Predicting the Future of Rare Plant Populations: Demographic Monitoring and Modeling

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ABSTRACT: Conservation biology desperately needs techniques to predict the future of small populations and endangered species, and to guide conservation strategy and management tactics. In particular, information is required on extinction probability and minimum viable population. Techniques in population viability analysis are just being developed; they have the potential for providing such information, but have not yet been applied to plants. Most focus on genetic factors rather than environmental or demographic, although the last two may constitute more immediate threats to most small plant populations.

This paper reviews modeling and data collection approaches to predicting plant population behavior, emphasizing matrix projection of stage-structured populations. The projections are driven by empirical data on life history components: mortality, growth, and fecundity of individuals grouped by defined life history stages.

To fully utilize the techniques, a long-term commitment (three years or more) to data collection of moderate intensity is required. Data collection issues and methods are illustrated by referring to an ongoing study of Furbish's lousewort in Maine. Stage projection of population dynamics allows estimation of extinction probability, future population size, and equilibrium population growth rate. The effects of various management treatments and environmental conditions on these qualities may be contrasted, guiding the manager to decisions that maximize population growth and/or minimize extinction probability. Management should focus on critical life history stages as defined by the projection techniques. A largely unexplored class of stochastic projection techniques, using empirically derived data in computer simulations, offers realistic predictions for populations affected by environmental and demographic variation. It also allows explicit calculation of extinction probability and minimum viable population. Preliminary results suggest that moderate variation in mortality can markedly increase the probability of extinction.

INTRODUCTION

The Need for Demographic Monitoring and Prediction

Natural areas containing rare plant populations are often deemed particularly valuable. But is preservation itself always sufficient to safeguard a rare species? Rarity is a state, but understanding extinction, which is a process, requires a dynamic viewpoint (Frankel and Soulé 1981). Although rarer species may have a greater probability of extinction (Terborgh and Winter 1980, Wilcox 1980, Diamond 1984), not all such populations are endangered. Once a species is protected in one or more preserves, effective management of populations and their habitats may minimize the risk of extinction (e.g., Soulé and Wilcox 1980, Synge 1981, Schonewald-Cox et al. 1983). Applied research should focus on dynamic aspects of each species' individual life history, environmental requirements, and vulnerability to threats, with specific management strategies the goal. But even a thorough understanding of rare species' life history does not always suggest to what extent extinction is a threat.

Individuals and organizations concerned with conserving biological diversity face difficult questions when financial resources or political realities limit the number and size of preserves. How does one decide whether a rare plant population is thriving or in danger of extinction? Is a given reserve large enough to support a viable population? Would additions safeguard a protected population? Is active intervention necessary to rescue a declining population? Should a small, unprotected population be ignored because it is doomed to extinction?

To assure that natural areas are fulfilling their role in rare species preservation, techniques are needed to predict or anticipate future population changes, and to analyze what interventions may be

necessary to assure species persistence. Tools are needed to understand what factors promote extinction and to predict the probability of extinction from obtainable and measurable population parameters. This paper outlines relevant methods of demographic monitoring and modeling that can advance our ability to predict the future of rare plant populations. In particular, it describes stochastic, demographic models based on stage-structured populations, that can use field-collected data on individual species to generate predictions of population dynamics.

Extinction Probability (EP) and Minimum Viable Population (MVP)

Developing a predictive understanding of the relationship between a population's size and its extinction probability is crucial to conservation biology (Shaffer 1981) because it indicates minimum reserve sizes and suggests when active intervention is essential. Conservation biology has a vocabulary to begin this understanding, even including a name for the subfield of "population viability analysis" (Soulé 1985). But it has not developed precise or predictive tools.

Extinction can be caused either by systematic or stochastic factors. The latter will be of primary importance once populations are protected on reserves. Among stochastic factors, one can delineate environmental, demographic, and genetic stochasticity, and natural catastrophes (Shaffer 1981; Table 1). Each of these stochastic factors is more important in small populations. A minimum viable population (MVP) is of sufficient size so that extinction probability (EP) from some or all forms of stochasticity over a long time period is acceptably small. Populations smaller than MVP may be handicapped in some way so that recovery is impossible.

The MVP concept has been developed largely in relation to genetic stochasticity (Frankel and Soulé 1981). Small populations may lose genetic variation, causing inbreeding depression and loss of evolutionary flexibility (Hamrick et al. 1979, Levin 1984). Inbreeding accumulates gradually over time at a rate of $1/2 N_e$ per generation, where N_e is the effective population size, taking variance in progeny number, uneven sex ratios, and population fluctuations into account (Franklin 1980, Frankel and Soulé 1981). Inbreeding has negative effects on survival and reproduction, termed inbreeding depression. Small populations also are prone to a net loss of genetic variation (losses exceeding the mutation rate) that could limit evolutionary flexibility. However, low genetic variability can be advantageous for exploiting specialized conditions (Antonovics 1968); some genetically depauperate populations have persisted for some time (Babbel and Selander 1973).

Estimates of genetic MVP so far are general and based on approximations derived from *Drosophila* and cattle rather than for endangered species. For example, $N_e = 500$ is an often-cited MVP value necessary to maintain equilibrium between additive genetic variance gains through mutation and losses due to small population size. This value is based on bristle characteristics in homogeneous lines of *Drosophila* (Franklin 1980) and obviously may be inappropriate for other organisms or situations.

In formulating MVP's for plant species, genetic considerations may be secondary to demographic and environmental stochasticity, for several reasons. First, not all rare, isolated, or small populations are genetically depauperate, although some widespread species are. Electrophoretic data from very rare species, however, often show virtually no detectable protein variation, suggesting little overall genetic variation (e.g., Bonnell and Selander 1974, Gawler and Menges 1986). Most scientists agree that small and isolated populations usually develop lower within-population genetic variance

TABLE 1. Sources of Uncertainty for Populations*	
Source of Uncertainty	Causes
Demographic Stochasticity	Chance events in survival and reproduction, not related to the environment
Environmental Stochasticity	Variation in habitat, competitors, predators, parasites, and other external factors, acting on demographic properties of a population
Genetic Stochasticity	Changes in gene frequencies due to founder effect, drift, and small population size, and their effects on inbreeding depression and evolutionary flexibility
Natural Catastrophes	Floods, fires, droughts, etc.
* After Shaffer 1981.	

(Stebbins 1942, Solbrig 1972, Nei et al. 1975, Levin et al. 1979, Soule' 1980, Soltis 1982, Ledig and Conkle 1983, Moran and Hopper 1983, Levin 1984, Prentice 1984, Karron 1985, Rice and Jain 1985). However, exceptions are not uncommon (Mosquin 1971, Meagher et al. 1978, Stebbins 1980, Hamrick 1982, Griggs and Jain 1983, Loveless and Hamrick 1984).

Secondly, plant species may be innately tolerant to lowered genetic variance because of small neighborhood sizes (Ehrlich and Raven 1969, Schaal and Levin 1978, Levin 1981, Rai and Jain 1982), local genetic differentiation (e.g., Linhart 1974, Schaal 1975, Turkington and Harper 1979, Givnish 1981, Hamrick 1982, Davy and Smith 1985, Silander 1985), and greater occurrence of and tolerance to inbreeding, apomixis, and vegetative reproduction (e.g., Antonovics 1968, Jain 1976, Park et al. 1984). In plants, a direct link between low electrophoretic variation and inbreeding depression or loss of evolutionary flexibility has not been established. Stronger evidence of such links comes from animals like the cheetah (O'Brien et al. 1985). A final practical point argues for explicit consideration of nongenetic issues in modeling EP and MVP. If loss of genetic variation in small populations has deleterious effects, they should be expressed through mortality and fecundity rates. This means that it should be possible to predict population dynamics of genetically disadvantaged populations without having to know the mechanisms by which they are disadvantaged.

MODELING POPULATION BEHAVIOR

The remainder of this paper summarizes modeling approaches that may be used to predict extinction probability (EP) and minimum viable population (MVP) in individual plant populations based on demographic, not genetic, considerations. This review does not include the extensive literature using a multispecies island biogeographical approach to predict EP, considering instead the ecological properties of individual species (Jarvinen 1982, Wright and Hubbell 1983).

The simplest population model considers all individuals of a population the same (i.e., no population structure) and simulates their growth through time as exponential, logistic, or some other function. Extensions of the basic models have considered the effects of stochasticity in population growth rate or environmental carrying capacity (Levins 1969, Lewontin and Cohen 1969, Richter-Dyn and Goel 1972, May 1973, Keiding 1975, Roughgarden 1975, Fritz 1979, Leigh 1981, Ginzburg et al. 1982, Wright and Hubbell 1983, Strebel 1985), yielding results largely of theoretical interest. They do suggest that both the average population size and extinction probability increase with greater stochasticity in growth rate or carrying capacity.

Unfortunately, individuals of different ages, sizes, or sexes vary in such demographic properties as reproductive output and probability of survival, making nonstructured models inadequate for most predictive purposes. More useful models subdivide the population into groups based on age or life history stage (Lefkovitch 1965). In predicting an individual plant's demographic properties, size/stage generally is superior to age (Werner 1975, Sohn and Policansky 1977, Werner and Caswell 1977, Gross 1981) although both may interact in affecting population dynamics (Young 1985). Stage classifications are also essential for species with multiple modes of reproduction or complex modes of dormancy and establishment. To project the future dynamics of the population using stage-structured population growth, two mathematical approaches have been used: differential calculus or matrix algebra. These alternatives correspond to a continuous versus a discrete view of population growth (Charlesworth 1980). In matrix projections, life cycles and population growth are modeled as discrete steps, a formulation appropriate to most life histories, especially those in seasonal environments. Discrete-time models also typically allow a more varied set of solutions than continuous-time models based on calculus (Roughgarden 1979) and are generally easier to fit with available data.

Both approaches are hampered by a number of unreasonable assumptions. For example, much of their power derives from equilibrium assumptions, including constancy of demographic parameters over time and among individuals of the same life history stage. More realistic predictions may be obtained by using stochastic approaches, allowing life history components to vary over time or among individuals of the same stage. The stochastic approach also allows explicit calculation of EP and MVP, qualities of great interest to those studying or managing rare plants.

A stage-structured, stochastic, nonequilibrial model of the population dynamics of individual species could, in theory, be based on analytical methods or computer simulation. Analytical solutions to stochastic, age-structured population growth have appeared in theoretical and mathematical journals (e.g., Bartlett 1960, Pollard 1966, Sykes 1969, Cohen 1979, Tuljapurkar and Orzack 1980, Wu and Botkin 1980, Ginzburg et al. 1984, Goodman 1984, Tuljapurkar 1985). However, most arguments depend on crucial assumptions, special cases, or difficult mathematics. Many theoretical papers rely on a combination of analytical mathematics and numerical simulations (e.g., Boyce 1977, Tuljapurkar and Orzack 1980). Truly realistic analytical models of this type may be impossible (Turelli 1977). Computer simulation models are not only more tractable and flexible, they can incorporate compensatory mechanisms and systematic pressures on a species or its habitat. This article will outline the use of such stochastic models after describing how classic, deterministic models function and what their limitations are to understanding rare plant biology.

FIELD DATA COLLECTION

The projections described here require mortality, growth, and reproduction data

gathered by following individual plants over time. (These methods have been well used by academic plant ecologists, especially Harper (1977) and his colleagues). Measurements may include reproductive status, number of stems, stem diameter, height, number of leaves, leaf size, and rosette size. Since determination of the age of individuals is no longer required for these matrix projections, destructive or intrusive sampling (e.g., excavations, tree coring) is not necessary. Correlation analysis of one growing season's data can show which measurements are uninformative and can streamline future data collection. Grouping of individuals into stages is flexible, and alternate formulations are always possible. The choice of group definitions should minimize the variation in life history components (Vandermeer 1978), but such theoretical considerations may be overridden by practical matters of sample size. Subdividing the classes too finely (i.e. with too few individuals per class) can produce unreliable estimates of demographic parameters.

In the field, one needs to mark, map, or otherwise identify individuals. (The definition of an individual is not crucial as long as it is consistent.) Many approaches are possible, including marking locations with wire tags, swizzle sticks, markers, or the like, as well as detailed mapping and (for woody plants) metal markers affixed to the plants themselves. Common sense is important, with redundancy and appreciation for natural hazards (e.g., floods, fires, trampling) recommended. Incorporation of demographic monitoring into other levels of data collection (e.g., cover type, community composition, population structure) allows interrelation of environmental, community, and population data (Menges and McCune, in prep.).

The fate of individuals (mortality and growth to other stages) should be regularly followed, often annually, supplemented by an assessment of life history stages that cannot be measured so casually: seed production, seed dormancy, seed germination, and clonal spread. Seed production can be estimated by

destructive subsampling of fruits or infructescences, followed by allometric regressions of seed number on plant dimensions. Other aspects of seed behavior may require field experiments, as, for example, sowing known numbers of seeds and assessing the quantity of viable seeds in the soil by sampling and germination/viability tests. Biological interpretation of the species' life cycle is particularly important in deciding what quantities to measure.

If one suspects that life history components vary significantly with the environment, then stratify sampling by environmental class or measured environmental features. The environmental data need not be technologically sophisticated, and much may be learned by measuring life history components as a function of vegetation cover, soil depth, grazing intensity, burning history, community composition, or the like. Comparisons of calculated demographic parameters across experimental treatments, for example, will be of great interest to reserve managers.

Data from two field seasons can be enough to make preliminary analyses, but predictions are only as good as that time period is typical of the future. This implies that, if important events happen once a decade, any five-year monitoring plan can give misleading answers. Longer-term measurements also minimize procedural problems when individual plants "skip" a year (Gilbert and Lee 1980). In addition, stochastic approaches require enough measurements to estimate both temporal and spatial variability in life history components. This requires long-term monitoring.

Sufficient data to construct projection matrices for plant species is surprisingly uncommon, despite the number of long-term plant demographic studies that have been published. Static information gained from analysis of size or age structures is insufficient, because they imply dynamic rates only if conditions have not changed during the past history of the population. Dynamic data are often published, but in many cases does not encompass the entire life cycle of the

species. Statistics on seed dormancy, seed germination, reproductive output by size or age, and probability of flowering are commonly missing. Reproductive output is commonly measured as biomass produced, but propagule numbers and viability data are essential for demographic analysis. Even fewer data are available on variation in demographic parameters with environment or population or over time. Almost without exception, however, when multiple environments, sites, or years are investigated, parameters vary (e.g., Bierzychudek 1982, Werner and Caswell 1977).

CONSTRUCTING THE PROJECTION MATRIX

Matrix techniques project population age or stage structures forward through time (see Leslie 1945, Lefkovitch 1965, Keyfitz 1968, Roughgarden 1979, Charlesworth 1980). The projections begin with the structure of a population at one time. The structure then changes over one time step (often one year) as some individuals remain at that stage, while others grow to another stage or die. Stage-specific survivorships, fecundities, and transfer (growth) rates project the future of the population. Each is an element in a square matrix and is termed a life history component whose value (demographic parameter) can be empirically measured for a given population.

Generally, the population projection is expressed in matrix notation $n_{t+1} = \tilde{A}n_t$ where n represents the vector of stage distribution, $\tilde{A}$ is the projection matrix that includes as matrix elements the life history components, and t is time. Population projection and life history analysis depend on estimation of life history components and formation of the projection matrix $\tilde{A}$.

First, construct a diagram of the life history of the species. As an illustration, consider the life cycle of the endangered *Pedicularis furbishiae* of the St. John River in northern Maine and adjacent New Brunswick (Figure 1A). This perennial, iteroparous herb has no
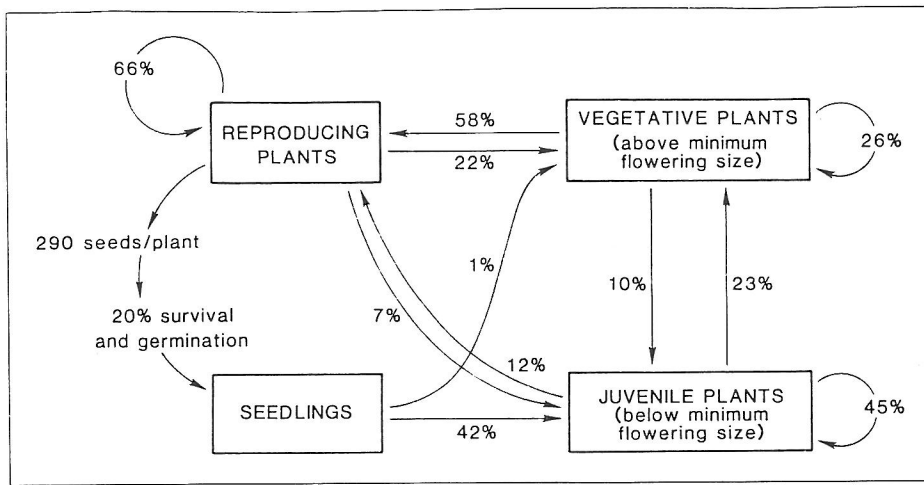
FIGURE 1A. Life cycle of *Pedicularis furbishiae*. Diagram of life cycle. Boxes show four stages present each August. Arrows show transfers each year. Reproductive output based on 1983 data, seed survival and germination on 1983-1984 data, and other transfers based on 1984-1985. Assume no seed dormancy.

al. 1985, Gawler and Menges 1986, Menges et al. 1986). In addition, these values represent populations not catastrophically disturbed by ice scour and bank slumping. Because these disturbances are crucial to large scale population dynamics (Menges and Gawler 1986), realistic models for Furbish's lousewort need to consider dynamics at two scales (Gawler, in prep.). Such realism is beyond the scope of this paper, so the projection matrix in Figure 1B is used for illustration only, and does not realistically represent the complete population dynamics of this species.

POPULATION BEHAVIOR UNDER DETERMINISTIC MATRIX PROJECTION

clonal growth, little or no seed dormancy, and produces seeds only after several years of vegetative growth. The four stages represented are seedlings, juveniles, vegetative plants, and reproductive plants. Juvenile and vegetative plants are both nonreproductive, but are divided by a size cutoff representing the minimum size for flowering (Menges et al. 1985).

Field techniques described above were used to generate the life history components shown in Figure 1A (Menges et al. 1985, Gawler and Menges 1986). In Figure 1B, each number represents a

transfer from the column stage to the row stage. For example, in one year, 42 percent of seedlings (stage 1, column 1) survived to become juveniles (stage 2, row 2) but only 1 percent became large enough to be classified as vegetative (row 3) and none became reproductive (row 4). The other 57 percent died. An average reproductive plant produced 290 viable seeds (column 4, row 1) and 20 percent of seeds survived, germinated, and survived until the next August (Menges et al. 1985). Each demographic parameter varied from year to year, from population to population, and as a function of microenvironment (Menges et

Under unvarying, deterministic conditions (limiting behavior analysis), matrix projection simulates a population tending asymptotically toward a stable stage distribution (constant percent of individuals in each stage) with population size constant, or growing or declining at a steady exponential rate. Either age and stage structured models yield analogous results and both can be considered general cases of populations structured by both age and stage (Law 1983). Even more generally, matrix projections are possible when demographic parameters depend on several factors (Goodman 1969). Deterministic

TO:	FROM:			
	Seedling	Juvenile	Vegetative	Reproductive
Seedling	0	0	0	290 x 0.2
Juvenile	0.42	0.45	0.10	0.07
Vegetative	0.01	0.23	0.26	0.22
Reproductive	0	0.12	0.58	0.66

FIGURE 1B. Projection matrix corresponding to life cycle in Figure 1A. See text for further explanation.

matrix projection analyses have been used to devise harvesting schedules in managed forests (Usher 1969) and evaluate the effects of harvesting on endangered animals (Goodman 1980, Flipse and Veling 1984).

At equilibrium, matrix algebra allows the calculation of several useful measurements of population behavior (see Table 2 for a summary and for key references, see Charlesworth [1980] for additional calculable values). The equilibrium finite growth rate ($\lambda = e^r$) is equal to the largest eigenvalue of the the projection matrix (Leslie 1945, Caswell 1982a). The equilibrium finite growth rate (λ) of the *Pedicularis furbishiae* population modeled by Figure 1 is 2.05, representing slightly more than a doubling of population size each year. A positive growth rate indicates that a population is demographically healhty, $\lambda < 1$ indicates that the population is destined for extinction unless conditions change. In fact, its high growth rate, typical of weedy plants such as *Dipsacus sylvestris* (Werner and Caswell 1977), emphasizes that Furbish's lousewort depends on natural disturbance for establishment, growth, and reproduction (Menges et al. 1985). It also points out the inadequacy of deterministic modeling, which predicts that we will be knee-deep in louseworts in just a few years. More realistic, but specific, models of *P. furbishiae* population dynamics are currently being formulated (Gawler, in prep.).

The equilibrium results are only reasonable under several conditions. Probabilities should only depend on the current, not past stage of each individual, a condition seldom tested (Usher 1979, Bierzychudek 1982). Results also depend on conditions which define the projection matrix remaining the same. For example, these analyses generally

TABLE 2. Calculable Demographic Results Using Deterministic Matrix Projection

Results	How Calculated (References)	Meaning/Limitation
Equilibrium Population Growth Rate (λ)	Dominant eigenvalue (Leslie 1945, Lefkovitch 1965, Hubbell and Werner 1979)	Population will reach equilibrium and grow or decline exponentially at this rate
Equilibrium Stage Structure	Dominant right eigenvector (Goodman 1967, 1982, Caswell 1982b, Silander 1983)	Proportion of population in each stage at equilibrium, can be compared to current structure
Reproductive Value (by stage)	Dominant left eigenvector (Goodman 1967, 1982, Mertz 1970, Caswell 1982a, b)	Relative importance of each stage to population growth; contribution to future generations of individuals in particular stages
Rate of Convergence to Equilibrium Stage Structure	Ratio involving first two eigenvalues (Goodman 1980)	Rate of approach to equilibrium
Density-Dependent Results	Additional terms, or by simulation (Leslie 1948, Pennycuick et al. 1968, Usher 1979, Smouse and Weiss 1975, Roughgarden 1979, Charlesworth 1980)	Given knowledge of density-dependence, more realistic results
Transient Results	Simulation (Caswell and Werner 1978, Law 1983)	Pre-equilibrium results may show greater and more realistic fluctuations
Sensitivity Analysis	For each matrix element (i, j) product of reproductive value of stage i and proportion of stage j at equilibrium; or by simulation (Caswell and Werner 1978, Goodman 1980, Caswell 1982b, Bierzychedek 1982, Piñero et al. 1984)	What effect does depressing or augmenting a process have on population growth? What are the pay-offs for specific management tactics that augment a particular process?
Interrelationship of Stages	Covariance analysis (Pielou 1974)	How do stages interact?

are independent of density, but survivorship probabilities may actually be density-dependent. Density-dependent modifications of matrix projections are possible (Leslie 1948, Guckenheimer et al. 1977) but are often constrained by inadequate knowledge of the form of density-dependence. Different formulations of density-dependence may lead to different population dynamics. The most general theoretical solution allows feedback among all stages (Smouse and Weiss 1975), but relevant data are very difficult to obtain without extensive experimentation, and analytical solutions lead to "mathematical terra incognita" (Roughgarden 1979).

Transient or short-term predictions avoid the worst assumptions of deterministic projections and thus may be more dependable than equilibrium predictions (Caswell and Werner 1978). Because these also address immediate concerns, a manager may be particularly interested in short-term predictions of population size and growth rate. These values are easily obtained by projecting population growth into the immediate future, beginning with the current stage structure or with an episode of colonization by a few propagules.

LIFE HISTORY ANALYSIS

Matrix projection techniques are valued not only for advancing predictive powers, but for understanding life histories. For example, population growth rates can be compared between burned and control treatments in a prairie. The demographic results of such a treatment cannot be ascertained merely by subtracting (adult) mortality from (juvenile) recruitment because an adult contributes relatively more to population growth than a juvenile. Matrix projection techniques can predict not only the overall effects of the treatment, but can quantify the relative importance (reproductive value) of various life history stages and the importance of transfers among stages (e.g., successful seedling establishment) (Caswell 1978, 1982a, b). Thus the analysis might suggest that better results would accrue from a burn timed to

minimize harm to adults, even if it does not maximize seed germination. Reproductive value can be calculated analytically, but sensitivity analyses using simulations are generally used for other aspects of life history analysis (Table 2).

These approaches can be used to suggest novel management strategies. We can quantify, for example, the relative importance of seed germination for the growth of a population. If important, we can explore the causes of its variable success. If related to plant cover, experimental thinning or mowing could be suggested. If related to soil moisture, modification or restoration of the site's hydrologic regime could be in order. Although a more casual approach could hit on a solution, limited resources could be wasted on a treatment that is demographically irrelevant. Identifying the bottleneck in a life cycle is crucial to finding an appropriate solution.

INCORPORATING VARIABILITY IN LIFE HISTORY

Empirical Evidence for Variability

The analyses described above are deterministic and based on point estimates of life history components (mortality, growth, and fertility values). Field biologists recognize that life history components vary among individuals, populations and subpopulations, and over time, and this variation may be more important to population dynamics than the average rates (Smith and Mead 1980). Even the average behavior of populations subject to variation differs from deterministic behavior (Tuljapurkar and Orzuck 1980, Goodman 1984). Therefore, stochastic models are more realistic, perhaps particularly for rare organisms exhibiting chaotic population behavior (cf., Vandermeer 1982). Plant populations generally do exhibit marked fluctuations in numbers (e.g., Tamm 1972a, b, Inghe and Tamm 1985, references in Austin 1981). Rare plants are not exceptions, judging from thirteen years of monitoring ten species at Tees-

dale, Great Britain (Bradshaw and Doody 1978, Bradshaw 1981) and a fifteen-year study of orchid species, also in Great Britain (Wells 1981). Variation in numbers over time is due to fluctuations in mortality and reproduction between and within populations (e.g., Bradshaw 1981, Davy and Jeffries 1981, Klemow and Raynal 1981, Wells 1981, Bierzychudek 1982, Lewis and Zenger 1982, Pinerō et al. 1984, Waite 1984, Menges et al. 1986).

Full stochastic simulation modeling of populations has not yet been attempted for real plant populations. (Bierzychudek [1982] alternated two matrices to simulate population growth of jack-in-the-pulpit.) Two studies explore these methods using data from grizzly bears. Other stochastic stage-structured simulation approaches include an explanation of why certain barnacles are not present on rocky New England shores (Wethey 1985), an exploration of the effects of skewed larval survivorship on spruce budworm population growth (Slade and Levenson 1984), and predictions of crane populations under stochastic birth and death processes (Miller and Botkin 1974).

Modeling Grizzly Bear EP and MVP

The well-studied grizzly bear has provided the best example of demographically based EP and MVP calculations. Shaffer and Samson (1985) varied demographic parameters (death, reproduction) to achieve stochastic population projection of a discrete population with age and sex structure. Both demographic and environmental stochasticity were simulated. Given a criterion of a 95 percent probability of survival for 100 years, an MVP of fifty to ninety bears was estimated, considerably more pessimistic than previous estimates of about twenty for MVP. Given environmental stochasticity, a population of twenty bears would have only a 36 percent chance of survival for 100 years. Unfortunately, an MVP of fifty bears implies a need for a reserve size larger than Yellowstone National Park, which now supports a declining bear population (Newmark 1985).

Knight and Eberhardt (1985) have also applied stochastic population projections to grizzly bear data. In this case, rather than varying demographic parameters for the entire population, individuals varied annually in survival and reproduction (demographic stochasticity). This alternate sort of variability was less extreme and predicted a lower EP.

Preliminary Results with Plant Species

I have made a rather generic and preliminary study of the effects of introducing variation into life history projections of plant populations (see Menges 1987 for more details). In doing so, two types of stochasticity are distinguished, which, if treated analytically, would involve different mathematics. Demographic stochasticity is modeled by applying matrix probabilities independently to each individual (Pollard 1966), causing fluctuation of populations because of minor variation in mortality, growth, and reproduction unrelated to environmental variation (May 1973, Roughgarden 1979). Environmental stochasticity describes variation in the external environment, which affects the demographic properties of the entire population. Environmental variation can encompass many factors important to population dynamics, such as competition, predation, parasitism, microenvironmental heterogeneity, and catastrophic disturbance. When added to a deterministic model, environmental stochasticity tends to disperse the "cloud" of possible results (May 1973). In stage-structured models, environmental stochasticity is simulated by varying matrix elements over time and applying them to the entire population (Sykes 1969 model 3, Boyce 1977, Cohen 1979). The form of environmental stochasticity modeled by Menges (1987) is conservative in that different elements vary independently (e.g., a bad year for seedlings may be a good year for reproductive plants) and that there is no environmental autocorrelation or cyclic behavior (Tuljapurkar and Orzack 1980, Leigh 1981, Tuljapurkar 1985).

To date, I have applied these methods to twenty-eight published projection matrices representing mean conditions, with the following general results (Menges 1987):

1) Stochastic modeling can reproduce realistic fluctuations and population sizes without density-dependence for populations with modest deterministic equilibrium growth rates ($\lambda <$ 1.05). Because density-dependence is difficult to quantify, these results suggest that modeling efforts can be based on modest levels of data collection.

2) Environmental stochasticity limits population sizes and increases extinction probability. Slow-growing populations are most vulnerable to environmental variation. Because this variation is important, long-term monitoring is desirable.

3) Environmentally induced variation in reproductive output is inconsequential compared to environmentally induced variation in mortality and growth for perennial plants. Therefore, the greatest amount of monitoring effort should be focused on following the fates of established plants.

4) Demographic stochasticity is significant in causing extinction only for some species with deterministic growth rates near one. Even these populations are more sensitive to environmental stochasticity. This means that for most populations, quantification of environmental stochasticity is important.

One practical extension of stochastic simulations of population growth will be the designation of MVP's with respect to environmental and demographic stochasticity. This is possible because, given quantification of a mean life history and its variation over time, extinction probability will decrease with increasing initial population size. If initial size is large enough (for many life histories), EP will drop to acceptable levels. Populations of this size should be secure and are MVP's. For modest environmental stochasticity, these MVP's are generally greater than published genetically based MVP's (Menges 1987), implying that environmental stochasticity may be a greater threat to plant populations than genetic stochasticity.

Practical application of demographic modeling is data-limited at the present time. The required data are straightforward to collect (as described previously) but require attention to the entire life cycle and perseverance for several years if detail on variation is desired. However, monitoring efforts directed at endangered species may succeed in creating suitable databases in the near future. A union of efficient, continuing data collection and realistic modeling can soon be expected to provide MVP's for rare plant populations and answer the practical questions posed at the beginning of this paper.

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