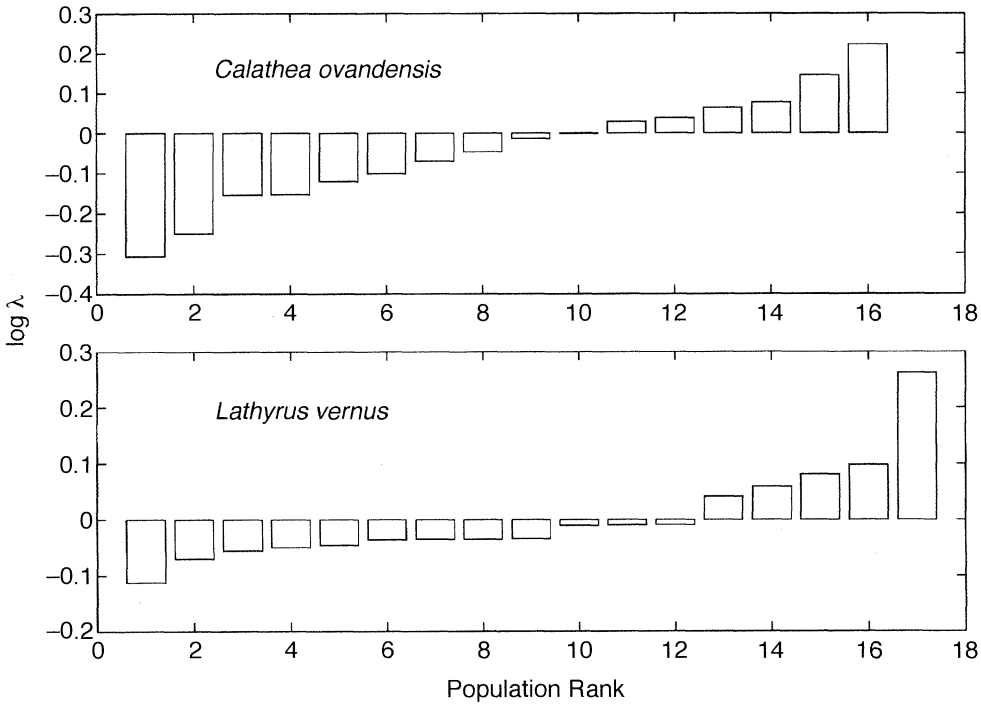

FIG. 1. The values of log λ for 16 populations of *Calathea ovandensis* (Horvitz and Schemske 1995) and 17 populations of *Lathyrus vernus* (Ehrlén 1995).

covariance surface for *C. ovandensis* is the positive values representing the variances in, and covariances among, the fertilities. In this sample of environments, a good year or a good location for fertility of one size class tends to be good for all size classes. The covariance surface for *L. vernus* is dominated by variance in, and covariance among, seed production by large plants and germination of dormant seeds.

Figs. 2 and 3 also show the contributions of the variances and covariances to $V(\lambda)$. It is apparent that the pattern of contributions is different from the pattern of covariances (because of the role of sensitivity) and that off-diagonal elements, corresponding to contributions from covariances, are prominent for both species.

In *C. ovandensis,* the largest contribution to variance in λ comes from the variance in a_{31}, the transition from seeds to juveniles. The large positive covariances among the fertilities make only a tiny contribution to $V(\lambda)$. In *L. vernus,* the largest contribution is from the variance in a_{65}, the growth from intermediate to large plants. There are also large contributions from the variances in a_{54} and a_{66} and from the covariance between a_{65} and a_{66}.

The elasticities are only weakly related to these contributions. Fig. 4 plots the summed contributions (χ_{ij}) against the elasticities e_{ij}. For each species, the vital rate with the highest elasticity (a_{55} for *C. ovandensis* and a_{44} for *L. vernus*) and that with the highest contribution to variance (a_{31} in *C. ovandensis* and a_{65} in *L. vernus*) are indicated. The vital rates with highest elasticities make negligible contributions to $V(\lambda)$.

Note that, in both species, the highest elasticities are for stasis of intermediate-sized plants, while the largest contribution to $V(\lambda)$ is in one case a growth rate and in the other a seed germination probability. The elasticities reflect the life histories (which happen to be similar for these two forest understory herbs) and the functional dependence of λ on the life history. The contributions to $V(\lambda)$ reflect the particular range of environments observed, which happen to be different.

Now suppose that a perturbation, such as might be produced by a management intervention, increases or decreases one of the vital rates. How much can the variance contributions tell about the effect of such changes? Not much. Fig. 4 compares the response of λ to changes (from −10% to +10%) in the vital rate with the highest elasticity and in the vital rate with the highest contribution to variance. (These curves were calculated by actually varying the matrix entries. That they are nearly linear shows how well the elasticity can predict the results of changes of even this relatively large magnitude.) In each species, the effect on λ of a change in the vital rate with high elasticity is large, even though its contribution to variance is small. If you, as a manager wanted to increase the growth rate of *C. ovandensis* or *L. vernus,* the message is clear.

DISCUSSION

Difficulties with prospective and retrospective analyses in demography are no surprise; the same issues

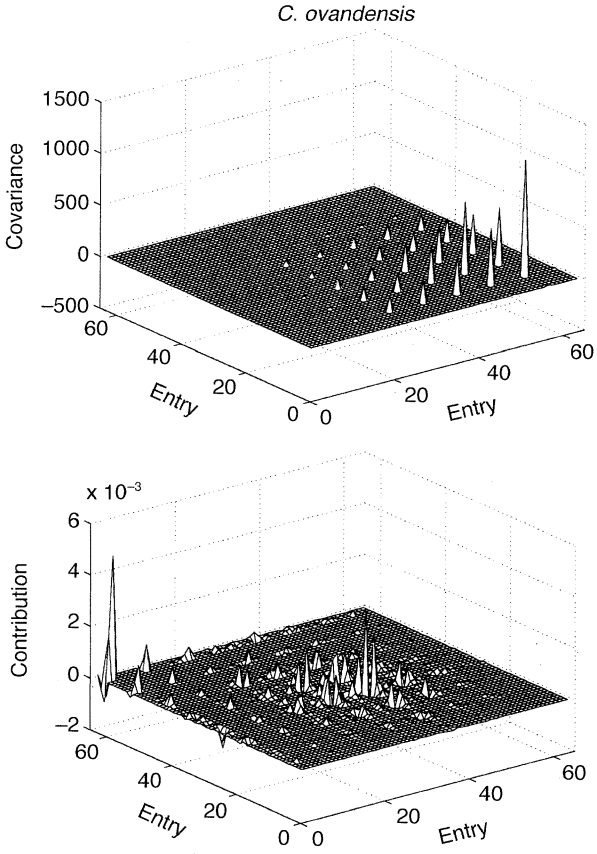

FIG. 2. The covariances of matrix entries, $\mathrm{cov}(a_{ij}, a_{kl})$, and the contributions of those covariances to the variance $V(\lambda)$ for *C. ovandensis*. The matrix entries are plotted in column order, i.e., the entries in the first column, followed by the second column, and so on.

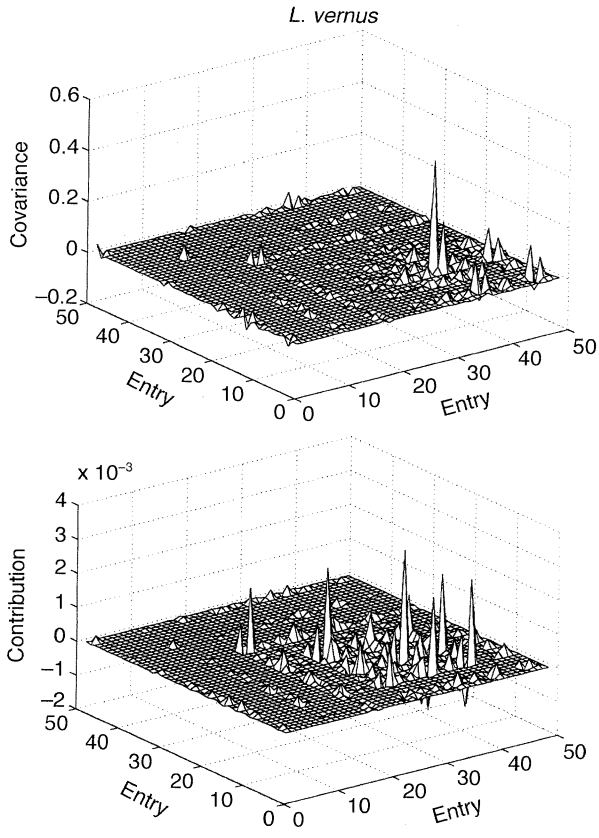

FIG. 3. The covariances of matrix entries, $\mathrm{cov}(a_{ij}, a_{kl})$, and the contributions of those covariances to the variance $V(\lambda)$ for *L. vernus*. The matrix entries are plotted in column order, i.e., the entries in the first column, followed by the second column, and so on.

have long plagued the interpretation of heritability in quantitative genetics. Heritability is the contribution of additive genetic variance to the total phenotypic variance. As a variance contribution, it is a retrospective calculation, specific to the population and the range of environments observed. Great controversy has been generated by the common mistake of interpreting heritability (e.g., of IQ) in a prospective sense, concluding that environmental interventions (e.g., education) cannot change traits with high heritability. Lewontin (1974) points out that this belief is erroneous:

> . . . *the fallacy is that a knowledge of the heritability of some trait in a population provides an index of the efficacy of environmental or clinical intervention in altering the trait.*

Lewontin (1974) also emphasized the same distinction between functional relationships and variance contributions that I am making here:

> . . . *[variance decomposition] is a local analysis. It gives a result that depends upon the actual distribution of genotypes and environments in the particular population sampled . . . and is not a statement about* functional *relations.*

Unlike geneticists, demographers have ready access to the functional relations between λ and the vital rates. Prospective analysis in genetics would require a theory connecting genotype and environment, through the developmental system, to the eventual phenotype. Despite many people's efforts, no such theory exists.

Prospective and Retrospective Analysis in Conservation Biology

The utility of prospective analyses, using sensitivity or elasticity, in conservation biology is clear. *If* you change a vital rate with a high elasticity by a given proportion, *then* you will change λ more than if you make the same proportional change in any rate with lower elasticity. Thus prospective analysis identifies the most effective potential targets for management interventions, if the goal of such intervention is to change λ.

Several recent papers have tried to apply retrospective analysis to conservation biology (Wisdom and Mills, 1997, Crooks et al. 1998, Ehrlén and van Gro-

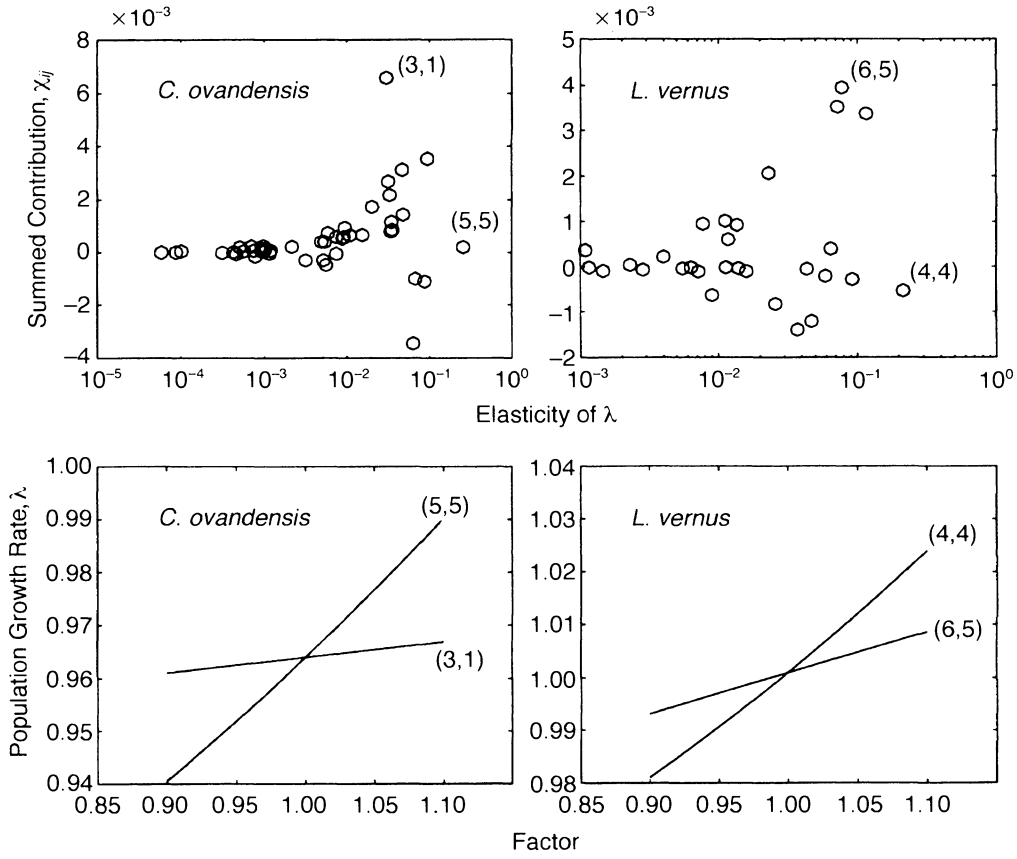

FIG. 4. Upper panels: the summed contributions χ_{ij} to the variance $V(\lambda)$ as a function of the elasticities e_{ij} of λ (note log scales for x-axes). The vital rates with the largest elasticities and the largest variance contributions are indicated. Lower panels: The effect on λ of changes (from -10% to $+10\%$) in the rate with the highest elasticity and the highest variance contribution.

enendael 1998). Careful study of these analyses convinces me that they are flawed.

Suppose some vital rate is under consideration as a management target. How should a conservation biologist interpret a retrospective calculation of the contribution of a vital rate to $V(\lambda)$? Wisdom and Mills (1997), as quoted above, believe that the contribution of a_{ij} to $V(\lambda)$ is a better guide to management than is the elasticity e_{ij}. Ehrlén and van Groenendael (1998) and Crooks et al. (1998) are more ambiguous, but seem to believe that the relative contributions to $V(\lambda)$ will show how likely it is that potential effects of a management intervention are actually realized.

Consider the following case. Suppose that a_{ij} is being considered as a target for management action. Suppose that the elasticity of λ to a_{ij} is large, so that a_{ij} is an attractive target, because all else being equal, a change in a_{ij} will have a big effect on λ. But suppose that a data set exists in which a_{ij} does not vary much, so that its variation makes only a small contribution to $V(\lambda)$. The implications of the small contribution of a_{ij} to $V(\lambda)$ depend on *why* a_{ij} does not vary much in the observations at hand.

On the one hand, a_{ij} might be physiologically or architecturally constrained; if so, it is a bad target for management, regardless of its elasticity, because it cannot be modified. Emperor penguins, for example, lay only a single egg. They hold it on top of their feet in the middle of the frigid antarctic winter. There is only room for one egg. Clutch size enlargement would be a poor target for penguin management, no matter what the elasticity of λ to clutch size, because it cannot be accomplished. But low variance in a_{ij} does not always make it a bad target. Suppose that a_{ij} was nesting success in a hole-nesting bird, and that the elasticity of λ to changes in nesting success was high (e.g., Heppell et al. 1994). Suppose that a_{ij} made only a small contribution to $V(\lambda)$ because the data for the retrospective analysis came from a forest with a fixed density of nesting holes. Improving nesting success would be an attractive option, if the manager knows how to increase the number of nesting cavities (by deploying nest boxes or drilling holes).

In these hypothetical examples, variance in penguin clutch size and in woodpecker nesting success both have low contributions to $V(\lambda)$. However, that fact does not define their potential as targets for management.

Similarly, vital rates with large contributions to $V(\lambda)$

may be unattractive targets for management. Recruitment in marine invertebrates and fishes, for example, is notoriously variable. I can imagine that it might make an overwhelming contribution to $V(\lambda)$ in some data set. But it might be an unattractive management target for management, because it is subject to so much environmental variability, due to so many impossible-to-control factors, that any management intervention would be swamped by environmental noise.

These examples prove that the contributions of the a_{ij} to $V(\lambda)$ by themselves say nothing about the merits of a_{ij} as a management target. In each example, the *potential* value of a_{ij} as a management target is revealed by the elasticity of λ to a_{ij} (the prospective question). Whether that potential can be realized is revealed, not by a retrospective analysis of variation, but by careful consideration of the biological mechanisms determining, and constraints limiting, the manager's ability to change the rate under consideration.

Suggesting that retrospective analyses can predict the effects of new management interventions obscures the demographic underpinnings of conservation biology and misleads managers confronted with difficult decisions about endangered species.

SPECIAL FEATURE

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