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# Reliability of Conservation Actions Based on Elasticity Analysis of Matrix Models

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**Abstract:** *Matrix population models have entered the mainstream of conservation biology, with analysis of proportional sensitivities (elasticity analysis) of demographic rates becoming important components of conservation decision making. We identify areas where management applications using elasticity analysis potentially conflict with the mathematical basis of the technique, and we use a hypothetical example and three real data sets (Prairie Chicken [*Tympanuchus cupido*], desert tortoise [*Gopherus agassizii*], and killer whale [*Orcinus orca*]) to evaluate the extent to which conservation recommendations based on elasticities might be misleading. First, changes in one demographic rate can change the qualitative ranking of the elasticity values calculated from a population matrix, a result that dampens enthusiasm for ranking conservation actions based solely on which rates have the highest elasticity values. Second, although elasticities often provide accurate predictions of future changes in population growth rate under management perturbations that are large or that affect more than one rate concurrently, concordance frequently fails when different rates vary by different amounts. In particular, when vital rates change to their high or low values observed in nature, predictions of future growth rate based on elasticities of a mean matrix can be misleading, even predicting population increase when the population growth rate actually declines following a perturbation. Elasticity measures will continue to be useful tools for applied ecologists, but they should be interpreted with considerable care. We suggest that studies using analytical elasticity analysis explicitly consider the range of variation possible for different rates and that simulation methods are a useful tool to this end.*

Confiabilidad de las Acciones de Conservación Basadas en Análisis de Elasticidad de Modelos de Matrices

**Resumen:** *Los modelos de matrices de poblaciones han incursionado en el medio de la biología de la conservación, con el análisis de sensibilidades proporcionales (análisis de elasticidad) de tasas demográficas volviéndose un componente importante del proceso de toma de decisiones en la conservación. Identificamos áreas donde las aplicaciones de manejo utilizando análisis de elasticidad potencialmente conflictúan con las bases matemáticas de la técnica y utilizamos un ejemplo hipotético y tres juegos de datos reales (la gallineta de pradera [*Tympanuchus cupido*], la tortuga del desierto [*Gopherus agassizii*] y la orca [*Orcinus orca*]) para evaluar la extensión a la cual las recomendaciones basadas en elasticidades pueden ser mal interpretadas. Primero, los cambios en una tasa demográfica pueden cambiar el valor de rangos de los valores de elasticidad calculados de una matriz poblacional, un resultado que empantana el entusiasmo por asignar rangos a acciones de conservación basados únicamente en las tasas que tienen los valores de elasticidad más altos. Segundo, aunque las elasticidades frecuentemente proveen predicciones precisas de cambios a futuro en las tasas de crecimiento poblacional bajo perturbaciones de manejo grandes o que afectan más que una tasa concurrente, la concordancia frecuentemente falla cuando tasas diferentes varían en diferentes cantidades. En particular, cuando las tasas vitales cambian a sus valores más altos o más bajos observados en la naturaleza, las predicciones de crecimiento a futuro basadas en elasticidades de una matriz promedio pueden conducir a errores, hasta llegar a predecirse un incremento cuando la tasa de crecimiento poblacional realmente disminuye después de una perturbación. Las medidas de elasticidad seguirán siendo herramientas*

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*muy útiles para la ecología aplicada, pero deberán ser interpretadas con extrema cautela. Sugerimos que los estudios que utilizan análisis de elasticidad explícitamente consideren el rango de variación posible para tasas diferentes y que los métodos de simulación son una herramienta útil para este fin.*

## Introduction

The use of mathematical tools to analyze population viability has increased rapidly over the last decade, and modeling efforts have focused on two overlapping goals: estimating extinction times or probabilities and targeting the best ways to improve population growth. For the latter goal, one of the most effective and popular tools is the analysis of matrix population models. Although matrix models can be used in many ways, most recent applications include the calculation of age- or stage-specific sensitivities or elasticities to indicate factors that most affect population growth (Caswell 1978; 1989a). These approaches have shown us that demographic vital rates differ in their effects on population growth and have become an elegant way to evaluate and prioritize conservation research and management (Wootton & Bell 1992; Crowder et al. 1994; Doak et al. 1994; Escos et al. 1994; Heppell et al. 1994; Olmsted & Alvarez-Buylla 1995; Marschall & Crowder 1996; Ratsirarson et al. 1996; Silvertown et al. 1996). Furthermore, these analyses of matrix models have served as the foundation for increasingly complex methods of exploring aspects of demographic change (van Groenendael et al. 1994; van Tienderen 1995; Caswell 1996; Horvitz et al. 1997).

Unfortunately, the precise mathematical definitions of sensitivities and elasticities are in sharp contrast to the ways these quantities are often used and interpreted in applied ecology. Many authors have noted the mismatch between the mathematical basis and potential interpretations of analytical sensitivity analyses for management (Crouse et al. 1987; Doak et al. 1994; Olmsted & Alvarez-Buylla 1995; Burgman et al. 1996; Horvitz et al. 1997; Wisdom & Mills 1997), but there remains a pressing need for a systematic evaluation of the extent to which these approaches provide robust predictions for conservation actions (Dixon et al. 1997; Ehrlén & van Groenendael 1998; Matos & Silva Matos 1998).

We investigated potential concerns arising from the mismatch between the definition and use of analytical sensitivity analysis by evaluating whether the most commonly used form of sensitivity analysis—elasticities—are robust in the same sense that many statistical tests are robust: can these metrics be used and interpreted with confidence over a wide range of realistic situations, even though their derivation relies upon narrow, restrictive definitions? To this end, we reviewed both the mathematical properties of analytical sensitivity analyses and

how ecologists use and interpret elasticities for conservation. We then used a simple hypothetical example to elucidate some of the potential problems in applying this technique to real-world situations. Finally, using data from field studies on three vertebrate taxa with different life histories, we explored the seriousness of these concerns for biologically realistic situations.

## Definitions and Common Use of Sensitivities and Elasticities

The sensitivity of a population's finite growth rate ( $\lambda$ ) to a change in matrix element  $a_{ij}$  is defined as the partial derivative of  $\lambda$  with respect to  $a_{ij}$  (Caswell 1978, 1989a):

$$\frac{\partial \lambda}{\partial a_{ij}} = \frac{v_i w_j}{\langle \mathbf{w}, \mathbf{v} \rangle},$$

where  $v_i$  and  $w_j$  refer to the  $i$ th and  $j$ th elements of the stage-specific reproductive value ( $\mathbf{v}$ ) and stable stage distribution ( $\mathbf{w}$ ) vectors, respectively, and where  $\langle \mathbf{w}, \mathbf{v} \rangle$  is the scalar product of  $\mathbf{w}$  and  $\mathbf{v}$ . The elasticity,  $e_{ij}$ , of  $\lambda$  to element  $a_{ij}$  is simply the sensitivity rescaled to account for the magnitude of both  $\lambda$  and the matrix element (Caswell 1989a):

$$e_{ij} = \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}}$$

Thus, elasticities predict the proportional change in growth rate given a proportional, infinitesimal change in a matrix element, while all other elements remain constant. The growth rate,  $\lambda$ , is the dominant eigenvalue of the matrix.

For many problems in applied ecology, it is not enough to focus on the sensitivities and elasticities of the matrix elements; rather, it is more appropriate to consider the actual vital rates that underlie each element (Wootton & Bell 1992; Brault & Caswell 1993; Doak et al. 1994). In stage-based models, for example, annual survival for most stages is not itself a matrix element but rather a part of at least two elements, that for surviving within a stage and that for surviving and growing to the next stage. Similarly, in age-based Leslie matrices, reproduction elements must contain some aspect of survival (Jenkins 1988; Caswell 1989a), so management for survival will affect not only survival but also reproduction. Using the chain rule, the elasticity of an underlying vital rate  $x$  can be expressed as (Caswell 1989a)

$$\frac{x \partial \lambda}{\lambda \partial x} = \frac{x}{\lambda} \sum_{i,j} \frac{\partial \lambda}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial x}.$$

Analogous approaches for calculating elasticities of underlying rates include small perturbations instead of analytical solutions (Crowder et al. 1994; Heppell et al. 1994) or rescaling the partial derivatives directly calculated from a matrix characteristic equation. (This method, however, is quite difficult for larger and more complicated matrices.)

Because elasticities are partial derivatives, they predict the effect on  $\lambda$  of infinitesimally small and linear changes. Elasticities of matrix elements can be added together to obtain combined effects of multiple changes in vital rates because their proportional nature means that the elasticities of all elements in a matrix sum to one (de Kroon et al. 1986; Mesterton-Gibbons 1993). Elasticities of component vital rates need not sum to one (Caswell 1989a:136) but may still be added to determine a relative net effect on  $\lambda$ .

Applications of elasticity analysis to conservation problems represent a laudable increase in quantitative approaches to management. In this case, however, the applications may not conform to the underlying mathematical assumptions. Elasticities, and consequent management recommendations, are usually calculated from a single population matrix constructed from average, or even "best guess" vital rates. The demographic rate in the mean matrix with the highest elasticity is then recommended for highest management or research priority, with correspondingly less emphasis recommended for management of low elasticity rates (Crowder et al. 1994; Heppell et al. 1994; Maguire et al. 1995; Olmsted & Alvarez-Buylla 1995). Similarly, specific changes in  $\lambda$ , or extinction probability, are inferred from each rate's sensitivity or elasticity, as implied by the mathematics (e.g., Doak et al. 1994; Escos et al. 1994). Finally, the joint consequence of management of multiple rates is often evaluated by adding elasticities to project change in growth rate (Kalisz & McPeck 1992; Silvertown et al. 1993, 1996; van Groenendael et al. 1994). Thus, in applying elasticities to population management, the presumption is that the instantaneous, one-change-at-a-time basis of the elasticity analysis will still give robust insights into the effects of larger, multiple changes in specific vital rates resulting from management of rare or endangered species.

The difference between the mathematical definitions and the conservation applications of elasticity analysis raises several potential concerns. It is not clear whether substantial changes in vital rates induced by management, measurement error, or natural spatial and temporal variation will yield new matrices with the same ranking of elasticities as the original. If not, the identification of optimal interventions will be complicated at best (Benton & Grant 1996). Even if the ranking of elasticities is unaffected, real changes in vital rates may result in population growth rates that are poorly predicted by the

infinitesimal perturbations assumed by the mathematics (for initial consideration of this problem see Caswell 1996). Both of these inferences—the stability of relative ranking of elasticities and their ability to predict change in population growth when vital rate changes are larger than infinitesimal—depend crucially on the linearity of responses of  $\lambda$  to changes in vital rates over the relevant range of values being considered.

When more than one rate changes simultaneously, as will typically be the case, the assumption of additivity of elasticities becomes critical for correct prediction of future growth rate. Also, even if effects are additive, different vital rates are likely to be highly correlated in their fluctuations due to life-history tradeoffs or common responses to environmental effects, which can also affect predictions of changes in growth rate based on summed elasticities (van Tienderen 1995).

A final concern has to do with the relationship between the sensitivity or elasticity of vital rates and the likely range of variation in these rates (Brault & Caswell 1993; Silvertown et al. 1996; Horvitz et al. 1997; Gaillard et al. 1998). Many studies using analytical sensitivity analysis focus exclusively on elasticities because they allow comparison of responses to a certain proportional change in demographic rates measured on different scales. Different vital rates, however, are not equally susceptible to change. The averages for some rates are closer to biological limits, for example, and some rates are simply less plastic in their response to environmental or management perturbations. Pfister (1998) has found that vital rates with low elasticities tend to have high variance, and Gaillard et al. (1998) notes that vital rates with high variation can have larger effects on population growth than rates with high elasticity. Given that there are rate-specific constraints, how well do elasticity values alone predict the effects on population growth of realistic changes in vital rates?

Several methods have been developed to deal with the problem of rate-specific range of variation and the correlation between variation in different rates. Probably the most common of these methods involves "life table response experiment" (LTRE) approaches (Caswell 1989b; Brault & Caswell 1993; Horvitz et al. 1997; Ehrlén & van Groenendael 1998). These methods lead to predictions of proportional change in  $\lambda$  based upon both elasticities of the changed rate and the proportional change in the rate. Although these extensions of sensitivity analysis can incorporate information on the amount, form, and correlations of changes in different vital rates, all incorporate the assumptions of linear, additive effects inherent in the use of elasticities. Thus, although they use more extensive data to overcome some problems of simple elasticity predictions, they may still be subject to some of the same potential limitations.

These concerns led us to use realistic matrix formulations to evaluate the following potential questions in the

application of sensitivity analysis to conservation and management (Fig. 1): (1) Will the ranking of elasticity values change qualitatively when vital rates undergo realistically large changes from their mean values? (2) Do elasticities accurately represent expected quantitative or qualitative changes in future population growth when realistically large or multiple changes occur in the mean matrix? (3) How robust are elasticity predictions (and therefore management recommendations) based on a mean matrix when vital rates have different constraints on their ability to change?

## A Hypothetical Example

Our hypothetical example explores these three questions in the context of conservation recommendations. Consider an organism whose demographic events are structured by age, although only two stages (juveniles and adults) are distinguishable in the field. Only adults breed, and reproduction is censused via a "pre-birth pulse" sample so that adult contribution to the juvenile cohort (fertility, or  $F$ ) incorporates both fecundity and survival through the first year to becoming a juvenile. Juveniles remain in the juvenile stage class for an average of  $T$  years. We used Caswell's (1989a:84) simplest ap-

proximation for partitioning annual juvenile survival ( $s_j$ ) into annual probabilities of surviving as juveniles versus surviving and becoming adults: the probability of growing out of the juvenile stage and becoming adults is a constant ( $1/T$ ). With these assumptions, juveniles can either survive to be adults with probability  $[(s_j)(1/T)]$  or survive and remain juvenile nonbreeders with probability  $(s_j)[1-(1/T)]$ . Adults have an annual survival probability of  $s_a$ . These life-history characteristics give the following population matrix:

$$\begin{bmatrix} (s_j)[1 - (1/T)] & F \\ s_j/T & s_a \end{bmatrix}$$

To make this scenario analogous to one of conservation interest, we considered a case in which the population exhibits a severe decline ( $\lambda = 0.81$ ) and in which we have sufficient data to determine the upper and lower biological limits of each vital rate (Table 1). Adult survival has the highest elasticity of rates in the mean matrix (Table 1), so conservation actions would typically be aimed toward improving adult survival as the most effective strategy for reversing population decline. Using this example, we address the three questions regarding typical conservation inferences based upon elasticity (Fig. 1).

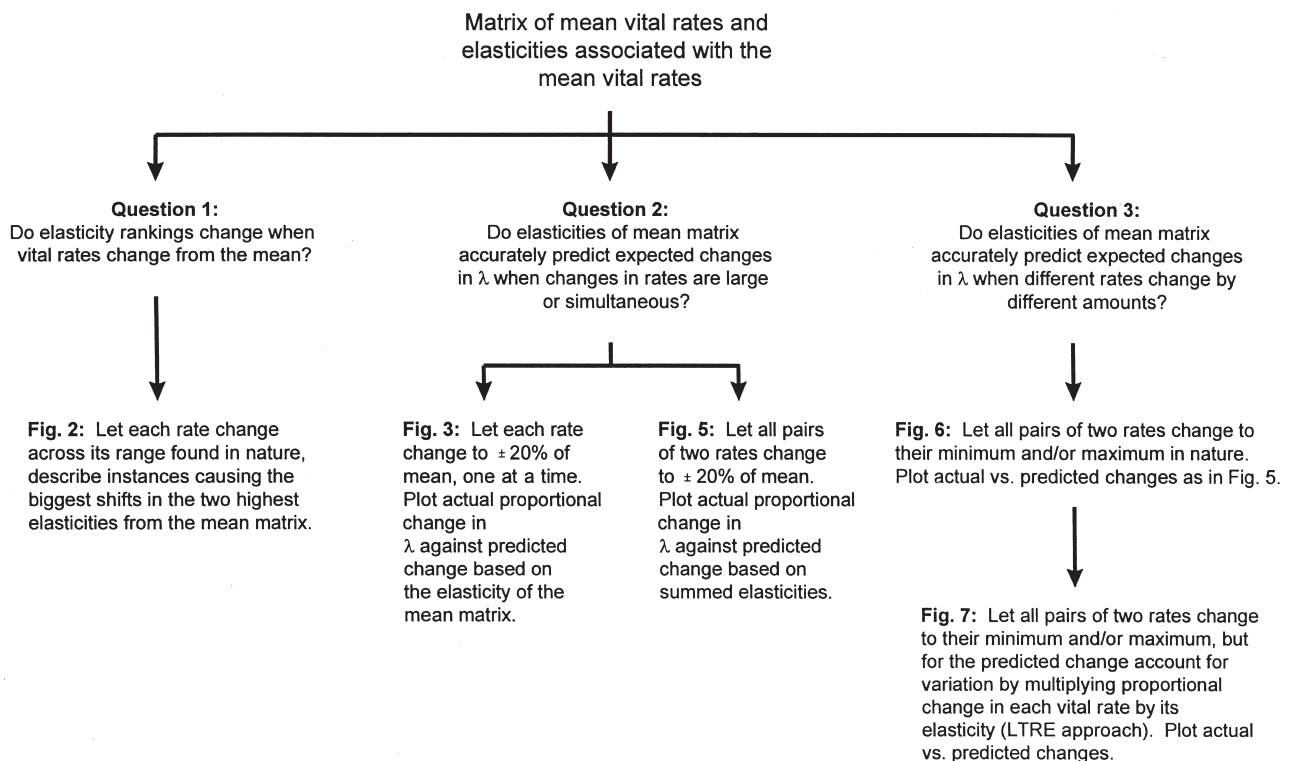


Figure 1. Flowchart showing approach taken to explore the application of elasticity analyses in a conservation biology context.

**Table 1.** Definitions of vital rates and their associated elasticities for a hypothetical declining population ( $\lambda = 0.81$ ).

Vital rate description	Mean vital rate	Vital rate elasticity given the mean matrix	$\pm 20\%$ of mean <sup>a</sup>	Hypothetical range of variation <sup>b</sup>
$s_a$ = adult survival	0.5	0.395	0.4–0.6	0.4–0.7
$s_j$ = juvenile survival	0.3	0.359	0.24–0.36	0.20–0.35
$T$ = mean time spent as juveniles	7	–0.226	5.6–8.4	3.5–10.0
$F$ = production of 1 year olds	4	0.245	3.2–4.8	2.0–6.0

<sup>a</sup> Values used for large but proportionately equal changes to vital rates.

<sup>b</sup> Values used to represent “natural” minimum and maximum values for each vital rate. As is likely to be the case in field studies, the mean does not necessarily fall in the middle between the high and low values.

### Changes in Ranking of Elasticity Values when One Vital Rate Changes

Suppose that management intervention, or natural variation, changes a vital rate relative to that used in the mean matrix. For example, imagine that the mean time spent as juveniles ( $T$ ) varies (Table 1), perhaps because the transition to breeding is altered by weather or changes in available habitat for territories or nesting sites (Heppell et al. 1994). For our example life history, the qualitative ranking of the elasticity values changes as  $T$  decreases from the mean of 7.0; below about  $T = 5.5$ , juvenile survival replaces adult survival as the vital rate with the highest elasticity (Fig. 2a). Thus, both the absolute value of elasticity and the “highest ranked” elasticity can shift with the particular values used to construct a matrix, implying that management-induced changes in one rate or simple uncertainty in estimates of a mean rate can alter conclusions drawn from elasticities. To test if these shifts in the importance of different rates were exaggerated by the low  $\lambda$  in this example (Meats 1971), we also performed this analysis with an altered matrix with  $\lambda = 1.01$  (all rates except  $T$  increased by 25%); the result was unchanged.

### Predicting Changes in Population Growth with Large or Multiple Changes in Vital Rates

How well do elasticities based on infinitesimal changes in the mean matrix predict the proportional change in  $\lambda$  when a single vital rate changes by a large amount? For our hypothetical organism, all vital rates were changed one at a time to  $\pm 20\%$  of the mean, and predicted proportional changes in  $\lambda$  (either the elasticity or negative elasticity, depending on whether the rate is increased or decreased, of each rate in the mean matrix) were plotted against the actual proportional change in  $\lambda$  after changing that rate:  $(\lambda_{\text{modified matrix}} - \lambda_{\text{mean matrix}})/(\lambda_{\text{mean matrix}})$ . If the elasticity of the mean matrix were a perfect predictor of change in population growth rate, the points would correspond to a straight line. Deviation from a straight line would indicate a mismatch between the predictions of simple elasticities and the actual changes in growth rate after the vital rates were modified. In this case, the correspondence between predicted and observed changes was excellent for these

equal 20% changes (Fig. 3a). (The numerical values of the predicted and actual change do not necessarily correspond because the predictions are for infinitesimal changes, whereas each rate was changed by 20%.)

Deviations between predicted and observed changes in  $\lambda$  may increase as the magnitude of the changes increase because of nonlinearities in the relationships between  $\lambda$  and underlying vital rates. For example, the actual  $\lambda$  for matrices with decreasing  $T$  values increased more than predicted based on the linear proportional changes assumed by elasticities (Fig. 4). This occurred mostly for changes in  $T$  larger than the 20% used in Fig. 3a. Figure 4 emphasizes that  $\lambda$  can change nonlinearly as a vital rate changes, so that the linear, proportional changes predicted by elasticities of the mean matrix can be misleading when the underlying relationships are nonlinear and changes in vital rates are realistically large in size.

We next extended the question of accuracy of quantitative predictions of population growth changes to more than one rate changing simultaneously, as would be the case with conservation management or any inclusion of environmental variability. If two rates change by the same proportional amount (20%), the predicted proportional change in  $\lambda$  is obtained by adding or subtracting elasticities of the mean matrix according to whether vital rates are altered up or down (Silvertown et al. 1993; van Groenendael et al. 1994), and the actual change is again calculated from  $(\lambda_{\text{modified matrix}} - \lambda_{\text{mean matrix}})/(\lambda_{\text{mean matrix}})$ . As an example, if adult survival and juvenile survival were both decreased by 20%, the expected proportional change in growth rate (from elasticities of the mean matrix in Table 1) would be  $(-0.395 - 0.359) = -0.754$ , whereas the actual proportional change would be  $(0.686 - 0.81)/0.81 = -0.153$ . Although in this case summed elasticities did not precisely reflect the actual change in population growth rate, the qualitative predictions were still quite good (Fig. 5a).

### Predicting Changes in Population Growth when Vital Rates Change by Different Amounts

We again considered all combinations of two vital rates changing simultaneously, but in this case the rates changed

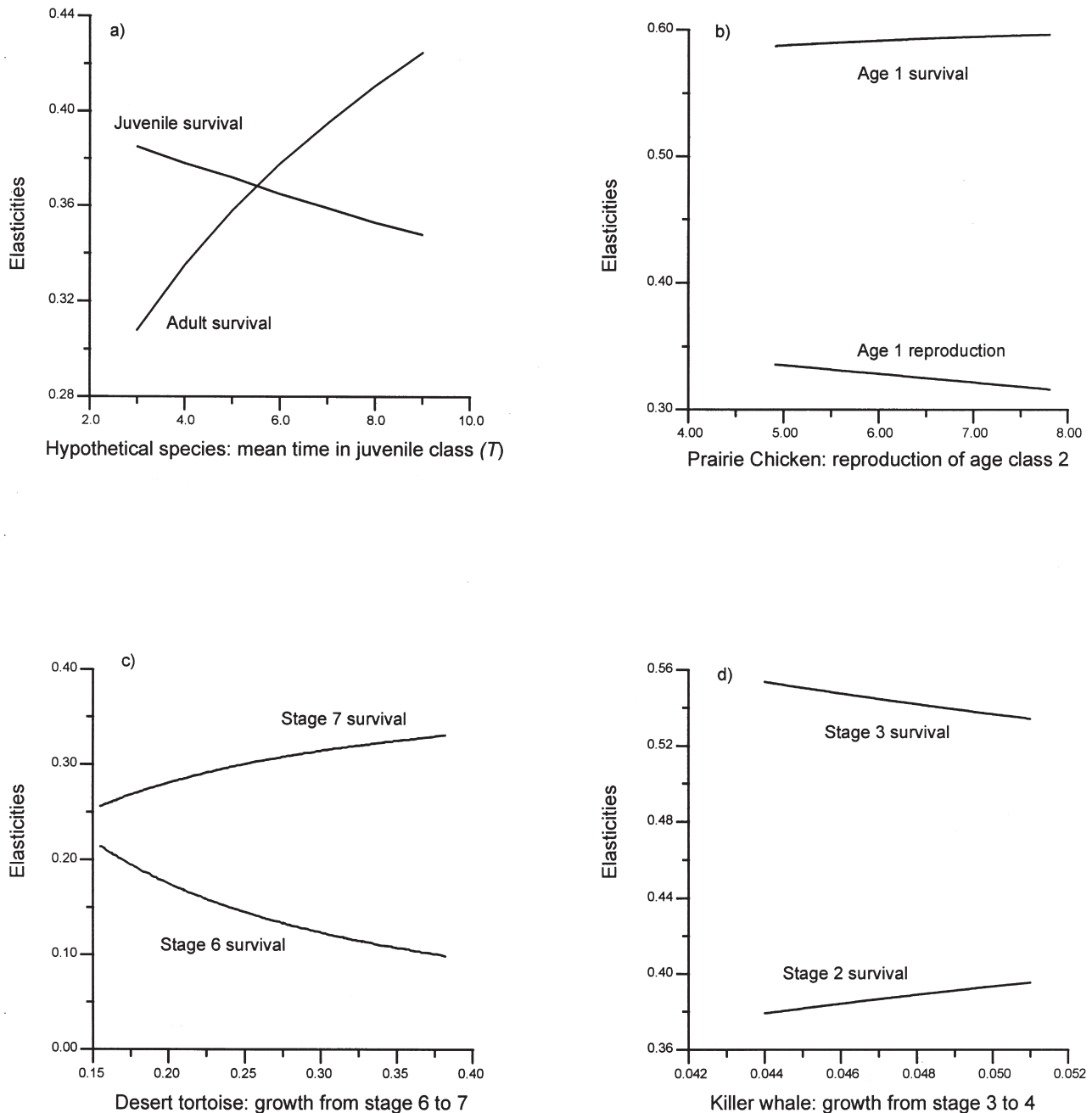
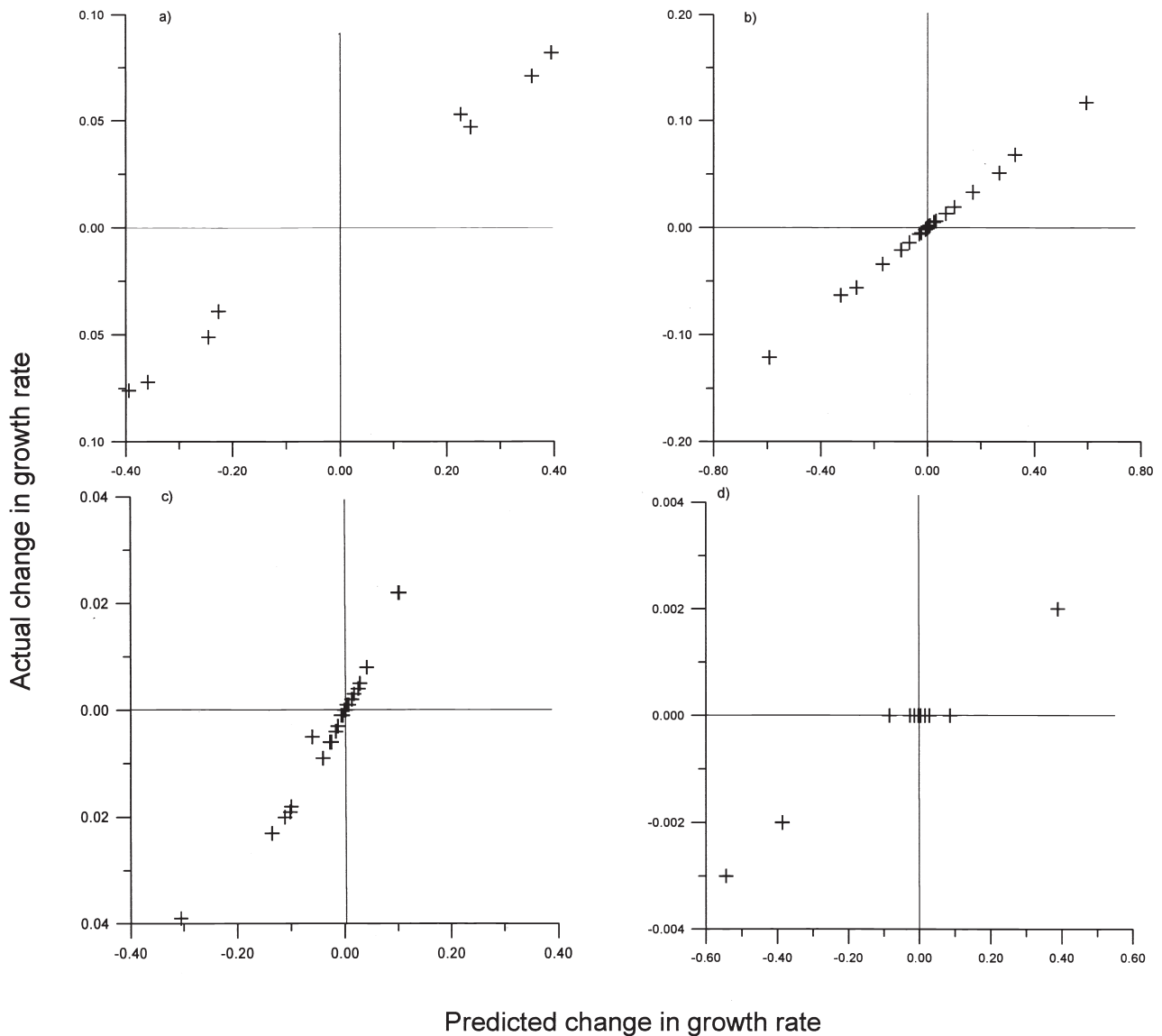


Figure 2. Effect of changes in one vital rate on the rankings of the two highest ranked elasticities calculated from the mean matrix. The vital rate on the x-axis is the one whose variation resulted in the greatest change in relative values of the two largest elasticities. Data used for calculations are (a) hypothetical example; (b) Prairie Chicken; (c) desert tortoise; (d) killer whale.

not by the same amount but to the minimum and maximum found in "nature" for our hypothetical species (Table 1). Thus, we emulated the common case in which predictions of change in future growth rates are made on the basis of elasticities from the mean matrix, despite the fact that different vital rates change by different amounts due to life-history or logistical and political fea-

sibility constraints. In this case, elasticities can be quite misleading (Fig. 6a). In fact, in several cases the predictions from the summed elasticities were positive, predicting an increase in  $\lambda$  if certain rates were changed, but the actual change in growth rate was negative; the reverse also occurred (Fig. 6a). Thus, not only was there quantitative disparity in predicted and actual changes



**Figure 3.** Relationship between predicted proportional change in growth rate (based on elasticity of each vital rate in the mean matrix) and actual change when each vital rate was changed one at a time by relatively large but proportionally equal amounts. Predicted changes in growth rate (elasticities) on the x-axis are symmetrical around zero according to whether the vital rate is increased or decreased; when the change would exceed biological limits (0 or 1 for survival, for example), that point was deleted. Data and extent of perturbation are (a) hypothetical example ( $\pm 20\%$ ); (b) Prairie Chicken ( $\pm 20\%$ ); (c) desert tortoise ( $\pm 20\%$ ); (d) killer whale ( $\pm 0.5\%$ ; see text).

in growth rates, but the actual direction of predicted population change—the qualitative prediction—could be wrong.

Can this problem be solved by incorporating knowledge of the limits of change into elasticity predictions? We consider LTRE-type approaches (Caswell 1989b; Brault & Caswell 1993; van Tienderen 1995; Horvitz et al. 1997; Ehrlén & van Groenendael 1998) as a best-case scenario in which not only elasticities but also the change in rates are known. For all combinations of two

rates changing to their highs and lows, we plotted the actual proportional change in growth rate versus the predicted proportional change under LTRE: (elasticity of mean rate)(proportional change in that rate) summed for the altered two rates. We called these the LTRE graphs (Fig. 7) and noted that this is analogous to an LTRE approach that multiplies the sensitivity of mean rates times the absolute change in the rate (Ehrlén & van Groenendael 1998). To give a numerical example for the case of adult and juvenile survival going from their mean

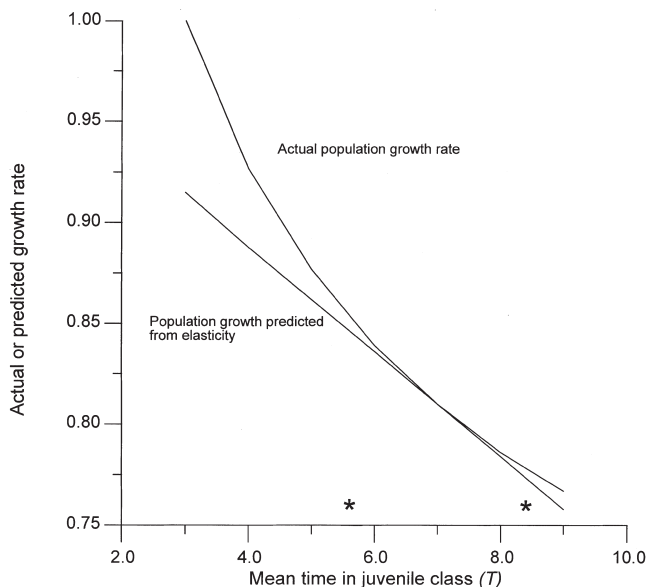


Figure 4. A demonstration of nonlinearities between  $\lambda$  and changes in one vital rate ( $T$  = mean time spent as juveniles) for the hypothetical example. A linear change in  $\lambda$  (as assumed by elasticity analysis) is shown for comparison. The values of  $T$  used in Fig. 3a ( $\pm 20\%$  of the mean) are shown by an asterisk, indicating that nonlinearities would more substantially decrease the good fit shown in Fig. 3a if changes were  $>20\%$ .

values to their minimum (a change of 0.1 in this case; Table 1), the predicted proportional change would be  $(-0.395)(0.1)/0.5 + (-0.359)(0.1)/(0.3) = -0.199$ . The actual proportional change would be  $(0.643 - 0.81)/0.81 = -0.206$ . In the LTRE comparison for the hypothetical data, the predictions were qualitatively correct—and much better than for the simple elasticity prediction—with some imperfect fit between predicted and actual proportional change in  $\lambda$  but only two predictions that were wrong in sign (Fig. 7a).

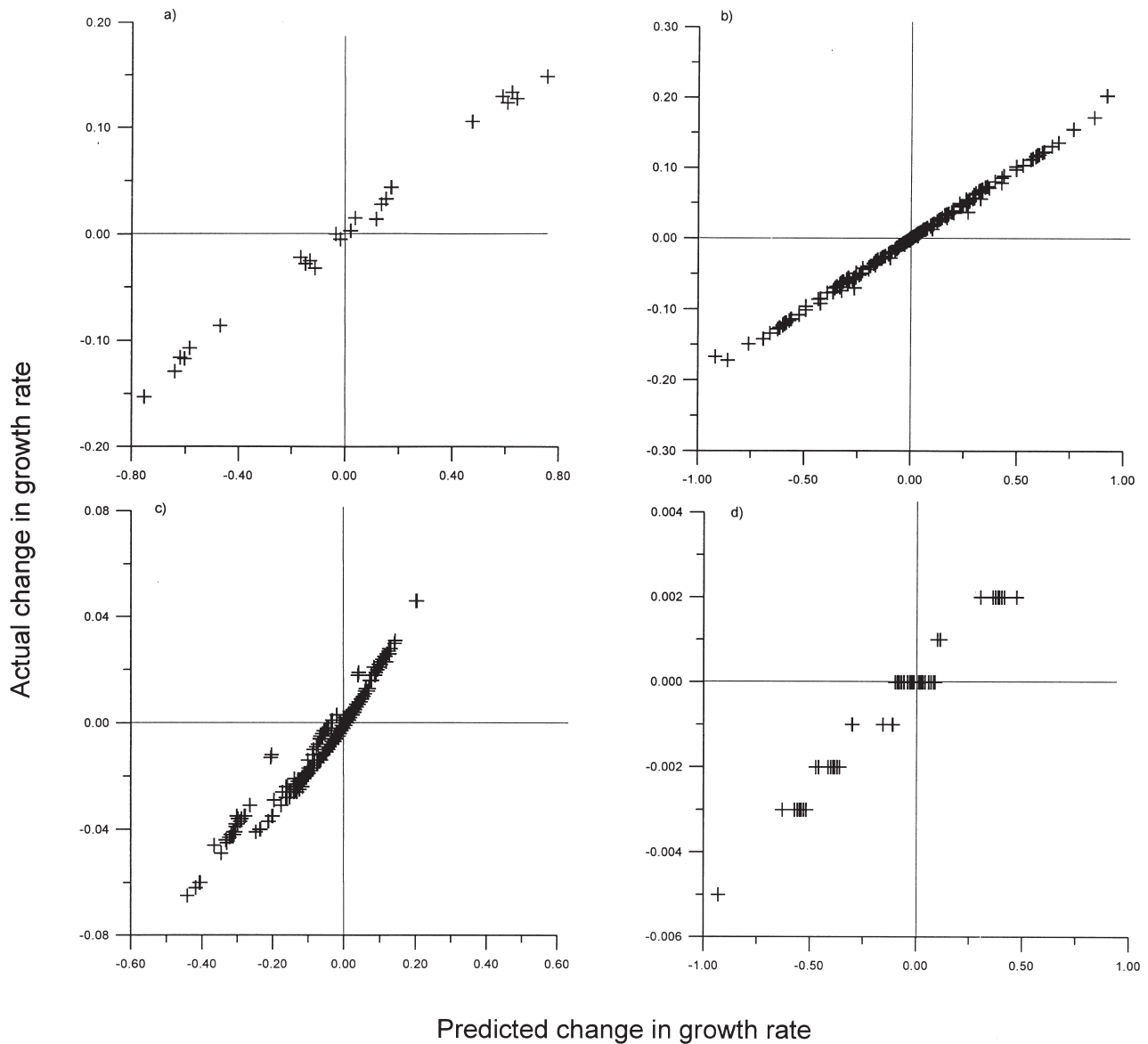
For this hypothetical example, both the ranking and the qualitative predictions of elasticities alone hold up rather well, giving roughly accurate estimates of most population changes in the face of variation and simultaneous changes. It is also clear, however, that whether or not elasticity analysis produces qualitatively correct insights into population growth in the hypothetical example depends on how much vital rates change. If users make predictions of growth without accounting for the range of variation (Fig. 6a), the predictions can be substantially wrong. If the user is lucky enough to know the range of variation and takes steps to incorporate it into the predictions (Fig. 7a), the predictions improve considerably. Given these conflicting possibilities for the utility of analytical sensitivity analysis, it is important to extend the examination to actual case histories.

## Analytical Elasticity Analysis for Three Vertebrate Species

To extend the analysis of limitations of elasticity analysis beyond the hypothetical example, we addressed how well elasticities predict the effect of demographic perturbations on the matrix growth rate using data from three field studies that span a range of vertebrate life histories: Prairie Chicken (*Tympanuchus cupido*), desert tortoise (*Gopherus agassizii*), and killer whale (*Orcinus orca*). We reevaluated the performance of elasticity in these cases under conditions typically used in conservation applications, whereby a single matrix is constructed from mean or “best guess” vital rates and inferences based on that matrix are assumed to be robust to the sometimes large and/or concurrent changes in vital rates. As in the hypothetical example, we considered changes to underlying vital rates and not to matrix elements. This allowed us to examine, in a practical setting, the importance of each of the three main questions identified above. Mean vital rates, as well as reasonable upper and lower bounds for vital rates, were extracted from published matrix analyses of field data (Appendix). For each set of empirical data, we changed vital rates using the same approaches outlined for the hypothetical example (Fig. 1).

To address the question of the stability of elasticity rankings with changes in vital rates, we varied the values for each vital rate across its observed range (Appendix). As a worst-case scenario, we report only the case that led to the biggest change in the rankings of the two highest elasticities for each species. For the second question, the accuracy of predicted changes in  $\lambda$  as vital rates change by equal but large amounts, we changed each vital rate one at a time to  $\pm 20\%$  of the mean (or to the specified biological limits for that species) and we evaluated the relationship between the predicted proportional change in population growth (determined from the elasticity in the mean matrix) and the actual proportional change in  $\lambda$  following the change in that vital rate. The effects of simultaneous changes in the two rates were evaluated, as in the hypothetical example, by changing all rates two at a time  $\pm 20\%$  and comparing the expected additive proportional change in  $\lambda$  (from summed elasticities of the mean matrix) to the actual change  $(\lambda_{\text{modified matrix}} - \lambda_{\text{mean matrix}})/(\lambda_{\text{mean matrix}})$ . Finally, to evaluate the effects of different ranges of variation in different vital rates, we used changed combinations of two rates but allowed vital rates to vary to the maximum or minimum observed in nature for each species (Appendix). Again, we plotted the actual proportional change in growth rate in separate graphs against predicted growth rates based on either summed elasticities of the two rates altered to their high or low values (Fig. 6) or the summed elasticities weighted by the proportional change in the rate (Fig. 7; the LTRE scenario).





**Figure 5.** Relationship between the predicted proportional change in growth rate (based on summed elasticities of two rates in the mean matrix) and actual change when pairs of rates were changed simultaneously by relatively large but proportionally equal amounts. For each matrix, all two-way combinations of positive and negative changes in pairs of vital rates are shown. Thus, summed elasticities on the x-axis are symmetrical around zero, except that points are deleted when the changes would exceed biological limits (0 or 1 for survival, for example). Data and extent of perturbation are (a) hypothetical example ( $\pm 20\%$ ); (b) Prairie Chicken ( $\pm 20\%$ ); (c) desert tortoise ( $\pm 20\%$ ); (d) killer whale ( $\pm 0.5\%$ ; see text).

### Prairie Chicken

For Prairie Chickens, changes in any single vital rate did not alter the relative elasticity values for juvenile survival and juvenile fecundity, the two highest-ranked elasticities (Fig. 2b). Furthermore, even when vital rates were changed one at a time by 20% (Fig. 3b), or two at a time by 20% (Fig. 5b), elasticities of the mean matrix did an excellent job of predicting future growth rate. When we added the real-world aspect of unequal ranges of varia-

tion for different vital rates, however, the clean relationship between the mathematical prediction and actual change did not hold (Fig. 6b). Not only did some combinations give very different changes in  $\lambda$  for the same predicted change (summed elasticity), but the overall relationship between elasticities and realized growth rates changed (Fig. 6b). The nonlinear jump in change in  $\lambda$  relative to elasticities arose from changes in juvenile survival because juvenile survival had both the highest elas-

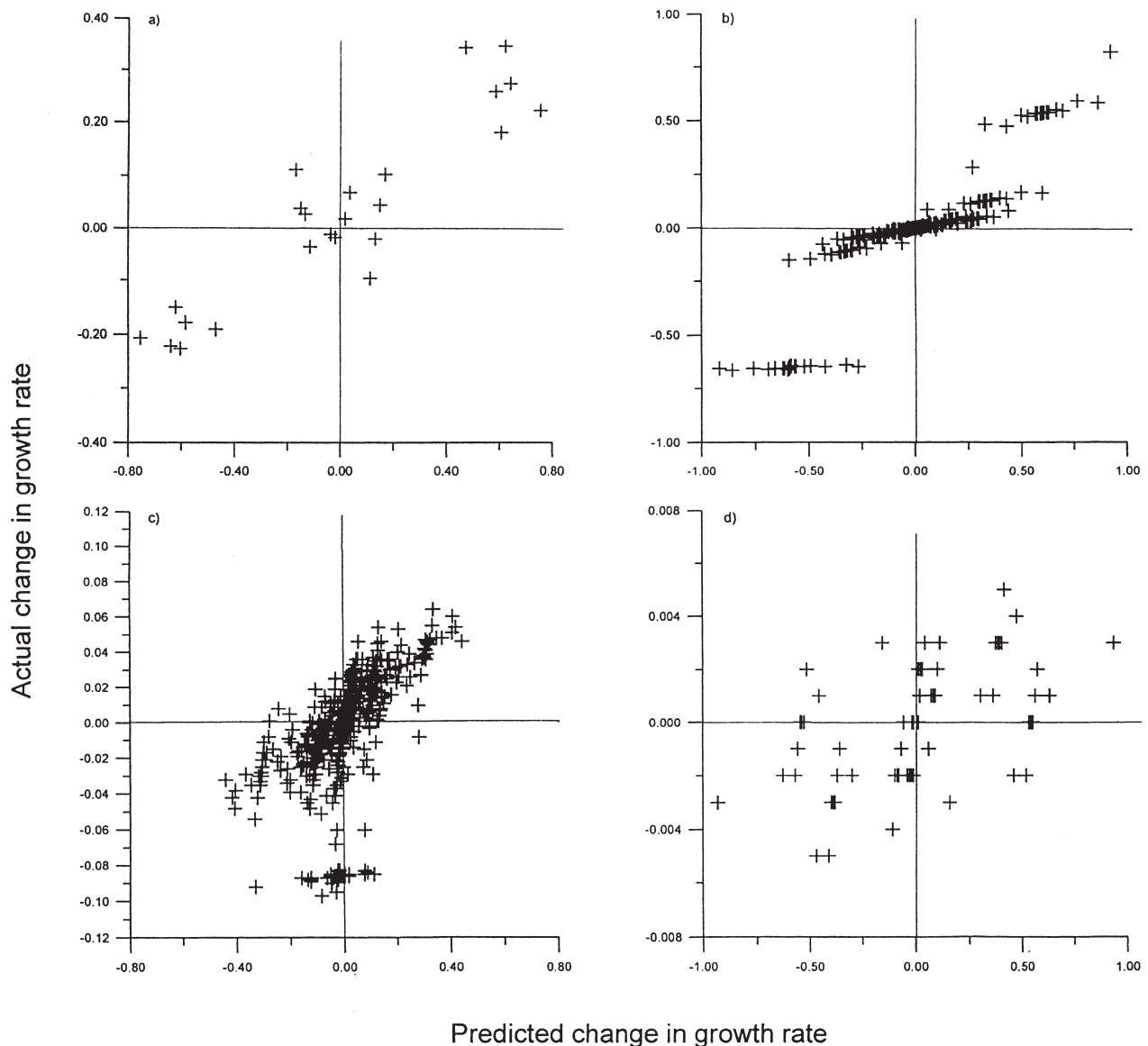


Figure 6. Relationship between predicted proportional change in growth rate (based on summed elasticities of two rates in the mean matrix) and actual change when pairs of rates were changed simultaneously to the minimum or maximum found in nature. Data are for (a) hypothetical example; (b) Prairie Chicken; (c) desert tortoise; (d) killer whale.

ticity and the widest range of variation. When the ranges of different vital rates were incorporated by the LTRE approach, combining elasticities with range of variation, the actual change in growth rate was much closer to that expected (Fig. 7b).

#### Desert Tortoise

Elasticity metrics based on the mean matrix were more problematic for the desert tortoise. Changes across a realistic range of variation in the transition from class 6 to class 7 almost changed the ranking of the two highest elastic-

ties (Fig. 2c). Changes in growth rate corresponded closely to elasticity predictions when single rates changed by 20% (Fig. 3c), and proportionally equal changes in any two rates also retained a fairly predictable relationship between summed elasticities and proportional change in  $\lambda$  (Fig. 5c). There were instances, however, in which changes in vital rates with nearly equal combined elasticities resulted in quite different proportional changes in  $\lambda$  (Fig. 5c). This became more striking when simultaneous changes occurred across the unequal ranges of variation for different vital rates (Fig. 6c). Many changes led to qualitatively wrong predictions, whereby the summed elastic-

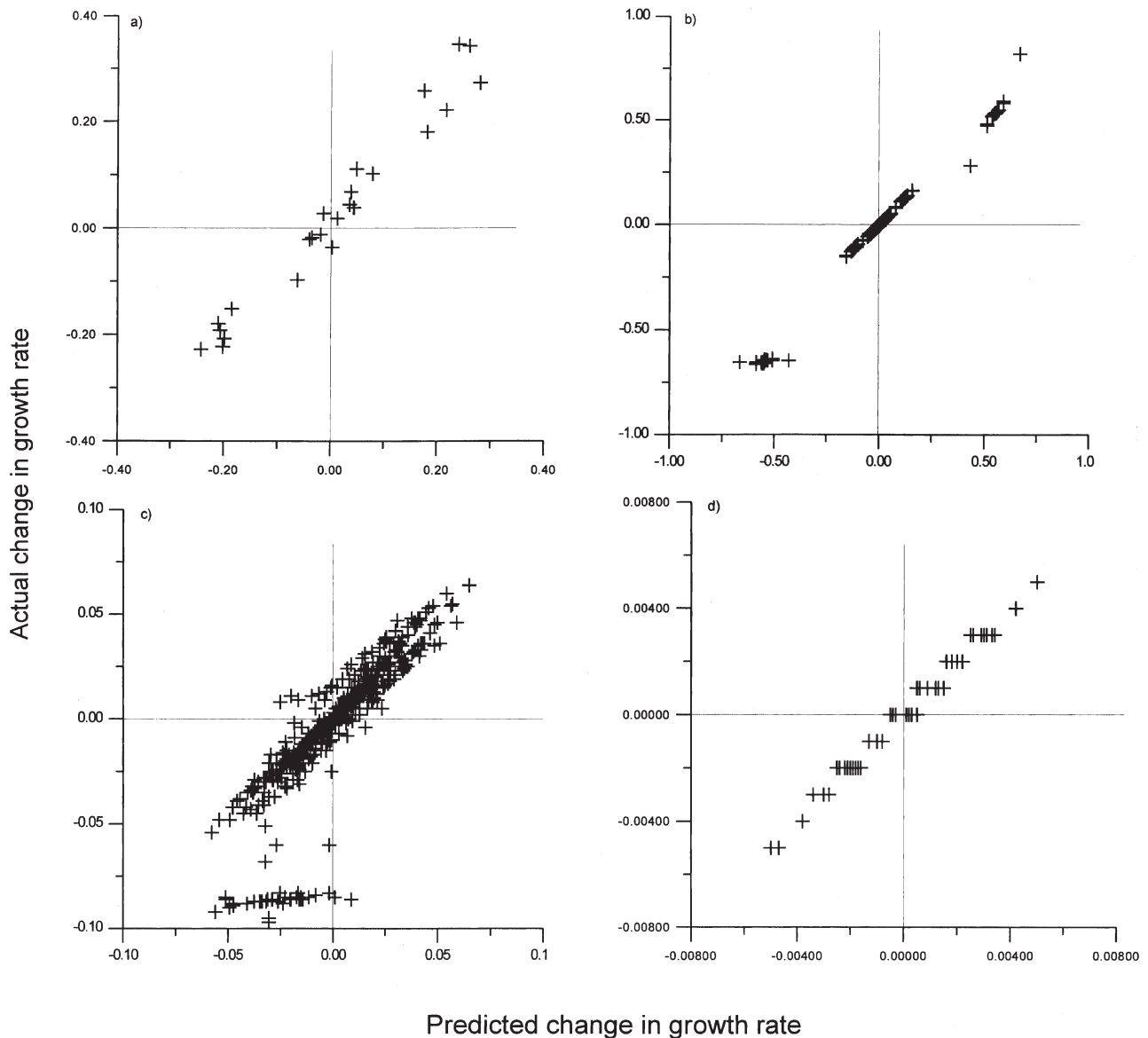


Figure 7. Relationship between predicted proportional change in growth rate (based on LTRE approach) and actual change when pairs of rates were changed simultaneously to the maximum or minimum value observed in nature. Data are for (a) hypothetical example; (b) Prairie Chicken; (c) desert tortoise; (d) killer whale.

ities predicted increases (or decreases) in  $\lambda$ , yet the actual change was the opposite. In fact, the sign of the expected change in  $\lambda$  was incorrectly predicted in 15% of the cases. The cluster of points with strongly negative changes in  $\lambda$  ( $< -0.08$ ) in Fig. 6c contains vital rates for growth of stage 2 or stage 3, both of which have moderate elasticity values and large ranges of variation ( $>100\%$  difference between the mean and the maximum or minimum). Thus, the pairing of a large range of variation with a relatively large elasticity gave stages 2 and 3 unexpectedly large negative effects on population growth. When range of

variation was explicitly incorporated into the elasticity analysis (LTRE scenario), scatter was reduced but some combinations of changes still led to qualitatively wrong predictions (Fig. 7c).

#### Killer Whales

The two highest elasticity values (survival for stage 3 [S3] and stage 2 [S2]) converged as the probability of maturing from stage 3 to stage 4 [G3] increased, but the tiny range for G3 limited the crossover potential (Fig.

2d). An important result was that when we increased the upper range of  $G_3$  by only 0.03, so that  $G_3$  ranged from 0.044 to 0.080, elasticity for  $S_2$  surpassed that of  $S_3$ , even though in the mean matrix the elasticity of  $S_3$  was 40% greater than that of  $S_2$ .

It was not possible to test the accuracy of projected changes in  $\lambda$  with large (20%) changes in one or two vital rates with this data set because too many of the mean rates were too close to biological limits (e.g., 0 and 1 for survival; Appendix) to allow imposition of 20% changes. Therefore, we set our fixed percentage changes at 0.5%, a very small proportional change that converges on the “infinitesimal” change assumed by the elasticity calculations. Not surprisingly, with this very small, fixed change, elasticities were for the most part accurate in predicting both the sign and actual values for changes in growth rate when either one (Fig. 3d) or two (Fig. 5d) vital rate changes were made at 0.5%.

Elasticities performed poorly for killer whales, however, when we used the empirically observed bounds for the different vital rates (Fig. 6d). As in the hypothetical example and in the desert tortoise case, there were numerous instances of predicted positive changes when negative changes in growth rate actually occurred, and vice versa. The LTRE approach that incorporated vital-rate variation improved predictions considerably (Fig. 7d).

## Discussion

Several important results emerged from our analysis. First, we validate and extend the implications of recent suggestions that sensitivities and elasticities for a population may vary across space and time (Kalisz & McPeck 1992; Shea et al. 1994; Horvitz & Schemske 1995; Lesica 1995; Benton & Grant 1996; but see Gotelli 1991). We found that variation in vital rates can change the values of elasticities expected from a mean matrix and in the worst case could cause a change in the qualitative rankings of elasticities. It is not known how often such shifts in elasticity rankings occur in the wild; the only theoretical study to consider this in detail (Benton & Grant 1996) detected relatively few ranking changes. Even if such crossovers in elasticities are not common, the potential problem is worth careful consideration, given the consequences of incorrect management recommendations.

Second, it is clear that elasticities can provide robust predictions to large proportional changes in vital rates (20% of the mean in our case), as long as the changes are equal for different vital rates. Biologically plausible responses to environmental change in natural or managed populations, however, will almost never be of the same proportional or absolute magnitude for all vital rates. When we allowed just two vital rates to change simultaneously to the high and low levels observed in nature, the relationship between predicted and actual change in

growth rate broke down. In the worst cases the predictions indexed by elasticities were of the wrong sign, with elasticities falsely leading to expected increases or decreases in population size that were opposite to the real changes.

Therefore, elasticities from a mean or best-guess matrix are not enough, by themselves, to accurately predict how population growth will change as vital rates change. If matrices are simple and the coefficients of variation for all vital rates are roughly the same, then elasticities are probably good qualitative indicators of growth-rate changes when the underlying rates are changed (Dixon et al. 1997). Where matrices are complex or vital rates change by different amounts, however, as will often be the case, elasticity values can give misleading predictions of growth-rate changes when vital rates change. Because vital rates with low elasticities may typically have higher variance than rates with high elasticities (Pfister 1998), it may be generally true that rates with low elasticities changing over wide ranges could affect growth rate as much as rates ranked as “most important” based on elasticities alone (Gaillard et al. 1998). Thus, our results substantiate suggestions that assessing the effects of conservation actions on population growth rate must account for not only how sensitive  $\lambda$  is to a specific vital rate but also how much variation in that rate can or does occur and how it covaries with other rates (Meats 1971; Nichols et al. 1980; Emlen & Pritchard 1989; Noon & Biles 1990; Schemske et al. 1994; Nations & Boyce 1997; Ehrlén & van Groenendael 1998).

In some instances, such as the tortoise and the whale, imposing even identical changes on different vital rates, or accounting for variation with an approach similar to LTRE, did not result in an acceptably good fit between predicted and realized growth rate. Such a mismatch could occur because the change in  $\lambda$  with a change in a vital rate may not be symmetrical around zero, or it may differ across the range of the vital rate (Fig. 4). In models with complex transitions to multiple alternative states, any nonlinearities between rates and  $\lambda$ , or interactions among rates, may lead to a disparity between elasticity and change in  $\lambda$ . In turn, LTRE and related approaches fail to consistently yield robust predictions because they still rely on the assumptions of additivity and linearity of population responses to changing vital rates. Extending LTRE-like approaches to include nonlinearity is straightforward in theory (van Tienderen 1995) but is perhaps most easily accomplished through simulations (Wisdom & Mills 1997; Crooks et al. 1998; Wisdom et al., in press).

What does our analysis mean for the use of formal elasticity analysis of matrix models in conservation biology? In addressing this broad question, it is important to reiterate why these approaches are usually used. The appeal of elasticities has been based on the perception that they yield strong management recommendations on the

relative importance of different demographic rates with minimal data requirements. Management priorities are then ranked based on an assumption that elasticities provide a robust and consistent index of life-stage importance. Our results call for caution in such use of elasticities: certain changes may alter the relative elasticities as calculated from a mean matrix, and, if the relative amount of change in each rate is not specified, elasticities can give inaccurate predictions of the response of  $\lambda$ .

In an attempt to clarify the appropriate use of elasticities, Horvitz et al. (1997) distinguished between prospective and retrospective analyses, defining prospective analysis as an evaluation of life-stage importance that addresses the potential effects of future changes in vital rates on population growth. Horvitz et al. (1997) identified elasticity analysis as a prospective technique because perturbations to vital rates are hypothetical and do not address past effects of empirical or experimentally induced variation. By contrast, they defined retrospective analysis as an evaluation of life-stage importance that measures the response of population growth to observed variation and covariation in vital rates, such as is done under LTREs.

These definitions of prospective versus retrospective analyses further emphasize the severe limitations of elasticities as a "stand-alone" measure of life-stage importance in an applied setting. If, in fact, elasticities are accurate only under a very constrained scenario (i.e., with equal and small levels of variation, occurring one rate at a time), then they offer little advantage over simply calculating the actual growth rates predicted by each altered matrix. If data on variation are available (Nichols et al. 1992), an alternative approach may be to simply calculate expected changes in growth rate or extinction probability using simulations that include the distribution and range of variation and any known correlations among vital rates (McCarthy et al. 1995; Ferrière et al. 1996). For example, Wisdom and Mills (1997) describe a simulation-based procedure to examine how frequently the rankings of elasticities change when vital rates fluctuate within reasonable bounds of field data. If certain vital rates always have the highest elasticity across the range of vital rates simulated, then confidence in the relative "qualitative importance" for different vital rates increases. Such a simulation approach goes beyond the strict use of elasticities by directly calculating  $\lambda$  for a wide range of possible matrices associated with a given population and evaluating how much variation in growth rate is accounted for by variation in each vital rate (Wisdom et al., in press). To the extent that covariation or correlations between rates are known (van Tienderen 1995), moreover, these could also be incorporated into a simulation-based approach.

One difficulty with any of these analytical or simulation-based methods is the need to use estimated ranges of vital rates to infer the biological range for each rate. Wide confidence limits can be generated by poor data or by real

variation. Conversely, a limited range of conditions during sampling may not accurately reflect the possible scope for a rate. Furthermore, ranking the "importance" of vital rates by means of any of these matrix-based tools does not account for the many complexities of nature that could alter the effects of vital rates on population growth (such as density dependence or deviation from stable age distribution) nor does it indicate the factors causing population decline (Beissinger & Westphal 1998) or incorporate factors such as the logistics or politics of modifying different rates (Goodman 1980; Nichols et al. 1980; Silvertown et al. 1996; Citta & Mills 1999). Any of these complications must therefore be explicitly examined during the process of evaluating and interpreting the results of a matrix analysis.

Finally, although elasticities may give misleading information over realistic ranges of changes in vital rates, we are not dismissing all uses of this elegant technique. Our purpose is to present an evaluation of the somewhat obvious, often overlooked, and seldom carefully analyzed limitations to the interpretations of formal sensitivity analysis in applied contexts (Silvertown et al. 1996). Such complications are to be expected in the use of ecological tools to address applied questions (e.g., Doak & Mills 1994; Royama 1996). Elasticity values are surprisingly robust under some circumstances and can be a useful first step in establishing qualitative guides to population dynamics. Nevertheless, they can also give quite misleading results if interpreted without a clear understanding of their assumptions and limitations.

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## Appendix: Sources of Vital Rates for Matrix Examples

### Prairie Chicken (*Tympanuchus cupido*)

Estimates for Prairie Chicken demography came from Wisdom and Mills (1997; see Tables 1 and 2). Vital rates for eight age classes were parameterized into a Leslie Matrix under a post-birth pulse formulation (Caswell 1989a). Mean vital-rate estimates follow (age classes are 1-8, survival and reproduction respectively follow age class, and numbers in parentheses are lower and upper limits recorded in published studies [Wisdom & Mills 1997]): 1, 0.158 (0.012-0.304), 3.858 (2.8028-4.914); 2, 0.445 (0.38-0.51), 6.905 (5.96-7.85); 3, 0.51 (0.45-0.57), 6.905 (5.96-7.85); 4, 0.42 (0.38-0.46), 6.905 (5.96-7.85); 5, 0.34 (0.24-0.44), 6.905 (5.96-7.85); 6, 0.345 (0.24-0.45), 6.905 (5.96-7.85); 7, 0.17 (0.00-0.34), 6.905 (5.96-7.85); 8, 0.145 (0.00-0.29), 6.905 (5.96-7.85).

Wisdom and Mills (1997) use the following notation for these age classes: survival of the first age class is S0 (age-zero survival), second age class is S1, and so on. Reproduction of the first age class, post-birth pulse, is R1, second age class is R2, and so on. This notation is in keeping with that for a post-birth pulse matrix model.

### Desert Tortoise (*Gopherus agassizii*)

Our estimates of vital rates for desert tortoises came from Doak et al. (1994). For growth and survival we used the means provided in their Table 3, and we used the standard deviations listed there to calculate standard errors and thus the 95% confidence limits around the means ( $\pm 1.96$  SE). We used these limits as our high and low parameter estimates for growth and survival. Some lower growth rates calculated in this way were negative, so we set these lower rates equal to 0.001.

We treated reproduction somewhat differently. Doak et al. (1994) provided four estimates for each reproductive rate. We used their low and high estimates as our low and high values. To have a mean estimate, we calculated the simple mean of the four values provided for each reproductive rate. This mean value was not the same as the one in Doak et al. (1994); so our mean matrix provides somewhat different results than shown in their work.

In matrix construction, we followed Doak et al. (1994; Table 5), with eight size classes (Table 2) and with the elements for continued presence in class  $x$  equal to  $s_x(1 - g_x)$  and the probability of making a transition to a larger class equal to  $s_x g_x$ . Reproductive elements in the first row are equal to reproductive rates because these rates are calculated as the production of surviving yearling tortoises. Although Doak et al. (1994) denote the eight size classes as 0-7, in this as in our other examples we begin numbering classes at 1 and thus refer to classes 1-8.

Mean vital rate estimates follow (age classes are 1-8; survival, growth, and reproduction respectively follow age class; and numbers in parentheses are lower and upper limits recorded in Doak et al. [1994]): 1, 0.716 (0.555-0.877); 2, 0.716 (0.555-0.877), 0.208 (0.001-0.422); 3, 0.716 (0.555-0.877), 0.208 (0.001-0.422); 4, 0.839 (0.717-0.961), 0.280 (0.187-0.373); 5, 0.785 (0.683-0.887), 0.287 (0.117-0.458); 6, 0.927 (0.878-0.976), 0.269 (0.153-0.385), 0.996 (0.042-2.22); 7, 0.867 (0.778-0.956), 0.018 (0.001-0.035), 1.530 (0.069-3.38); 8, 0.860 (0.775-0.945), 1.927 (0.069-4.38).

### Killer Whale (*Orcinus orca*)

We took estimates for orca demography from Brault and Caswell (1993). We followed these authors in matrix form and construction of matrix elements from the underlying vital rates that we varied (Brault & Caswell 1993).

To estimate means and ranges for vital rates, we first calculated the mean and standard error for vital rates contributing to matrix elements, using the sample of 18 pods listed in Brault and Caswell's Appendix and their equations (p. 1446). Thus, we first calculated the pod-specific vital rates and then determined their mean and SE values (we used a simple average and did not weight by within-pod sample sizes). As estimates of high and low values for each vital rate, we used the 95% confidence limits of the mean for each rate ( $\pm 1.96$  SE). Two high survival rates calculated in this way were  $>1$ ; we set these equal to 0.9999.

Because we used pod-specific means, our mean values are not identical with those listed in Brault and Caswell (1993:1447) or those listed in van Tienderen (1995, his Table 1), which are mean values of all animals surveyed, regardless of pod. (This is especially confusing in van Tienderen's table because his means over all animals are followed by pod-specific standard deviations over pods). Our means, however, are quite close to those used by these authors.

In all, this matrix is based upon seven vital rates, as follows (the mean is followed by the upper and lower limit): annual probability of yearling survival, 0.9848 (0.9643-0.9999); annual probability of juvenile survival, 0.9883 (0.9807-0.9958); annual probability of reproductive adult survival, 0.9996 (0.9989-0.9999); annual probability of post-reproductive adult survival, 0.9817 (0.9756-0.9876); annual probability of maturation from class 2 to class 3, given survival, 0.0746 (0.0723-0.0770); annual probability of maturation from class 3 to class 4, given survival, 0.04726 (0.0437-0.0509); mean annual reproductive output of reproductive females, 0.1186.

No variance estimate is provided for reproduction, so we treated it as a constant in the orca analyses.

