

ELASTICITIES: A REVIEW OF METHODS AND MODEL LIMITATIONS

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Abstract. Elasticity is a perturbation measure in matrix projection models that quantifies the proportional change in population growth rate as a function of a proportional change in a demographic transition (growth, survival, reproduction, etc.). Elasticities thus indicate the relative “importance” of life cycle transitions for population growth and maintenance. In this paper, we discuss the applications of elasticity analysis, and its extension, loop analysis, in life history studies and conservation. Elasticity can be interpreted as the relative contribution of a demographic parameter to population growth rate. Loop analysis reveals the underlying pathway structure of the life cycle graph. The different kinds of results of the two analyses in studies of life histories are emphasized. Because elasticities quantify the relative importance of life cycle transitions to population growth rate, it is generally inferred that management should focus on the transitions with the largest elasticities. Such predictions based on elasticities seem robust, but we do identify three situations where problems may arise. The mathematical properties and biological constraints that underlie these pitfalls are explained. Examples illustrate the additional information that needs to be taken into account for a sensible use of elasticities in population management. We conclude by indicating topics that are in need of research.

Key words: conservation; elasticity; *Hypochaeris radicata*; life history theory; loop analysis; matrix population model; perturbation analysis; population growth rate; sensitivity; trade-offs.

INTRODUCTION

Population growth rate quantifies the changes in the numbers of individuals in a population through time. Vital rates such as survival and reproduction are responsible for these changes and determine the demographic parameters that describe the development of individuals throughout the life cycle (Caswell 1989b, Roff 1992, Stearns 1992). Species differ in the life histories that they can exhibit. Some species are semelparous and others iteroparous, the age and size at first reproduction may differ, and some species have an additional (asexual) mode of reproduction, while others do not. Even within species, individuals differ in life history options. Demographic parameters are a function of the individual's age, size, developmental state, or a combination of any of these.

Matrix population models assume that populations can be fruitfully subdivided into classes of individuals that share certain values of these demographic parameters; they calculate population growth rates on the basis of transitions between these classes, as reflected in the structure of the life cycle (Caswell 1989b). Elas-

ticities (proportional sensitivities) quantify the relative changes in population growth rate resulting from small relative changes in the matrix transition elements.

In this paper, we review and discuss two different, but related, topics. First, we define elasticities and demonstrate how elasticity analysis, and its extension, loop analysis, quantify the relative contributions of life cycle transitions and alternative life history pathways to population growth rate (see *Elasticity and loop analyses in life history studies*). Knowledge about the contributions of different stages of the life cycle to population growth rate enhances our understanding of the life histories of species. In the second part of the paper, we explore how elasticity analyses may be used to make predictions about the effects of perturbations in demographic parameters on population growth rate, as in the management and control of populations (see *Elasticities in population management: caveats and limitations*). We discuss the limitations and caveats with this application that follow from the mathematical properties of elasticities, and illustrate them with examples.

STRUCTURING THE LIFE CYCLE: THE LIFE CYCLE GRAPH

In matrix population models, the basic units are classes, i.e., groups of individuals with similar demography (*nodes* in the life cycle graph). The demographic parameters that determine the fates of individuals are rep-

Manuscript received 9 October 1998; revised 4 May 1999; accepted 4 June 1999. For reprints of this Special Feature, see footnote 1, p. 605.

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resented by transitions from one class into another (*arcs* in the life cycle graph). Two basic vital rates underlie these transitions: survival of individuals from one time step to another (which may or may not be accompanied by growth, shrinkage, change in demographic status, etc.), and reproduction events by which new individuals are formed. Note that vital rates may be spread over multiple transitions (survival from one class into a number of other classes), and that transitions may be composed of multiple vital rates (seed production, germination, and establishment of seedlings in one compound transition).

The structure of the life cycle reflects the a priori choices about the subdivision of the individuals in the population (age, size, demographic state, or combinations of these), the time step over which the model is iterated (usually one year), and, in the case of a size-classified matrix, the number of classes. These choices may determine the values of the elasticities that are generated by the model (Enright et al. 1995, Wardle 1998), and they should be made on the basis of sound ecological and statistical arguments. Appropriate tools to assist in these choices include log-linear analysis to discriminate between age vs. size (Caswell 1986, 1989b), and algorithms to identify the number of size classes that minimize error. (Vandermeer 1978, see also Easterling et al. 2000). By repeated multiplication of the transition matrix with a distribution vector of the abundances of the classes, the population growth rate converges asymptotically to a constant that equals the dominant eigenvalue λ of the matrix. The corresponding left or right eigenvectors represent the stable reproductive value distribution and the stable state distribution, respectively. For basic information on the properties of projection matrices, and the computation of these limit properties and their biological interpretation, see Caswell (1986, 1989b, 1997) and van Groenendael et al. (1988).

Individuals are part of life history *pathways* or *loops* (Caswell 1982). We define a life history pathway (or “reproductive path” [Hubbell and Werner 1979]) as a closed circuit of arcs (transitions) that returns to its starting node and does not encounter any node more than once (see Fig. 1). Certain nodes in the life cycle are part of a number of different loops. For example, a node may be part of one or more reproductive loops but, in a stage-based model, individuals of the same class may also survive and remain in the same class (*stasis*), forming a *self-loop*. Life history loops represent the actual trajectories used by individuals in the population (Caswell and John 1992, McGraw and Caswell 1996) Starting with a reproduction event, a new individual passes through a number of age and or size classes, ending up as a mature individual of the same class as its parent, which closes the loop. As a rule, a life cycle can be decomposed into several distinct pathways, i.e., at least one arc in the pathway is not shared by another pathway (van Groenendael et al. 1994, War-

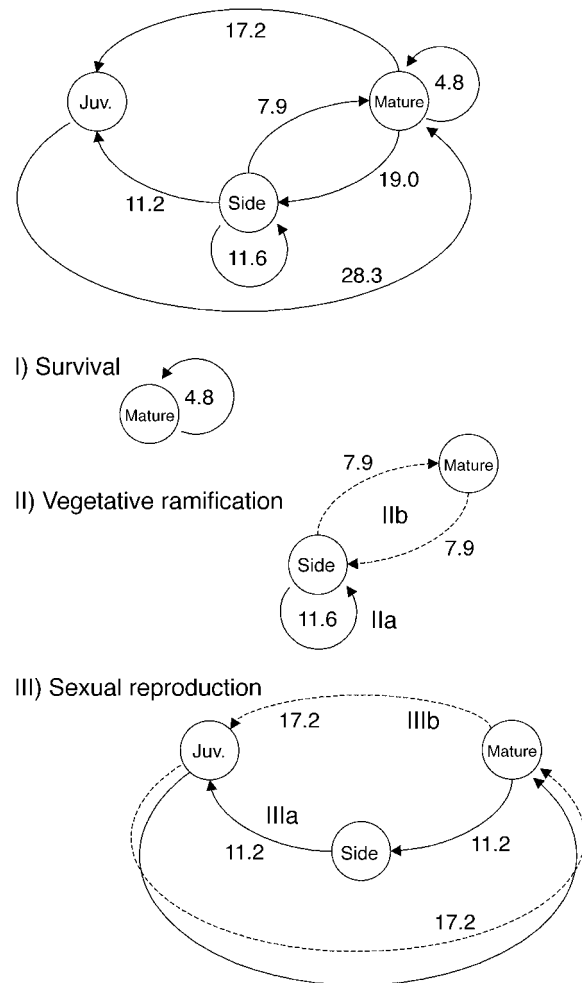


FIG. 1. Simplified life cycle graph for a population of *Hypochaeris radicata*, consisting of juvenile rosettes (juv.), side rosettes, and mature rosettes (after de Kroon et al. [1987] and van Groenendael et al. [1994]). Elasticities are given (as percentages) for a recently established (colonizing) population, in a site with no mowing. The life cycle is subdivided into five loops belonging to three categories: (I) survival of mature rosettes, (II) vegetative ramification (by side rosettes, IIa; or by mature rosettes, IIb), and (III) sexual reproduction (by side rosettes, IIIa; or by mature rosettes, IIIb). The elasticities of the transitions belonging to the loops are given. These are the characteristic elasticities of the pathway and are identical for all transitions of the same loop.

dle 1998). Formulated this way, a life history pathway represents a useful categorization of all the possible individual trajectories, and this allows a comparison of the major life history alternatives within a given life cycle structure. This is especially useful when a life history trait cannot be represented by a single life history transition, but is part of the whole life cycle, such as the timing of reproduction (late vs. early).

The life cycle graph and the life history pathways not only accurately reflect the biology, but are also the mathematical building blocks of any projection matrix. While dominant eigenvalue and eigenvectors are usu-

ally computed numerically, life cycle graph analysis yields analytical formulas for these limit properties. Such analysis shows how the limit properties depend on the structure of the life cycle. Essentially, the life cycle graph is a system of linear difference equations that, in principle, can be solved analytically by transformation (the so-called z -transform) (Lewis 1976, Hubbell and Werner 1979, Caswell 1982, 1989b). This solution shows how each life history path contributes to the overall rate of growth of the population (Hubbell and Werner 1979). The contributions of the pathways, in turn, are built up of the contributions made by the transitions making up the pathways. Only pathways (loops) contribute to λ . Transitions to and from classes in the transition matrix that are not part of a pathway, such as postreproductive age classes, have no impact on the eigenvalue of the matrix (Caswell 1989b: 64). An example of such classes can be found in Moloney (1988), who modeled the population dynamics of the perennial grass *Danthonia sericea* with a size-classified matrix model. He showed that, in some years, some transitions did not occur, thereby isolating a number of classes from loops in the matrix. The transitions to or from these isolated classes had an elasticity of zero. Isolated classes are usually omitted from projection matrices, which makes the matrices *irreducible*, i.e., there is a succession of arcs from each node to every other node in the matrix.

ELASTICITY AND LOOP ANALYSES IN LIFE HISTORY STUDIES

Elasticities: decomposing the population growth rate

Elasticity analysis is an analytical tool for decomposing the population growth rate into the contributions made by the life cycle transitions. Mathematically, elasticity e_{ij} quantifies the *proportional* change in λ resulting from a infinitesimal *proportional* change in matrix transition a_{ij} (Caswell et al. 1984, de Kroon et al. 1986):

$$e_{ij} = \frac{\partial(\log \lambda)}{\partial(\log a_{ij})} = \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}} \quad (1)$$

where all other elements of the transition matrix are held constant during partial differentiation. Elasticities thus compare the relative effects on λ with the same relative changes in the values of the demographic parameters. Elasticities are derived from the sensitivity index of Caswell (1978), given by

$$s_{ij} = \frac{\partial \lambda}{\partial a_{ij}} = \frac{v_i w_j}{\langle \mathbf{w}, \mathbf{v} \rangle} \quad (2)$$

with \mathbf{w} and \mathbf{v} as the dominant right and left eigenvectors of the transition matrix, respectively. Sensitivity s_{ij} quantifies the *absolute* change in λ of an infinitesimal *absolute* change in matrix transition a_{ij} . In other words, sensitivities compare the absolute effects on λ of the

same absolute changes in the values of the demographic parameters.

An important characteristic is that all elasticities of a transition matrix sum to unity (see de Kroon et al. [1986] and Messerton-Gibbons [1993] for mathematical proof). This property has a number of interesting consequences. First, it permits comparison of the relative importance of different types of transitions (e.g., stasis, growth, and reproduction) within the life cycle. Elasticities of different transitions may be added, and comparisons of different groups are possible between populations and between species with similar or with very different growth rates (Silvertown et al. 1993, 1996, Cunnington and Brooks 1996, Oostermeijer et al. 1996, Heppell 1998, Hoffmann 1999). Second, it follows that elasticities also measure the contribution of a_{ij} to λ (Caswell 1986, de Kroon et al. 1986). Because $1 = \sum e_{ij}$ and multiplying both sides by λ , Eq. 1 may be rewritten as follows:

$$\lambda = \lambda \sum e_{ij} = \sum a_{ij} \frac{\partial \lambda}{\partial a_{ij}} = \sum a_{ij} s_{ij}. \quad (3)$$

Thus, each e_{ij} gives the proportional contribution of its corresponding a_{ij} to λ . In other words, multiplying the set of elasticities by λ produces a set of contributions of a_{ij} , where each is weighted by its sensitivity and which together sum to λ .

It should be emphasized that the mathematical properties and biological interpretation of elasticities are very different from those of sensitivities (Caswell 1978). Sensitivities estimate the effects on λ of absolute changes in parameter values that are measured on widely different scales, such as transitions that cannot exceed unity (e.g., growth and stasis), and reproductive outputs, which can take on larger values. Sensitivities are therefore unsuitable for comparing the contributions of transitions within the matrix to population growth rates (de Kroon et al. 1986, Horvitz et al. 1997). However, the "importance" of parameters can have many different meanings (Horvitz et al. 1997). Sensitivities do appropriately quantify the importance of transitions for evolutionary questions, in terms of the intensity and direction of selection. The product of sensitivities and the genetic variance in demographic parameters gives the rate of change of the phenotypic mean of the parameters under selection (Lande 1982, Caswell 1985, van Groenendael et al. 1988, van Tienenderen 1995, 2000). As with elasticities, sensitivities may be added to predict the results of simultaneous changes in multiple transitions, and compared between species with different life histories.

Loop analysis: contributions of life cycle pathways to population growth rate

Loop analysis is an extension of elasticity analysis (van Groenendael et al. 1994) that reveals the underlying pathway structure of projection matrices. The first step is to identify the pathways in the life cycle graph.

Wardle (1998) has recently developed a systematic procedure for deriving the loops for any complex life cycle, based on graph theory. The number of loops L in an irreducible matrix is given by $L = b - n + 1$, with b as the number of arcs, and n as the number of nodes in the matrix. The loops thus identified will depend on the biological comparisons that the model is designed to represent. One can decompose the life cycle graph into the loops of interest, as shown in Fig. 1 with the simplified life cycle of *Hypochaeris radicata*, a perennial rosette-forming herb. In this life cycle graph, juveniles and first-year side-rosettes are distinguished from mature rosettes. In the actual model, the two latter categories were subdivided into vegetative and generative classes and further split into four size classes (de Kroon et al. 1987). Due to the additive nature of elasticities, these subdivisions can be conveniently pooled for the purpose of comparing life histories by loop analysis.

In the example of *H. radicata*, five life history pathways are distinguished: survival of mature rosettes (a self-loop), two vegetative ramification loops, and two sexual-reproduction loops (Fig. 1). Several features of loop analysis are immediately apparent. Except for self-loops, pathways consist of more than one transition. In each loop, all transitions have the same elasticity value, denoted as the "characteristic elasticity" of the loop (van Groenendael et al. 1994). The summed characteristic elasticities of a pathway amount to the contribution of that pathway to population growth rate (the loop elasticity). Some transitions are part of more than one pathway, and the elasticities of such transitions are simply the summed characteristic elasticities of the loops involved (Fig. 1). The relative nature of elasticities is maintained in loop analysis, in that the summed elasticities of all the loops equal unity.

Given the pathway structure of the life cycle graph, it makes intuitive sense for all transitions of a loop to have the same elasticity value. The contribution of a pathway to population growth rate is the same, irrespective of where in the pathway the contribution is measured. Accordingly, the summed elasticities of transitions coming into and going out of a node are identical (see van Groenendael et al. [1994] for mathematical proof), indicating that elasticity is "conserved" by the effects of individuals that pass through the pathway and then complete the life cycle (Wardle 1998). It follows immediately that only transitions that are part of loops contribute to population growth rate.

Longer pathways with more transitions, and therefore with more elasticity values to contribute, do not necessarily have a greater loop elasticity. Self-loops that comprise only a single transition may have very high elasticities, as in long-lived organisms with a self-looping adult node. It is well known that, in growing populations, early reproduction (i.e., short reproductive pathways) stimulates population growth rate (Stearns 1992, Charlesworth 1994). With every additional tran-

sition, it takes an additional time step for the pathway to complete, and this slows the population growth rate. Indeed, in the z -transform each transition is multiplied by λ^{-1} , effectively reducing the contribution made by longer pathways. Consequently, shorter loops will tend to make a larger contribution to the population growth rate than longer loops in growing populations. The reverse is true for populations in decline, where delaying reproduction reduces the rate of decline.

Comparison of elasticity vs. loop analysis

While intimately linked, elasticity analysis and loop analyses provide two different ways of decomposing the population growth rate. Conventional elasticity analyses, of both simple and grouped transitions, have been successfully applied in comparisons of the demographic characteristics of groups of species. For example, Silvertown et al. (1992, 1993) have classified the demographics of perennial plant species on the basis of summed elasticities of growth (G), fecundity (F), and survival (L). These and other classifications allow life history comparisons among species with widely different life cycles, as well as between the life cycles, the population growth rates, and the habitats in which the species prevail (e.g., Cunnington and Brooks 1996, Saether et al. 1996, Heppell 1998, Hoffmann 1999, Heppell et al. 2000, Saether and Bakke 2000).

The advantage of loop analysis is that the contributions of life history options that are not apparent in conventional elasticity analysis can be quantified (van Groenendael et al. 1994). Different modes of reproduction (as apparent in Fig. 1), or early vs. late reproduction, are options directly linked to the pathway structure of the life cycle and are made explicit with loop analysis. The contributions made by each of such pathways, and the trade-offs between them, are fundamental in studies on the evolution of life histories. A trade-off involves the negative covariance between traits of a given stage in the life cycle (e.g., survival vs. reproduction), or in other words, between alternative outgoing transitions of a given stage in the transition matrix. Life history trade-offs are thus expressed between, not within pathways.

Examining the underlying patterns among individuals can best identify trade-offs between traits. Patterns emerging from conventional elasticity analysis do not reflect such trade-offs (Shea et al. 1994). When traits exhibit trade-offs and affect life history parameters that belong to different loops, loop elasticities will most likely also show a negative relationship. The reverse, however, does not hold: loop analysis cannot unambiguously reveal trade-offs between traits, either. One reason for this arises from the property that elasticities sum to one. Thus, they are not independent, and negative correlations may arise between the elasticities (Shea et al. 1994). Other mathematical constraints to the values of elasticities have been identified (Basilio de Matos and Silva Matos 1998). Another reason is the

usually complex relationship between an individual trait and a transition in a population matrix. Negative correlations may appear between traits, but without a trade-off relation between them (van Tienderen 1995). Therefore, although correlated shifts between loops are interesting in themselves, they need not indicate a relationship between the underlying traits. In *H. radicata* for instance, with increasing population density the contribution of the sexual reproduction loops decreased and the elasticity of the vegetative propagation loops increased (de Kroon et al. 1987, van Groenendael et al. 1994; Fig. 1). A numerical perturbation analysis of the relative changes in each of the transitions making up these loops was necessary to reveal that changes in the germination/establishment parameter in the transition matrix were the principle causes of the shifts in loop elasticities with increasing population densities. Hence, this negative correlation between loop elasticities was not induced by a trade-off between sexual reproduction and vegetative propagation. For an explicit analysis of trade-offs in matrix population models, taking into account the direct effects of changes in parameters as well as the indirect effects via correlations with other parameters, see van Tienderen (1995, 2000).

ELASTICITIES IN POPULATION MANAGEMENT: CAVEATS AND LIMITATIONS

Elasticities have become a popular tool in conservation biology. Because they quantify the relative importance of a matrix element to population growth rate, it is generally inferred that management should focus on those demographic parameters with the largest elasticities (e.g., Crouse et al. 1987, Menges 1990, Doak et al. 1994, Heppell et al. 1994, Schemske et al. 1994, Caswell 1996b). The effects of harvesting on population viability (Mendoza and Setyarso 1986, Olmsted and Alvarez-Buylla 1995, Zagt 1997), as well as control measures of pest and invasive species (Shea and Kelly 1998), can be analyzed with elasticities in similar ways.

We identify three areas where possible pitfalls may arise when elasticities are used to give directions for population management. First, we show that predicting the effects of management efforts on the development of the population in the future contrasts with the local definition of elasticities. Such predictions may be erroneous if large changes in transition values and growth rates are involved. Second, the implications of variation in demographic parameters are explored. Not all transitions are equally variable (Pfister 1998) and are not equally possible to influence by management practices. Elasticities do not consider these constraints. Third, elasticities vary systematically with population growth rate, giving rise to implications for the management of declining vs. growing populations (Oostermeijer et al. 1996, Silvertown et al. 1996). In all three cases, the interdependency of elasticities, due to

their summation to one, plays a significant role. Examples are used to point at additional information that needs to be taken into account for a sensible use of elasticities in population management.

Elasticities are local estimates

Elasticities are calculated directly from the limit properties of a linear time-invariant transition matrix (see Eq. 2). They are the analytical expression of the relative changes in λ as a result of infinitesimal relative perturbations in a matrix element. In other words, elasticities are derivatives that give the *local* slope of $\log \lambda$ as a function of $\log a_{ij}$ (Horvitz et al. 1997). Elasticities are thus typically a tool used in *projection*, in which the hypothetical consequences of maintaining the current environment are explored, in contrast to *prediction*, in which one is interested in the actual population dynamics in the future (van Groenendael et al. 1988, Caswell 1989b, 1997). Horvitz et al. (1997) have therefore coined the term *prospective* for elasticity analysis. It should be realized, however, that elasticities do incorporate the past in the sense that they are based on past demographic observations (instantaneous values or long-term mean population values). Thus, they depend on estimates of the mean demographic input parameters (Drechsler 1998, Wisdom et al. 2000), but not on past variation in these parameters.

Potentially, predictions based on elasticities may be false, because the relationship between λ and changes in transition elements is typically curvilinear (Boyce 1997; see also Caswell [1997]). Consequently, beyond the infinitesimal range around the value of a transition element, elasticities will change. The degree of curvilinearity is not the same for all types of elements. Fig. 2 shows the changes in the proportional changes in transition values, for three Leslie matrices (left column, all vertebrate species) and three Lefkovich matrices (right column, all plant species). The life spans of the species vary widely and increase from the top of the figure to the bottom. The degree of curvilinearity differs between transition elements and between species, but, apart from this, no general patterns are discernible. The rank in relative importance of each parameter remains the same, even as deviations in parameter values get larger, indicating that elasticities give robust *qualitative* predictions of large changes in λ as a result of large changes in demographic parameters.

The curves in Fig. 2 show that the degree of curvilinearity is generally not very large, suggesting that elasticities may also provide fairly accurate *quantitative* estimates of these changes. Indeed, as Fig. 3 shows for the three species of vertebrates and plants combined, the elasticities were highly significantly correlated with the percentage changes in λ as caused by reductions in parameter values approaching 50% (see Heppell 1998). Similarly, Mills et al. (1999) showed that elasticities give generally robust predictions for

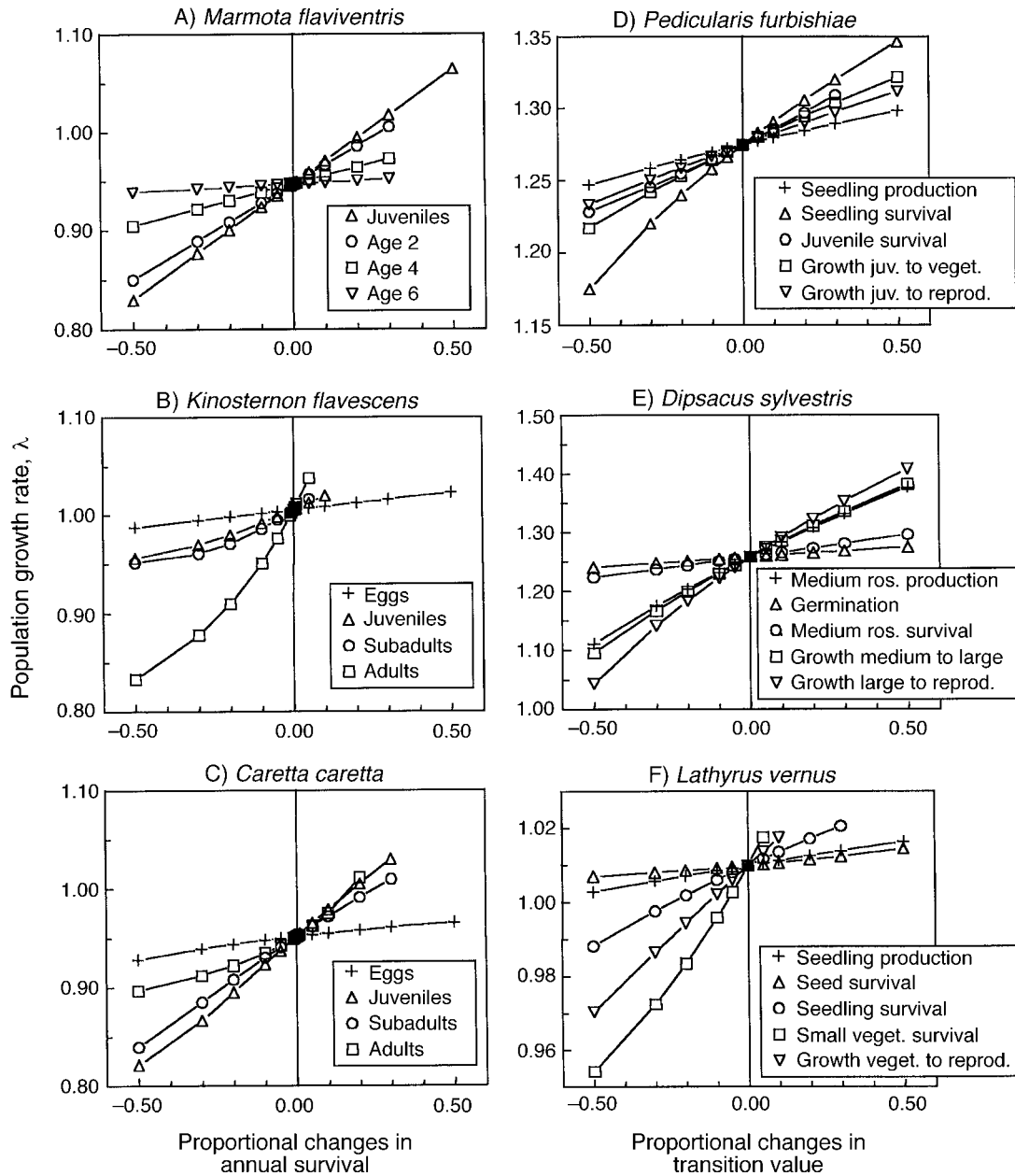


FIG. 2. The curvilinear relationships between transition values and the population growth rate, λ . (A–C) Comparisons of the sensitivity of λ to changes in survival rates of the Leslie matrices of three vertebrate species: *Marmota flaviventris* (yellow-bellied marmot; based on data from Armitage and Downhower [1974]), *Kinosternon flavescens* (yellow mud turtle; Heppell et al. [1996b]), and *Caretta caretta* (loggerhead sea turtle; Crowder et al. [1994]), respectively. (D–F) Comparisons of the sensitivity of λ to changes in reproductive, survival, and growth transitions in Lefkovich matrices of three perennial plant species: *Pedicularis furbishiae* (Menges 1990), *Dipsacus sylvestris* (Werner and Caswell 1977), and *Lathyrus vernus* (Ehrlén 1995), respectively. Enhanced survival rates were simulated for biologically realistic values only (survival ≤ 1); consequently, some of the lines to the right of the graphs are cut short.

changes in vital rates of 20% for three other vertebrate species and for a hypothetical population. Fig. 3 also shows that a linear approximation (percentage change in $\lambda \approx$ percentage change in transition element \times elasticity) predicts larger changes in λ quite accurately (see Heppell 1998, Caswell 2000), with the exception of

one transition with a very high elasticity (61.1%; Fig. 3A). Note that these predictions based on elasticities assume that other transitions remain unchanged.

The examples of Fig. 2 show that the elasticity e_{ij} of a matrix element a_{ij} depends on the value of that element (see also Drechsler [1998], Mills et al. [1999]).

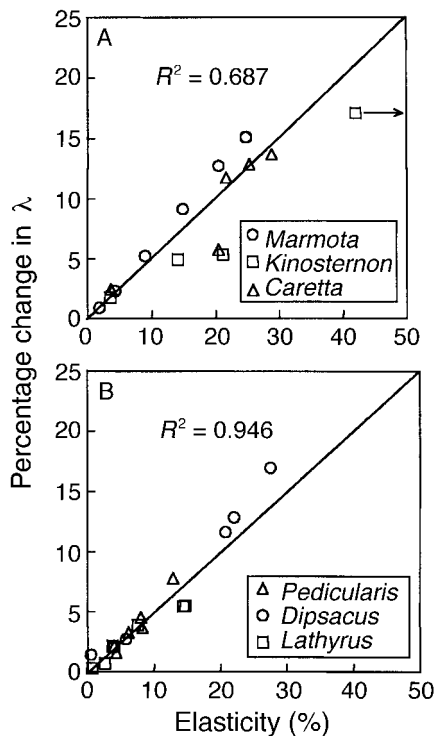


FIG. 3. The percentage change in population growth rate λ as a result of a reduction in demographic parameters of 50%, for (A) populations of the three vertebrate species and (B) populations of the three plant species of Fig. 2. All parameters displayed in Fig. 2 were included, supplemented with a few additional parameters to incorporate the full range of demographic parameter values. The relationships between percentage change in λ and elasticities were highly significant for both species groups ($P < 0.0001$), with regression coefficients of 0.317 (95% CI, 0.194–0.440; $R^2 = 0.687$, $n = 16$) and 0.573 (95% CI, 0.503–0.643; $R^2 = 0.946$, $n = 19$) for the vertebrate species and the plant species, respectively. The straight line represents the linear relationship between λ and elasticity (percentage change in $\lambda = \text{percentage change in transition element} \times \text{elasticity}$).

The second derivatives of the population growth rate quantify the changes in elasticity e_{ij} as the values of the other matrix elements a_{kl} change (Caswell 1996b). Caswell's (1996b) analysis of the second derivatives shows that the impact of different age or stage classes on elasticity values may vary widely, and that this influence may be positive or negative, i.e., that the elasticity e_{ij} may either increase or decrease with an increase in parameter value a_{kl} . We hypothesize that the pathway structure will be reflected in the values of the second derivatives. Transitions a_{kl} that are unique to the same life history pathway as a_{ij} will have a positive effect on e_{ij} , while transitions a_{kl} that belong to other pathways will have a negative effect. It would be most informative in the context of loop analysis to take the second derivative of the characteristic elasticities. In age-structured (Leslie) matrices, second derivatives of fecundity elements typically decrease with age, imply-

ing nonlinear rates of change in elasticity values, but other general patterns are still to be revealed (Caswell 1996b).

Elasticities and variation in demographic parameters

Demographic parameters vary in space and time, and this variation affects the population growth rate. Several different methods to analyze the impact of this variation have been suggested. First, life table response experiments decompose differences in λ among a fixed set of transition matrices into contributions from the variances and covariances of the transition elements (Caswell 1989a 1996a, Levin et al. 1996). A similar method for decomposing the variation in λ has been developed for random designs (Brault and Caswell 1993). These methods have been termed retrospective analysis by Horvitz et al. (1997). A second method to study the effects of variation is to examine the response of λ to changes in demographic parameters that are proportional to the standard deviation, instead of proportional to the mean, which is the perturbation used for calculating elasticities (van Tienderen 1995, Ehrlén and van Groenendael 1998). Lastly, the effects of variation on λ can be examined by randomization of parameters (Wisdom and Mills 1997). Note that elasticity analysis does not analyze the effects of actual variation in the transition elements of populations, but analyses the impact of hypothetical changes in these elements. For further discussion on analyses of the impact of actual variation in demographic parameters on population growth rates and its implications, see Caswell (2000) and Wisdom et al. (2000).

Variation in demographic parameters may be random, systematic among populations, or stochastically related to the favorability of the environment. Not all transitions are equally variable. Fig. 4 shows that, for three perennial plant species, variation is larger and mean elasticity is smaller for matrix elements with lower transition probabilities. Hence, the variability in demographic parameters is negatively correlated to their mean elasticity, which seems a universal pattern now observed for a great variety of life histories (Ehrlén and van Groenendael 1998, Gaillard et al. 1998, Pfister 1998, Saether and Bakke 2000). These patterns may indicate that natural selection buffers variation in traits that have a large impact on fitness (Pfister 1998), such as the high survival transitions in Fig. 4. Because low elasticity transitions are more variable, the actual contributions to the variance in population growth rate may be more evenly distributed among transitions than is suggested by the elasticities. Note that these analyses ignore covariances among transitions. To what extent covariances may modify these general patterns is yet unknown.

In variable environments, elasticities are usually based on the mean transition values and ignore the variation in these values and their impact (Wisdom and Mills 1997, Ehrlén and van Groenendael 1998, Saether

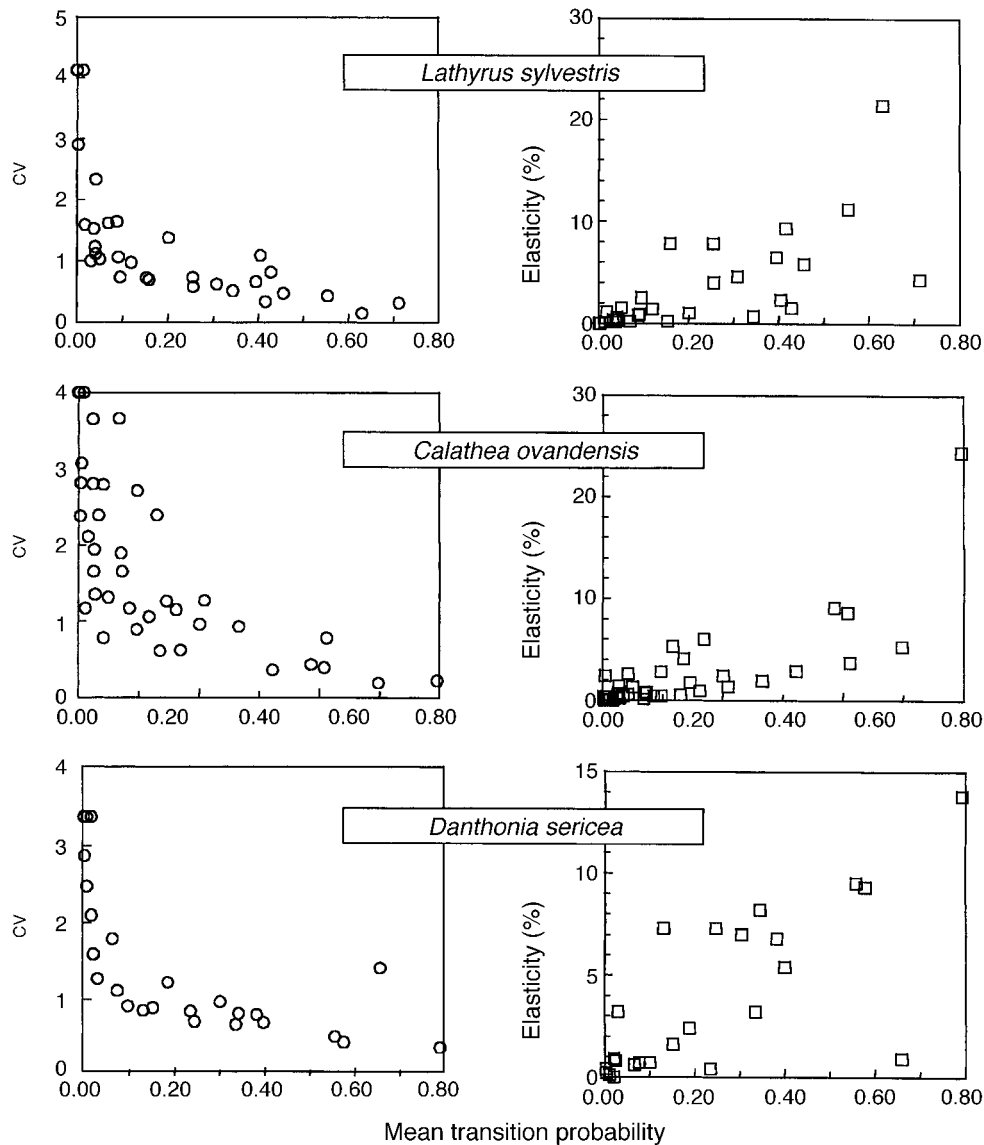


FIG. 4. The relationships of the coefficient of variation (CV) in transition values, and the mean elasticity, with the mean matrix transition values, for three perennial plant species. The results for the forest understory herb *Lathyrus vernus* were based on 17 matrices (5 sites \times 3 intervals + 1 site \times 2 intervals) with mean $\lambda = 1.008$ (range: 0.900–1.300; from Ehrlén and van Groenendael [1998]). The results for the tropical understory herb *Calathea ovandensis* were based on 16 matrices (4 sites \times 4 intervals), mean $\lambda = 0.978$ (range: 0.778–1.248; from Horvitz and Schemske [1995]). The results for the perennial grass *Danthonia sericea* were based on 10 matrices (5 sites \times 2 intervals), mean $\lambda = 1.077$ (range: 0.600–1.431; from Moloney [1988]). To limit the range of transition values in the comparisons, only survival and growth transitions are included. Elasticities were calculated for each matrix separately, and then means were evaluated.

and Bakke 2000, Wisdom et al. 2000). As we have shown, elasticities may give us a robust estimate of the impact of potential proportional changes. The variation in transitions in nature suggests, however, that the changes that we can actually induce will usually not be proportional, but vary to a great extent. Measures directed toward high-elasticity transitions will then be much less effective than indicated by their elasticities (Wisdom et al. 2000). We conclude that elasticities cannot be the sole tool to identify the life cycle phases to

which population-management effort should be directed (Ehrlén and van Groenendael 1998). Whether the actual causes of variation are random (due to environmental stochasticity) or manageable (e.g., related to habitat quality that may be manipulated) will determine the importance of this variation for population management (Wisdom and Mills 1997, Caswell 2000, Mills et al. 2000).

The constraints operating on the selection of the demographic parameters worthy of the most management

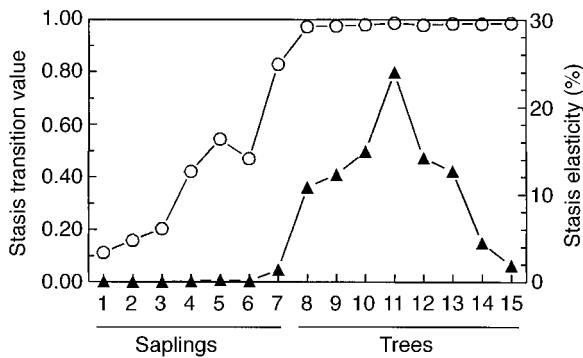


FIG. 5. Stasis transition values (circles; left-hand y-axis) and stasis elasticities (triangles; right-hand y-axis) for an undisturbed population of the tropical timber tree *Chlorocardium rodiei* (Greenheart) in Guyana (after Zagt [1997]). The population is subdivided into 15 size classes. The summed elasticities are 0.3% for reproduction, 2.5% for growth, 97.2% for stasis, and 0.1% for retrogression. The λ of this population was 0.998.

attention can be demonstrated well with populations of long-lived organisms, such as tropical trees. For example, beyond a given size, the survival rates of individuals of Greenheart (*Chlorocardium rodiei*) are very high, resulting in stasis transition values for adult trees that are close to unity (Fig. 5). Successful reproduction is a rare event in populations of this species (Zagt 1997). Consequently, stasis self-loops comprise the bulk of the total loop elasticity (97.2% for the population of Fig. 5). For management towards an increase of the growth rate of the population, such high elasticities are not particularly informative, because little incremental change in adult tree survival is possible. The values of growth and fecundity are more variable, and management efforts should rather focus on the stimulation of sexual reproduction or of tree growth. Though less conspicuous than in tropical trees, similar effects may operate in other life histories, such as those of long-lived vertebrates, in which survival may make large contributions to the growth rate of the population (e.g., Crouse et al. 1987, Doak et al. 1994, Heppell et al. 1994).

In these cases of long-lived organisms, however, one should be aware of the basic asymmetry in the variation of high survival rates. While there may be little opportunity to enhance the survival, there is plenty of scope for reducing such high values. The high elasticities of these values do point to the vulnerability of the population to changes in these demographic parameters (Heppell et al. 1996a,b, 1998). Continuous harvesting of the adults may result in major declines in population growth rates (Heppell et al. 1996b), and might critically affect the regeneration capacity of the populations, pointing to the need for a judicious use of elasticity analysis in management. Paradoxically, single harvests of mature tropical trees reduce the population size, but may actually increase the population growth rates, as

the populations are released from density-dependent control and growth, and as sexual recruitment is enhanced during the transient dynamics of population restoration (Zagt 1997, but see Batista et al. 1998).

These examples show that an evaluation of the elasticity landscape for the purpose of conservation should be accompanied by knowledge about the actual transition values, their biological constraints on variation, and management options (what transitions can most easily be enhanced). In some cases, this may reveal that management efforts should concentrate on transitions with the smaller, rather than the larger, elasticities (Heppell 1998).

Elasticities vary with population growth rate

There is a systematic variation in elasticity values of life cycle stages with population growth rate. Silvertown et al. (1993) showed a positive correlation between λ and the elasticity of fecundity among the transition matrices of 66 perennial plant species. Analyzing this relationship in more detail, Silvertown et al. (1996) compared the elasticities of growth (G), stasis (L), and fecundity (F) for populations of *Pedicularis furbishii* and *Cirsium vulgare* that differed in growth rate. They found a negative correlation between λ and the summed stasis elasticity, and positive correlations between λ and the summed growth and fecundity elasticities. This seems a general result, at least for plant life histories. Other species such as *Gentiana pneumonanthe* (Oostermeijer et al. 1996) and *Primula vulgaris* (Valverde and Silvertown 1998; Fig. 6A) show a similar pattern.

These correlations are easy to explain. The growth (G) and fecundity (F) groups together form the reproductive pathways in the matrix, and successful reproductive pathways (high fecundities, high establishment, and growth of recruits) may boost the growth rate of the population, which is a long-known fact (Lewontin 1965). Stasis transitions are always <1 , and a large contribution of these parameters will be typically associated with low growth rates or even declining populations (Fig. 6A). In one extreme case of a strongly declining population of *C. vulgare* ($\lambda = 0.18$), total elasticity was made up almost entirely of contributions from stasis transitions (Silvertown et al. 1996). Indeed, if fecundity fails completely, the elasticities of fecundity as well as of growth, being part of the same pathways, will become zero. In the case of a size-structured (Lefkovich) matrix, stasis of the largest size class will typically become the only loop contributing to λ . In such a situation, stasis elasticity will equal unity, and λ will take on the value of the highest stasis transition (Saether and Bakke 2000; R. Zagt, *personal communication*). Given the fact that parameters for growth and reproduction are intimately linked within the reproductive pathways of the transition matrix, changes in the elasticity landscape following changes in one or more matrix elements are even more clearly visible

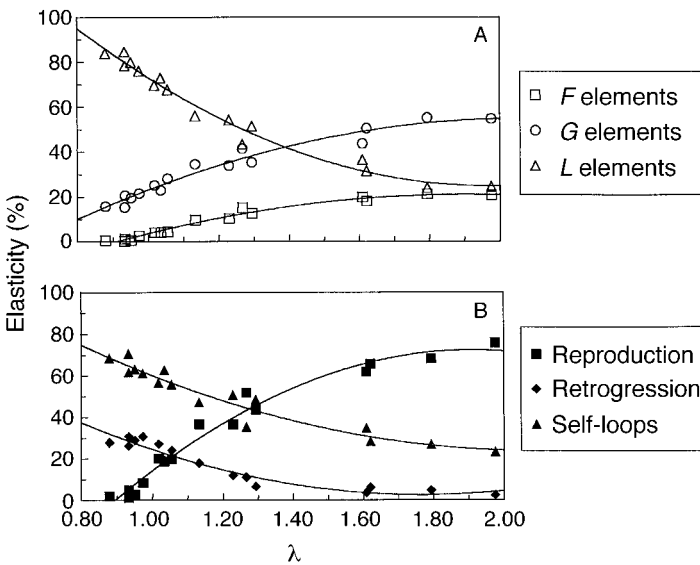


FIG. 6. The relationship between population growth rate and (A) summed elasticities and (B) loop elasticities, for nine populations of the forest understory perennial *Primula vulgaris* with different population growth rates. Two years of data are presented (except for two populations). Elasticities in (A) were summed in the categories fecundity (F), survival (L), and growth (G) (sensu Silvertown et al. [1996]). The life history loops in (B) are vegetative loops that involved shrinking (retrogression), self-loops, and reproductive loops (including growth). Lines are second-order polynomial curve fits. Data are from T. Valverde; for further details see Valverde and Silvertown (1998).

when expressed as changes in loop elasticities (see Fig. 6B). At low values of λ , delay mechanisms such as self-loops (stasis) and retrogression prevail at the expense of reproductive loops, which become important only at the higher population growth rates.

These patterns imply that caution should be taken to base management on elasticities of a matrix of a single population at a single time, especially if a population is declining (Silvertown et al. 1996). Silvertown et al. (1996) advocated considering a set of matrices and that intervention should take into account the relationship between elasticities of the major groups of transitions and λ (see Fig. 6). The choice of the appropriate measures will depend on the causes of the decline. In perennial plants, remnant populations with very little recruitment may only persist by the survival of some mature individuals (Eriksson 1996). Such situations would call for measures that enhance successful sexual reproduction, i.e., stimulation of life cycle parameters that have low, rather than high, elasticities. In contrast, if populations of long-lived turtles are threatened by human-caused mortality of adults, their decline can only be reverted by reducing adult mortality, rather than by stimulating recruitment (Crowder et al. 1994, Heppell et al. 1996a,b).

CONCLUSIONS AND UNSOLVED ISSUES

Elasticity and loop analyses decompose the population growth rate into contributions made by demographic parameters and life history pathways, respectively. As such, they not only provide important insight into the life history of the species, but also point to the parameters where population management should focus. However, for a sensible use of elasticities in conservation, additional information on the biology of the species and the options for management is required.

Such information may indicate that conservation measures should focus on parameters with the smaller, rather than the larger, elasticities.

Preliminary results suggest that elasticities are fairly accurate in predicting even large changes in growth rate as a result of large changes in transition elements. However, more information is needed about the robustness of elasticities in realistic settings, taking into account effects such as uncertainties in parameter estimates (Wisdom et al. 2000), model structure (Easterling et al. 2000), covariances between traits (van Tienderen 2000), and density dependence (Grant and Benton 2000). Moreover, we do not know to what extent environmental stochasticity (Benton and Grant 1996, Nakaoka 1997, Gaillard et al. 1998, Grant and Benton 2000) or catastrophes (Ludwig 1999), which may affect some transitions more than others, will blur predictions based on elasticities of time-invariant projection matrices. This calls for theoretical analyses, as well as broad comparative studies, extracting further information from the many transition matrices that are available today for a great variety of life histories (Silvertown et al. 1993, Pfister 1998, Heppell et al. 2000, Saether and Bakke 2000). Such analyses will be necessary to fully determine the reliability of elasticities for population management.

ACKNOWLEDGMENTS

We are grateful to Selina Heppell, Roderick Zagt, and Teresa Valverde for providing the data of Figs. 2A–C, 5, and 6, respectively. Together with Cathy Pfister, they also provided us with useful suggestions during the preparation of this paper and valuable comments on an earlier draft. This paper has further benefited from the comments of Hal Caswell, Pieter Zuidema, and two anonymous reviewers.

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