AN ABSTRACT OF THE DISSERTATION OF

Thomas N. Kaye for the degree of Doctor of Philosophy in Botany and Plant Pathology presented on May 18, 2001. Title: Population Viability Analysis of Endangered Plant Species: an Evaluation of Stochastic Methods and an Application to a Rare Prairie Plant.

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Transition matrix models are one of the most widely used tools for assessing population viability. The technique allows inclusion of environmental variability, thereby permitting estimation of probabilistic events, such as extinction. However, few studies use the technique to compare the effects of management treatments on population viability, and fewer still have evaluated the implications of using different model assumptions. In this dissertation, I provide an example of the use of stochastic matrix models to assess the effects of prescribed fire on *Lomatium bradshawii* (Apiaceae), an endangered prairie plant. Using empirically derived data from 27 populations of five perennial plant species collected over a span of five to ten years, I compare the effects of using different statistical distributions to model stochasticity, and different methods of constraining stage-specific survival to ≤100% on population viability estimates. Finally, the importance of correlation among transition elements is tested, along with interactions between stochastic distributions and study species, on population viability estimates.

Fire significantly increased population viability of *L. bradshawii*, regardless of stochastic method (matrix selection or element selection). Different processes of incorporating stochasticity (i.e., matrix selection vs. these statistical distributions for element selection: beta, truncated normal, truncated gamma, triangular, uniform, and bootstrap) and constraining survival (resampling vs. rescaling procedures) yielded divergent estimates of stochastic growth rate, and there was a significant interaction between these methods. These effects were largely explained by the degree of bias the different methods caused in transition elements. Incorporating correlation among elements caused a significant, but small, reduction in estimated stochastic growth rate in two of five species examined, yet there was no interaction with stochastic method in this effect. Much of the variation in average response to correlation structure among species was due to the relative balance between positive and negative associations among the vital rates. Although alternative techniques may lead to very strong differences in estimates of population viability, conclusions about the relative ranking of populations or treatments are robust to differences in stochastic methods.

Population Viability Analysis of Endangered Plant Species: An Evaluation of Stochastic Methods and an Application to a Rare Prairie Plant

by
Thomas N. Kaye

A DISSERTATION

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Completed May 18, 2001
Commencement June 2001

Doctor of Philosophy dissertation of Thomas N. Kaye presented on May 18, 2001

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Thomas N. Kaye, Author

ACKNOWLEDGMENTS

This dissertation is the result of a great deal of work on the part of many people over several years. I am grateful for financial support from Oregon Department of Agriculture's Plant Conservation Biology Program; Oregon State University; Institute for Applied Ecology; the Bureau of Land Management Eugene, Medford, Prineville, Salem, and Vale Districts; and the U.S. Forest Service Mt. Hood, Rogue River, Umpqua, and Willamette National Forests; the U.S. Fish and Wildlife Service, Portland Field Office; and the U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, Corvallis, Oregon. The Native Plant Society of Oregon helped finance conservation biology interns that assisted with data collection for all of the species studied in this project, and I thank NPSO and a long list of interns that have helped over the years, including (in chronological order) Tom Brophy, Mary Garrard, Eric Peterson, Ed Hoover, Margaret Evans, Steve Gisler, Lupin Loel, Melissa Peterson, Jill Van Winkle, Armand Rebischke, Shannon Datwyler, Kelly Cahill, April Cameron, Robin Russell, Jenny Tilson, Sue Kolar, Sarah Brown, Annie Turner, Sahni Burkhart, Carla Cole, Shannon Clery, Jeff Stephens, Madi Novak, Lisa Karst, Mitchell McGlaughlin, Cormac Collier, Diana Fodor, Seth Bond, Lauren Mathewson, and David Matlaga. I thank Bob Meinke and Chuck Craig for their support over the years and for the opportunity to work for the state of Oregon's Plant Conservation Biology Program since its creation in the late 1980s. Many people with the ODA program also helped with data collection and entry, including Sarah Brady, Sarah Brown, Shannon Clery, Jack Greenlee, Melissa Kirkland, Keli Kuykendall, Susan Massey, Wes Messinger, Kendra Mingo, Angie Ruzicka, and Annie Turner. I would especially like

to thank ODA staff Matt Carlson, Steve Gisler, and Kelly Amsberry for their help and friendship. The following individuals, through their positions with federal agencies, were instrumental in making my research possible: Cindy Barkhurst, Kat Beal, Paula Brooks, Clair Button, Cindy Cripps, Jenny Dimling, Aaron Drew, Jean Findley, Nancy Fredricks, Ron Halvorson, Richard Helliwell, Claire Hibler, Jerry Hustafa, Jim Irving, Dean Longrie, Cheshire Mayrsohn, Linda Mazzu, Cheryl McCaffrey, Maura Naughton, Kathy Pendergrass, Bruce Rittenhouse, Andy Robinson, Larry Schofield, Joan Seevers, Alice Smith, Bryce Smith, Marty Stein, Molly Sullivan, Julie Thiel, Brad Tong, Carl Urban, Molly Widmer, and Nancy Wogen. Staff of the Oregon Natural Heritage Program, including Jimmy Kagan and Sue Vrilakas, provided valuable assistance and information on the location of rare plant populations. I would also like to thank these colleagues in the Department of Botany and Plant Pathology at Oregon State University for their years of teaching, friendship, and fruitful discussions: Johanna Brunet, Henny Chambers, Ken Chambers, Deborah Clark, Stella Coakley, Cheryl Ingersoll, Richard Halse, LaRea Johnston, Aaron Liston, Dianne Simpson, Mark Wilson, and Don Zobel. Scott Sundberg, who works longer hours than most lawyers, endured sharing an office with me for the last several years. I am eternally grateful to Manuela Huso for her patience and help with statistics. Kathy Pendergrass, Karen Finley, and Boone Kauffman are co-authors on the fire ecology chapter, and I thank them sincerely for their work. I look forward to continuing working relationships with Keith Karoly (Reed College), Ed Guerrant (Berry Botanic Garden), Susan Kephart (Willamette University), and Dave Craig (Willamette University). I have been very fortunate to have had the opportunity to learn from and discuss my

dissertation work with Russ Lande (University of Oregon), Eric Menges (Archbold Research Station), Doug Schemske (University of Washington) and Scott Ferson (Applied Biomathematics), and I want to express particular gratitude to Hal Caswell (Woods Hole Oceanographic Institute) for giving me the chance to look over his shoulder into the nitty-gritty of matrix modeling and for reviewing portions of this dissertation. Many thanks to my committee members, Dave Pyke, Pat Muir, Mike Blouin, Steve Radosevich, and Ralph Berry, for taking the time to help me and guide my studies. Finally, I thank my mother and father, my wife, Keli Kuykendall, and our daughter, Lila.

CONTRIBUTION OF AUTHORS

Dr. J. Boone Kauffman was involved in the design of the prairie burning experiment with *Lomatium bradshawii* presented in Chapter 2. Kathy Pendergrass and Karen Finley collected data and also assisted with the analysis conducted in Chapter 2. David A. Pyke provided guidance in the implementation of the analyses and writing of chapters 3 and 4.

TABLE OF CONTENTS

TABLE OF CONTENTS, CONTINUED.

LIST OF FIGURES

LIST OF FIGURES, CONTINUED.

LIST OF FIGURES, CONTINUED.

LIST OF TABLES

LIST OF TABLES, CONTINUED.

Population Viability Analysis of Endangered Plant Species: An Evaluation of Stochastic Methods and an Application to a Rare Prairie Plant

Chapter 1. Introduction

STOCHASTIC POPULATION MODELS IN ECOLOGY AND CONSERVATION BIOLOGY

Rare organisms that inhabit variable environments appear to be at the greatest risk of extinction. Computer simulations illustrate that increases in environmental variation cause a corresponding increase in extinction probability (Menges 1992). In the *Origin of Species*, Darwin (1859:153) noted that "any form represented by few individuals will, during fluctuations in the season or in the number of its enemies, run a good chance of utter extinction." It is this chance of extinction and decline in viability of populations that forms the focus of this dissertation.

A key goal of conservation biology is to maintain viable populations of rare species (Soulé 1987). This dissertation utilizes knowledge of environmental variation to estimate extinction risk or stochastic population growth rate for populations of rare plant species. My approach centers on transition matrix modeling, using demographic information from structured populations to project their growth or decline. Because matrix models can incorporate observed levels of environmental stochasticity to simulate population dynamics through time, they can be used to calculate the chance of population loss under various conditions. Land stewards can use this information to determine whether a management action should be taken to benefit a species of concern

(Schemske et al. 1994). This type of analysis, therefore, is directly applicable to management and conservation of natural populations.

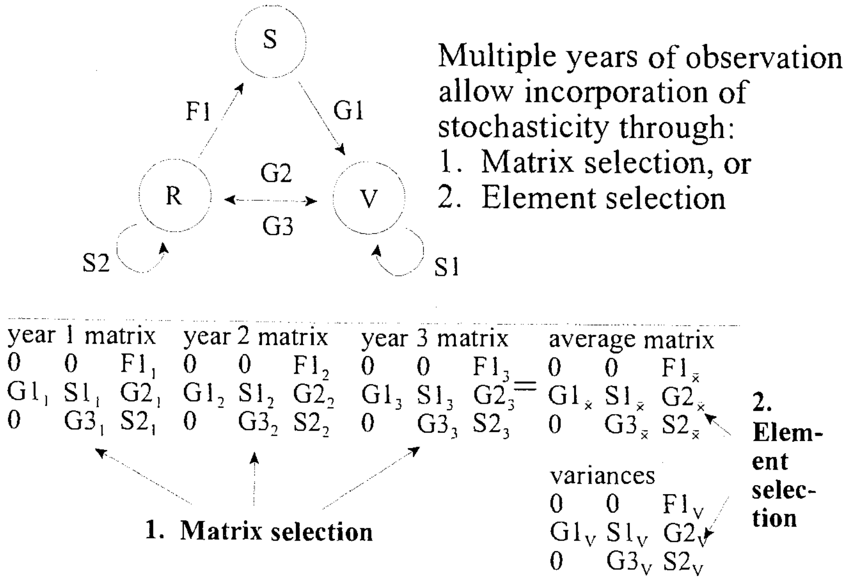
Transition matrix models are recommended widely as an effective method for evaluating demographic data, especially for calculating population growth rate, extinction probability, and sensitivities (e.g., Menges 1986, Burgman et al. 1993, Schemske et al. 1994, Caswell 2001). Such matrices are based on the Leslie matrix format (Leslie 1945), as modified by Lefkovitch to fit the more general form of a size or stage-structured population (Lefkovitch 1965).

Transition matrices have been used extensively to evaluate population dynamics of plants with various life histories, including trees (Hartshorn 1975, Namkoong and Roberds 1974, Enright and Ogden 1979, Pinero et al. 1984, Burns and Ogden 1985), herbaceous perennials (Sarukhan and Gadgil 1974, Bierzychudek 1982, Meagher 1982, Fiedler 1987, de Kroon et al. 1987, Kaye 1992, Menges 1986 and 1990, Gregg 1991), biennials (Caswell 2001), and annuals (Schmidt and Lawlor 1983). However, significant theoretical and practical issues pertaining to matrix models have not been resolved in the literature, thus limiting their application by managers and technicians. First, environmental stochasticity can be incorporated into matrix models through matrix selection (Menges 1990) or element selection (Ferson 1991; see also Burgman et al. 1993), but these methods may yield substantially different results (Greenlee and Kaye 1997). A formal comparison of stochastic methods is currently lacking in the published literature. Second, little attention has been given to the problem of constraining stage specific survival to 100%, a problem that arises in element selection for stage (but not age) structured models. Lastly, the effect of correlation among vital rates under theoretical conditions has been discussed by a few authors (e.g., Tuljapurkar 1982, Orzack 1993 and 1997, Ferson in prep.), but formal tests of the effect of correlation on multiple species are lacking.

A NOTE ON TRANSITION MATRIX METHODS

In this dissertation, transition matrix models will be constructed for each species by calculating the proportion of individuals that make the transition from one stage to another between years, and the fecundity of each stage (based on fruit production and seedling recruitment measurements). Separate matrices will be built for each pair of years available, e.g. 1992-93, 1993-94, etc. See Caswell (2001) for a complete description of matrix population models and their implementation. Extinction probabilities (calculated in Chapter 2) will be defined as the likelihood that a population will drop below 10 individuals in a 100-yr period, and stochastic growth (Chapters 2-4) rate will be approximated via long-run simulation (Caswell 2001).

Two methods of incorporating environmental stochasticity (and thus calculating extinction probability and stochastic growth rate) will be utilized in this dissertation: matrix selection and element selection. Burgman et al. (1993) review some matrix and element selection procedures. Matrix selection involves randomly selecting a whole matrix (from among a collection of matrices available from a series of years of observation) at each time-step in the model simulation (Figure 1.1) (e.g., Menges 1992). In contrast, element selection is implemented by building a new matrix at each time step with each new element drawn from a distribution with a specified mean and variance (calculated from the collection of individual matrices) (Figure 1.1). This procedure can employ various statistical distributions.



Multiple years of observation allow incorporation of stochasticity through:
1. Matrix selection, or
2. Element selection

Figure 1.1. A transition matrix model. Matrix selection involves randomly selecting whole matrices (e.g., year 1, 2 or 3) at each time step of the simulation, while element selection generally involves building a new matrix from the mean and variances of each element.

DISSERTATION SCOPE

In Chapter 2 of this dissertation, I present an in-depth evaluation of the effects of prairie burning on an endangered plant of Willamette Valley wetlands, *Lomatium bradshawii*, a near-endemic that appears to be declining due, in part, to fire suppression. Specifically, the impact of fire is evaluated in terms of its effect on extinction probability and stochastic growth rate of wild populations subjected to different fire frequencies. This chapter demonstrates the utility of the matrix model approach for assessing the impact of alternative management practices on population viability, and compares two methods of stochastic modeling.

Chapter 3 broadens the scope of the dissertation to a consideration of methodological issues, utilizing empirical data from 27 populations of five perennial plant species collected over periods ranging from 5 to 10 years. The effects of different methods of incorporating stochasticity are evaluated with stochastic growth rate as the response variable. These methods include matrix selection (also known as whole-matrix bootstrapping) and six statistical distributions for element selection (beta, truncated gamma, truncated normal, triangular, uniform, and observed/discontinuous). This evaluation also considers the effects of two different methods of constraining stage-specific survival to 100%, and tests for interactions between stochastic and survival constraint methods.

The issue of correlation among vital rates is considered in Chapter 4, along with an examination of interactions with species and stochastic methods. Correlation among matrix elements is a significant issue because it can increase or decrease estimates of population viability, such as stochastic growth rate, depending on whether the correlations are positive or negative (Orzack 1997). This creates some uncertainty in viability estimates and the need for including correlation structure, which can be an analytically cumbersome process. Even so, correlation structure has rarely been included in stochastic matrix models (Table 4.2). I use a method of generating correlated random numbers that employs a normal copula, a technique of specifying dependencies of variables that has been overlooked in the ecological literature.

Each successive component of this dissertation seeks to build on the last. A pervading goal among the chapters is to explore applications of ecological theory to some of the practical needs in conservation biology. These needs include improvements in management of endangered species and refinement of tools available to the practitioner of population viability analysis. By exploring both a specific case study and general methodological issues, I hope to contribute in some form to the advancement of the fields of ecology and conservation biology.

Chapter 2

The Effect of Fire on the Population Viability of an Endangered Prairie Plant

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Accepted by *Ecological Applications*

INTRODUCTION

Fire is a disturbance that influences plant population dynamics and can change plant community structure (Bond and van Wilgen 1996). Many rare plant species occur in fire-dependent communities (Myers 1989, Johnson and Abrahamson 1990, Campbell et al. 1991, Jacobson et al. 1991, Hardin and White 1992, Carlson et al. 1993, Menges and Kimmich 1996), and fire suppression is the principal threat to 4.1% of the endangered flora in the U.S. (Schemske et al. 1994). Conversely, some rare species are threatened by burning of their habitat, especially in tropical regions (e.g., Stone and Scott 1985). Therefore, managers can improve conditions for rare plants if they have specific knowledge of how populations of such species respond to fire (Hessl and Spackman 1995).

The effect of fire on life history processes has been explored for several rare plants. Burning can increase flowering and fruiting (Johnson and Blyth 1988, Hartnett and Richardson 1989, MacRoberts and MacRoberts 1990), seed germination (Borchert 1989, Boyd and Serafini 1992, Jacobs 1993), seedling establishment (Gankin and Major 1964, Barker and Williamson 1988), growth (Barker and Williamson 1988), or combinations of these processes (Lesica 1999, Menges 1995). In some rare plant species, burning has both positive and negative effects, such as increasing seedling recruitment while killing adults (e.g., Dunwiddie 1990, Menges 1992a). In others, fire has no clear effect on adult survival (Warren et al. 1992) or flowering (McClaran and Sundt 1992). Although prescribed burning is a recommended tool for rare plant conservation in various habitats (Folkerts 1977, Currier 1984, Jacobson et al. 1991, Kaye 1992, Phillips et al. 1992, Hawkes and Menges 1995), decisions to manage habitat with fire should be informed by careful experimentation, monitoring, and interpretation of results (Owen and Rosentreter 1992).

The overall impact of a disturbance on a population is a summation of its effects on various vital attributes (Noble and Slatyer 1980), and should not be inferred from a response at one or two points in a life cycle. Transition matrix models are an appropriate tool for assessing the impact of a management strategy on endangered species because they synthesize population dynamics at many life history stages (Schemske et al. 1994, Silvertown et al. 1996). They can be used to generate several useful statistics, such as population growth rate, extinction probability, and elasticities. However, only a few matrix-based evaluations of the effect of controlled burning on rare plants have been published to date (but see Manders 1987, Lesica 1997, Menges and Dolan 1998, Gross et al. 1998). In this paper, we use matrix models to evaluate burning as a management tool for an endangered plant. This approach integrates the influence of fire on plant growth, survival, fecundity, and mortality so that effects are measured at the level of population dynamics. We focus primarily on stochastic measures of population viability without burning and with two different fire frequencies to test the hypothesis that fire improves conditions for this species. In addition, we compare results derived from two widely-used methods of stochastic projection. We use elasticities to evaluate which demographic processes are most important to changes in growth rate caused by fire.

Lomatium bradshawii (Rose) Math. & Const. (Bradshaw's lomatium, Apiaceae) is listed by the U.S. Fish and Wildlife Service and the Oregon Department of Agriculture as an endangered species (Oregon Natural Heritage Program 2001). It is an herbaceous plant from a perennial taproot, reproducing only by seed. The seeds generally mature in June and passively disperse in July, then germinate by the following April. Its flowers are pollinated by a diverse assemblage of insects, especially solitary bees and flies (Kaye 1992). Most known populations of *L. bradshawii* occur in fragmented habitats in southwestern Washington and the Willamette Valley of western Oregon. Approximately sixteen populations are known, varying in size from less than fifty to 25,000 individuals, and less than one to about 40 ha (Parenti et al. 1993). The largest concentration of reported sites is in the southwestern Willamette Valley, west of Eugene, Oregon. A recovery plan for *L. bradshawii* (Parenti et al. 1993) identifies population enhancement as needed for the species' recovery.

Lomatium bradshawii occurs in remnants of two types of formerly widespread prairies. Seasonally saturated wetlands in shallow soil over basalt in Marion and Linn counties, Oregon, support a small number of populations (Alverson 1990). Most populations, however, occupy valley-bottom prairie dominated by *Deschampsia cespitosa* (tufted hairgrass) and characterized by deep pluvial clays and a perched water table. The latter habitat type has been described in some detail (e.g., Moir and Mika 1976, Kagan 1980, Alverson 1989, and Finley 1994), and typifies the sites included in our study. Both habitat types are part of the prairie-oak savannah ecosystem of western

Oregon interior valleys that was widespread before regional fire suppression and settlement in the mid- to late 1800's (Habeck 1961, Johannessen et al. 1977). Prior to Euro-American settlement, these prairies were maintained by frequent fall fires set by Native Americans to promote food plants, such as camas (*Camassia quamash* and *C. leichtlinii*), and to herd game for improving hunting success (Johannessen et al. 1977). Today, less than one percent of presettlement-composition prairies remain, and tools for managing this habitat for native and endangered species are urgently needed (Wilson et al. 1995).

METHODS

Study sites, burning treatments and plots

We used information from two populations to evaluate the effect of fire on the demography of *Lomatium bradshawii*. Both were within the southwest part of the species' range, in an area west and north of Eugene, Oregon, in valley-bottom prairie habitat that had not burned in several decades. These populations occurred within the Fern Ridge Research Natural Area at two sites: Fisher Butte (44°3' N, 123°15' W) and Rose Prairie (44°5' N, 123°15' W). The land is managed by the Army Corps of Engineers. Two additional populations were included for seed bank evaluation, Buford County Park (43°60' N, 122°56' W), east of Eugene, and the Long Tom Area of Critical Environmental Concern (ACEC, 44°9' N, 123°18' W), which is managed by the Bureau of Land Management. Throughout this report, these sites are referred to as Fisher Butte, Rose Prairie, Buford Park, and Long Tom, respectively.

Three burning treatments were conducted at Fisher Butte and Rose Prairie from 1988 through 1993 to determine the effects of fire on *Lomatium bradshawii* population dynamics. All burns were conducted in October. These treatments were control (no burning), burned twice in six years (1988 and 1991), and burned three times in six years (1988, 1989, and 1991). The population areas were divided into more or less equal strips, roughly four ha each at Fisher Butte and two ha each at Rose Prairie, and randomly assigned one of the three treatments prior to burning (see Pendergrass et al. 1998; and Pendergrass et al. 1999 for more details). Burn characteristics at each site, including flame length, height, depth and heat per unit area were recorded in 1988-1989 and are reported elsewhere (Pendergrass et al. 1998). Permanent monitoring plots were sampled annually in areas exposed to the three treatments. To establish these plots, mature *Lomatium bradshawii* plants (reproductive or large vegetative) were randomly chosen from throughout the population areas and tagged in 1988. These individuals were numbered, and a subset, ten at Fisher Butte and six at Rose Prairie, were randomly selected from each treatment type to serve as center points for permanent circular plots (2-m radius). All *L. bradshawii* individuals were mapped in each circular plot in May or June of each year (prior to burning) from 1988 through 1993. Seed production and umbel number were recorded annually for all tagged plants, including those at the center of each circular plot and outside the plots.

Transition elements and matrices

Two general approaches, analytical methods and biological classifications, have been used to define categories for stage-based models (Horvitz and Schemske 1995). Analytical methods maximize within-class sample sizes and minimize error of estimates (Vandermeer 1978, Moloney 1986, Fiedler 1987), and biological classifications rely on size, age, gender, reproductive states, development, or some combination of these (e.g., Lefkovitch 1965, Usher 1976, Bierzychudek 1982, Aplet et al. 1994, Maschinski et al. 1997). We used a biological classification that combined plant size and reproductive state to classify each *Lomatium bradshawii* individual into one of six stages: seedling (S), vegetative plant with one or two leaves (V2), vegetative plant with three or more leaves (V3), and reproductive plant with one (R1), two (R2), or three or more (R3) umbels. Reproductive plants were segregated by umbel number because one-umbel plants rarely produce seed (most of their flowers are male-only), while two-umbel plants produce seeds on the second umbel, and plants with three or more umbels may produce many seeds (T.N. Kaye, unpublished data). Thus differences in the size of reproductive plants affect their sexual function and fecundity rates, a pattern found in several members of the Apiaceae (Schlessman 1978, Lindsey 1982, Lindsey and Bell 1985). We combined vegetative plants with one or two leaves into a single stage because field observations indicated that plants with one leaf often produced a second leaf later in the year, and therefore leaf number of small plants may be a function of sampling date and/or variation in seasonal phenology, not plant vigor. Seedlings were defined as first year plants, often with cotyledons. All vegetative plants with one leaf were considered seedlings in 1988.

To construct transition matrices, we calculated the proportion of individuals in each stage that remained the same or changed to a different stage from one year to the next. To estimate the number of seedlings produced by individuals in each reproductive stage, we first determined the mean number of seeds produced by each stage (with data recorded for tagged plants) and the number of reproductive individuals within each plot to estimate the number of seeds produced in each plot in year t. Seedlings observed in year $t+1$ were then apportioned among the reproductive stages based on seed production and density of each stage in year t. These proportions and fertilities were organized as transition elements in a matrix following standard methods (Lefkovitch 1965, Menges 1986, Caswell 2001) and according to our conceptual model of population dynamics for this species (Figure 1). Annual transition matrices, hereafter referred to as detailed matrices, were constructed for each of five growing seasons from 1988-89 to 1992-93, and for each treatment at Fisher Butte and Rose Prairie. These detailed matrices can be found in Caswell and Kaye (in review). A mean matrix for each site and treatment combination was produced from each set of detailed matrices with a corresponding set of variances, one variance (representing environmental stochasticity) for each mean matrix element. Sample sizes for large reproductive plants (R3) were small because plants in this stage were uncommon in our study populations. In some cases (unburned plots at Rose Prairie in 1989 and 1992, and burned plots at that site in 1991), no R3 plants were observed, making it impossible

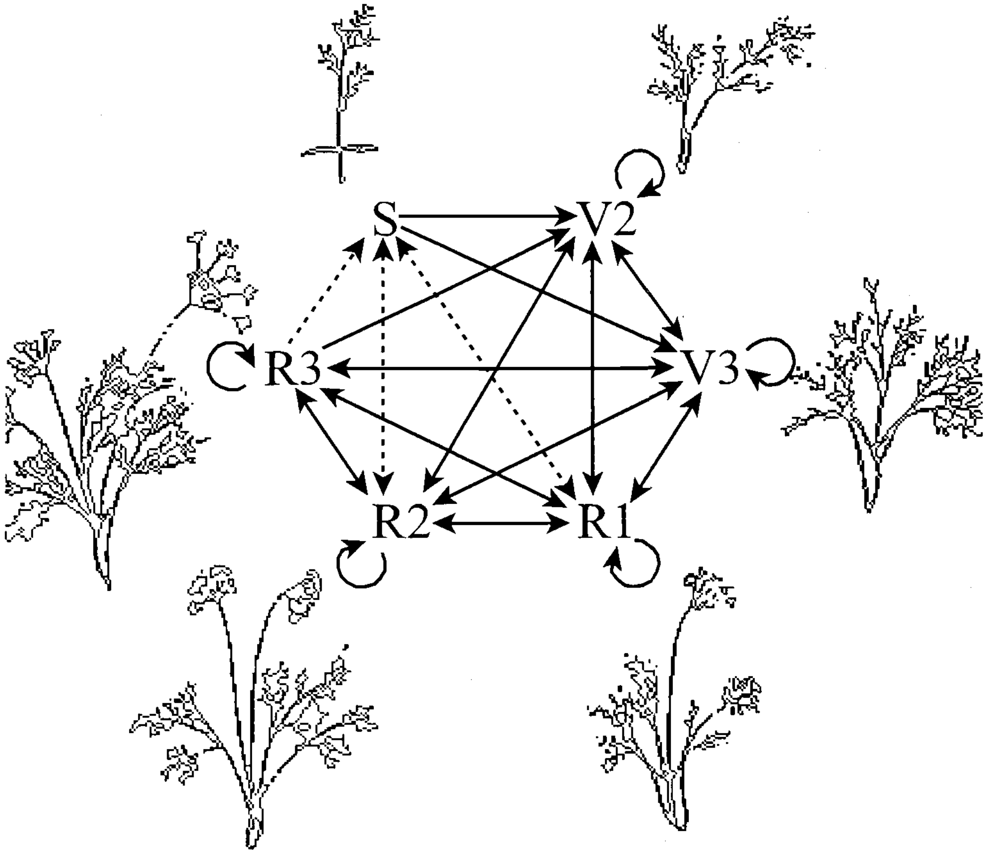

Figure 2.1. Conceptual model of the life cycle pathways of *Lomatium bradshawii*. Each arrow represents possible transitions plants can make from one year to the next. Dashed lines pointing to the seedling stage indicate reproduction. Double-headed arrows indicate regression to a smaller stage or growth to a larger stage. Stages identified in this model are first year seedling (S), one to two-leaved vegetative plants (V2), vegetative plants with three or more leaves (V3), and reproductive plants with one (R1), two (R2), or three or more (R3) umbels.

to estimate transitions for this stage. To resolve this problem, we replaced the R3-column of each of these detailed matrices with the average values from that stage for the appropriate site and treatment.

We used loglinear analysis to test for treatment and site effects on stage-specific survival and transitions. Count data (Table 2.1) for each transition were summed across all years. These data formed a 4-way transition frequency table with three explanatory variables: treatment (*T*, unburned, 2 burns, or 3 burns), location (*L*, Fisher Butte or Rose Prairie), and initial class (*C*, stages S through R3). The response variable was individual fate (*F*, stages V2 through R3 and death). A constant 0.5 was added to all cells prior to analysis (as recommended by Fingleton [1984]). In this analysis, the transition frequency table was modeled as a linear function of the logarithm of the cell frequencies (see Silva et al. [1990] for a detailed application of this analysis to demographic data). The presence of an interaction in these hierarchical models implies the presence of all lower order interactions involving those variables. Tests were performed by determining the reduction in the log-likelihood ratio, G^2, when a term was added to a model that excluded that term. For example, comparing a null model (*CTL, CF* for the null hypothesis that the fate of an individual is independent of treatment or location, conditional on its initial state) with a model that includes a location effect (*CTL, CFL*) can be used to calculate ΔG^2, which is compared to a chi-square distribution. This comparison tests for a location effect (see Table 2.2). Degrees of freedom for this test are equal to the difference in the degrees of freedom in

Table 2.1. Four-way transition frequency table used in the loglinear analysis (Table 2.2). Counts of individuals summed across the five years of the study are shown for each combination of six initial classes, six fates, two locations, and three burning treatments.

		Rose Prairie			Fisher Butte		
initial state	fate	no burn	two burns	three burns	no burn	two burns	three burns
S	V2	42	42	51	15	68	56
S	V3	15	22	24	5	16	8
S	R1	3	1	2	2	5	3
S	R2	0	0	0	0	0	1
S	R3	0	0	1	0	0	0
S	dead	185	86	96	91	411	226
V2	V2	37	58	26	18	44	22
V2	V3	34	50	45	5	23	9
V2	R1	7	12	10	0	4	5
V2	R2	3	3	6	0	4	1
V2	R3	0	0	0	0	1	1
V2	dead	98	76	57	28	83	51
V3	V2	17	22	27	6	9	2
V3	V3	150	72	126	24	27	26
V3	R1	49	38	52	16	26	17
V3	R2	18	26	21	2	23	10
V3	R3	1	1	4	0	0	0
V3	dead	162	135	131	21	64	38
R1	V2	6	5	3	0	6	0
R1	V3	33	18	16	12	9	9
R1	R1	53	28	33	24	20	12
R1	R2	26	33	29	10	21	14
R1	R3	2	3	6	0	1	0
R1	dead	72	47	49	21	37	29
R2	V2	2	3	1	0	2	1
R2	V3	11	9	6	2	12	3
R2	R1	23	23	20	13	15	16
R2	R2	18	33	45	5	40	20
R2	R3	4	7	13	1	4	1
R2	dead	32	54	57	7	38	21
R3	V2	0	0	0	0	1	0
R3	V3	2	0	1	0	1	1
R3	R1	1	1	4	0	2	0
R3	R2	3	5	8	2	4	1
R3	R3	7	17	24	1	3	2
R3	dead	2	10	20	0	4	2

Table 2.2. Loglinear analysis of the effects of burning treatment and location on stage-specific plant fates. The explanatory variables are initial class (C), treatment (T) and location (L), and the response variable is fate (F). Relevant comparisons for each test are shown as differences between two models, and their corresponding *P*-values are shown in bold type.

Effect	Model	Comparison	*df*	G^2	ΔG^2	*P*
	(1) CTL, CF (null)		150	252.5		<0.0001
	(2) CTL, CFL		120	167.6		0.0027
location		(1)-(2)	30		84.9	**<0.0001**
	(3) CTL, CFT		90	131.1		0.0031
treatment		(1)-(3)	60		121.4	**<0.0001**
	(4) CTL, CFL, CFT		60	41.18		0.9698
location		(3)-(4)	30		89.92	**<0.0001**
treatment		(2)-(4)	60		126.42	**<0.0001**
	(5) FCTL		0	0		1.0000
location × treatment interaction		(4)-(5)	60		41.18	**0.9698**

the two models. The effect of a factor is always estimated relative to a specified model, so there may be more than one way to measure the effect of any factor. Two different tests for each factor were, therefore, included in our analyses.

Stochastic measures of population viability

We explored two measures of population viability, stochastic population growth rate and extinction probability, using two methods of incorporating environmental variability. Stochastic growth rate (λ_s) was chosen over the more conventional deterministic growth rate, lambda (λ), because it incorporates environmental variability and does not assume a stable (equilibrium) population structure (Tuljapurkar 1990). The sampled *Lomatium bradshawii* populations may not be at equilibrium, especially when burned after several decades without fire. Further, λ_s is always less than λ (Caswell 2001), which makes it a more conservative estimate of population viability. Populations with λ_s greater than 1.0 are projected to grow, while those with λ_s less than 1.0 are projected to decline.

Environmental stochasticity was modeled in two ways, through element selection (e.g. Maschinski et al. 1997) and matrix selection (e.g., Bierzychudek 1982). Element selection used the average matrices and, at each time step of the simulation, varied each matrix element at random within its observed variance. Element selection allows population trajectories in time to follow an infinite number of pathways bounded only by observed variances, but our use of the method did not account for any inter-correlation of matrix elements. That is, “bad” years for one type of transition were not correlated with “bad” years for others, even though environmental correlation among demographic parameters occurs in some species (Horvitz and Schemske 1995, Oostermeijer et al. 1996, Horvitz et al. 1997, Caswell 2000). Matrix selection, on the other hand, preserves the observed correlation structure among transition elements by varying whole matrices, drawn at random from the set of five detailed matrices for each treatment/site combination, at each time step. This limits the number of possible trajectories a simulated population can follow (Burgman et al. 1993). We used RAMAS/stage software (Ferson 1991) to perform element selection simulations and POPPROJ2 (Menges 1986, 1990, 1992b) to implement matrix selection. For both methods, we used an initial population size of 800 plants distributed in the average observed structure for each treatment and site.

We calculated stochastic lambdas and 95% confidence intervals (following Caswell 2001:396) from simulations using both the element and matrix selection procedures. When the log of population growth is averaged over a very large number of time steps, it converges to a fixed value determined by vital rates and environmental processes (Caswell 2001, Tuljapurkar 1990). For each type of simulation, we ran the models for 2000 time steps to calculate the stochastic growth rate.

To calculate extinction probability, we ran 1000 simulations with 100 1-yr time steps. Extinction was defined as falling below ten individuals. For element selection, distributions were assumed to be normal and truncated to 0 and 1. If transition rates for a given stage summed to greater than 1.0 (suggesting greater than 100% survival) during element selection, the values were rescaled to sum to 1.0. In the matrix selection procedure, each detailed matrix had an equal probability at each time step. Extinction probability was calculated from the frequency of extinction events in the simulations. Confidence intervals were based on a normal approximation of a binomial distribution (Steel et al. 1997).

Our use of the transition matrix model assumed that fertility and transition rates are independent of intra-specific plant density. This is an acceptable assumption for populations below a density-dependent threshold (e.g., Shaw 1987), but only while they remain at low densities. Density dependence will eventually limit growth of populations with lambda greater than one. Therefore, we tested the effects of imposing a population ceiling on extinction probability and found that there was no effect on extinction probability of limiting population size to twice the initial size. We concluded that omitting density dependence from our models did not substantially alter our results. Demographic stochasticity was also ignored by our models, but it usually contributes much less to extinction probability than environmental stochasticity, except in declining populations with small (e.g., 50 individuals) initial size (Menges 1992b). In addition, these matrix models assume that population growth is a first-order Markov process, in which transition probabilities depend only on a plant's condition in the current year, not on its state in previous years (Lefkovitch 1965).

Elasticities

Elasticities are a proportional measure of the sensitivity of lambda to small perturbations in each transition element (de Kroon et al. 1986). One useful property of elasticities is that for a given matrix, they can be summed for each stage to provide a proportional measure of the importance of each stage for population growth (e.g., Caswell 2001). We calculated elasticities for each of the populations and treatments using weighted mean matrices and a parametric bootstrap process detailed in Caswell and Kaye (in review). This bootstrap procedure resamples matrices from a multinomial distribution for transition rates and a Poisson distribution for fertilities to generate 95% confidence intervals.

Seed bank analysis

Our models assume that seeds do not remain in the soil for more than 1 yr without germinating or dying. To test this assumption, we sampled soils from four *Lomatium bradshawii* populations to determine if the species maintains a persistent soil seed bank. Populations examined included Fisher Butte, Rose Prairie, Long Tom, and Buford Park. All soil samples were taken in 1993 after seedling emergence and prior to seed dispersal of the current season. At the first three sites, 20 x 20-cm by 3-cm deep samples were collected adjacent to randomly selected reproductive *L. bradshawii* plants, excluding plants that were included in monitoring plots. At each plant, a random direction and distance (up to 2 m) were selected for locating the sample. At Buford Park, 20 x 20-cm by 3-cm deep samples were taken at regular intervals along previously established monitoring transects in areas of high *Lomatium bradshawii* density ($\bar{x} \approx 50$ plants m^{-2}). Sample sizes ranged from 15 to 20 per site.

Soil samples were examined for *Lomatium bradshawii* fruits (single seeded mericarps) within two days of collection. Each sample was loosened into smaller fragments, then passed through a series of sieves to separate the size fragment appropriate for *L. bradshawii* fruits. The accuracy of this technique was evaluated by placing marked *L. bradshawii* fruits into the first three soil samples to determine if they could be found. All marked fruits were recovered quickly and without confusion. When *L. bradshawii* fruits were encountered, they were evaluated for overall condition and presence of endosperm or embryo. We tested for viability of embryos with tetrazolium chloride (following Heydecker [1973]).

RESULTS

Transition rates

Between 1988 and 1993, a total of 1,151 individual plants were recorded in sample plots at Rose Prairie and 1,273 were observed at Fisher Butte. Many kinds of transitions were observed among the stages of *Lomatium bradshawii*. From one year to the next, plants increased or decreased in size, or remained the same (Table 2.3). In a single year, some plants grew or shrank two or more stages. For example, at both sites and in all fire treatments, V3 plants grew to R1 or R2 or regressed to V2 stages in one year (Table 2.3). Some transitions were never or seldom observed, such as plants from

Table 2.3. Mean transition matrices and variances for each site, treatment, and year (1988-93, n=5). Fertilities are found on the top row of each matrix. Probabilities for stasis are along the main diagonals, regression to smaller stages are above the diagonals (excluding the top row), and growth probabilities are below the diagonals in each column. Stages are defined in Methods.

Stage at time t+1	Stage at time *t*											
	S	V2	V3	R1	R2	R3	S	V2	V3	R1	R2	R3
	Mean 1988-93						**Variance 1988-93**					
Rose Prairie, no burns												
S	0	0	0	0.362	3.462	4.035	0	0	0	0.0311	13.304	6.889
V2	0.068	0.244	0.108	0	0	0	0.0076	0.1079	0.0145	0	0	0
V3	0.094	0.130	0.390	0.228	0.044	0	0.0117	0.0298	0.0380	0.0114	0.0077	0
R1	0.018	0	0.278	0.432	0.584	0	0.0007	0	0.0262	0.0237	0.1112	0
R2	0	0	0.044	0.186	0.272	0.667	0	0	0.0077	0.0111	0.1409	0.2222
R3	0	0	0	0	0.100	0.333	0	0	0	0	0.0400	0.2222
Rose Prairie, two burns (88 and 91)												
S	0	0	0	0.764	4.138	10.178	0	0	0	0.3090	7.535	76.093
V2	0.318	0.408	0.108	0.078	0.022	0.125	0.0104	0.0095	0.0042	0.0055	0.0010	0.0469
V3	0.058	0.216	0.246	0.146	0.160	0.083	0.0027	0.0195	0.0290	0.0051	0.0154	0.0204
R1	0.012	0.016	0.254	0.348	0.150	0.100	0.0001	0.0004	0.0071	0.0191	0.0060	0.0300
R2	0	0.014	0.184	0.310	0.524	0.343	0	0.0008	0.0194	0.0267	0.0177	0.0674
R3	0	0.006	0	0.014	0.058	0.350	0	0.0001	0	0.0008	0.0039	0.1675
Rose Prairie, three burns (88, 89 and 91)												
S	0	0	0	0.692	4.800	10.540	0	0	0	0.2813	6.002	27.147
V2	0.336	0.316	0.028	0	0.014	0	0.0203	0.0852	0.0013	0	0.0008	0
V3	0.062	0.184	0.370	0.278	0.080	0.125	0.0029	0.0344	0.0223	0.0269	0.0084	0.0469
R1	0.020	0.156	0.228	0.278	0.240	0	0.0010	0.0329	0.0119	0.0262	0.0555	0
R2	0.012	0.034	0.124	0.342	0.488	0.250	0	0.0046	0.0055	0.0458	0.0469	0.1875
R3	0	0.006	0	0	0.050	0.375	0	0.0001	0	0	0.0100	0.1719
Fisher Butte, no burns												
S	0	0	0	0.322	1.718	5.984	0	0	0	0.1860	2.776	17.573
V2	0.236	0.242	0.054	0.030	0.016	0	0.0245	0.0156	0.0016	0.0014	0.0010	0
V3	0.102	0.220	0.496	0.206	0.140	0.240	0.0057	0.0130	0.0073	0.0058	0.0075	0.1504
R1	0.014	0.056	0.174	0.392	0.342	0.066	0.0002	0.0021	0.0040	0.0147	0.0089	0.0174
R2	0	0.042	0.062	0.180	0.326	0.174	0	0.0031	0.0014	0.0198	0.0304	0.0675
R3	0	0	0.002	0.014	0.048	0.414	0	0	0	0.0004	0.0022	0.1504
Fisher Butte, two burns (88 and 91)												
S	0	0	0	0.078	0.892	3.356	0	0	0	0.0045	0.3424	5.390
V2	0.286	0.328	0.106	0.060	0.018	0	0.0165	0.0063	0.0040	0.0013	0.0013	0
V3	0.170	0.262	0.362	0.168	0.090	0	0.0086	0.0145	0.0159	0.0169	0.0026	0
R1	0.006	0.070	0.180	0.278	0.220	0.040	0.0001	0.0032	0.0082	0.0064	0.0176	0.0064
R2	0	0.018	0.120	0.298	0.394	0.146	0	0.0005	0.0051	0.0723	0.0102	0.0325
R3	0	0	0.004	0.022	0.102	0.680	0	0	0.0001	0.0010	0.0135	0.0812
Fisher Butte, three burns (88, 89, 91)												
S	0	0	0	0.086	0.720	2.538	0	0	0	0.0020	0.2291	4.167
V2	0.334	0.196	0.084	0.046	0.012	0	0.0127	0.0077	0.0049	0.0027	0.0006	0
V3	0.146	0.326	0.496	0.106	0.056	0.028	0.0075	0.0229	0.0347	0.0178	0.0025	0.0031
R1	0.014	0.074	0.166	0.354	0.166	0.060	0.0003	0.0018	0.0027	0.0091	0.0147	0.0064
R2	0	0.050	0.070	0.316	0.458	0.192	0	0.0014	0.0029	0.0308	0.0166	0.0013
R3	0	0	0.018	0.046	0.142	0.632	0	0	0.0003	0.0044	0.0138	0.0279

S or V2 growing to R2 or R3 stages. The loglinear analyses (Table 2.2) suggest that fates of individuals in each of the six stages were affected by the burning treatments ($P < 0.0001$) and the locations of the populations ($P < 0.0001$). There was no evidence of an interaction between treatment and location ($P = 0.9697$).

In unburned environments at both sites, the most likely transition for all stages was survival in the same stage-class (matrix diagonals, Table 2.3) or decline in size. At Rose Prairie, stasis was most likely for V2 through R1 plants, while shrinkage to the next smaller stage class was most probable for R2 and R3 reproductive plants. Similarly, at Fisher Butte stasis was most likely for all stages except R2, which most frequently regressed one stage. Plants in burned environments most often remained the same or grew one stage. For example, plants remained the same size more often than any other transition in both fire treatments at Rose Prairie, except for V3 and R1 plants, which were most likely to grow one stage in the two-burn and three-burn treatments, respectively. Average matrices for the burn treatments at Fisher Butte also showed that stasis was the single most likely transition, except for one-step growth of R1 and V2 plants in the two-burn and three-burn treatments, respectively.

The effect of fire on individual plant fecundity (top row of the matrices, Table 2.3) was less clear, and appeared to differ between the two sites. Mean matrices for burned environments at Rose Prairie had higher fecundity values in most cases than those for unburned conditions, especially for R3 plants, but plants in the two burn treatments had very similar fecundities. At Fisher Butte, however, fecundity of R2 and R3 plants consistently declined with increasing fire frequency.

Population growth rates

Both estimates of stochastic population growth rate increased with burning frequency at Rose Prairie and Fisher Butte, but the magnitude of the fire effect differed from site to site, and, to a lesser degree, with the method of calculating λ_s. At Rose Prairie, for example, plant abundance was projected to decline in the absence of fire, but burning twice in six years resulted in growth rates well over 1.0. This increase continued in the three-burn treatment, especially for estimates from element selection (Figure 2), indicating that burned populations were projected to increase in size. Fire also had a positive effect on population growth rate at Fisher Butte, but its effect was less dramatic and a higher burning frequency was required to raise λ_s to 1.0. Population growth rate in the two-burn treatment at Fisher Butte increased over the unburned area, but remained less than 1.0 (Figure 2), with three burns in six years required to raise λ_s to 1.0. For either method of calculating λ_s, we rejected the null hypothesis that fire had no effect on λ_s at $P=0.028$ (i.e., the probability that we would observe a progressively positive effect of burning in three treatments at two sites if the effects of fire were random was $[1/6]^2=0.028$). Both measures of stochastic projection yielded roughly equivalent estimates of λ_s, except for computations for burn treatments at Rose Prairie. Growth rates were higher when calculated by element selection in the two- and three-burn treatments (95% confidence intervals: 1.13-1.17 and 1.18-1.20, respectively) than matrix selection (1.03-1.08 and 1.07-1.13, respectively) at that location.

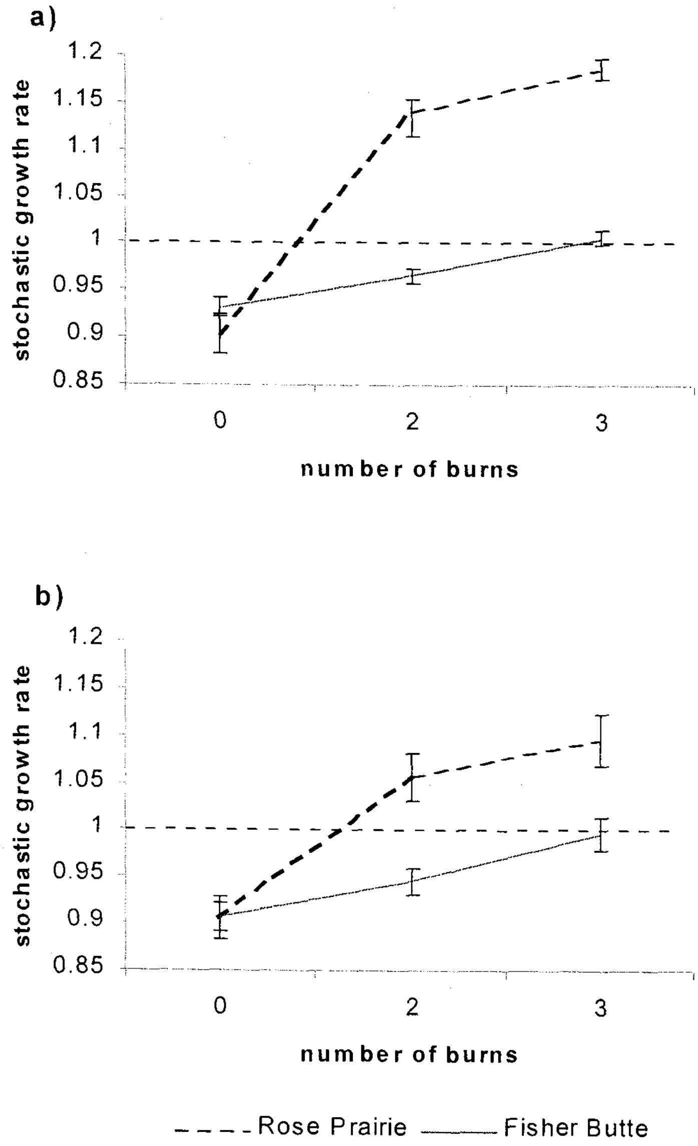

Figure 2.2. Stochastic population growth rate (λ_s) within each site and burning treatment for a) element selection (calculated with RAMAS/stage) and b) matrix selection (POPPROJ2). Each value is a median of 2,000 iterations with 95% confidence intervals.

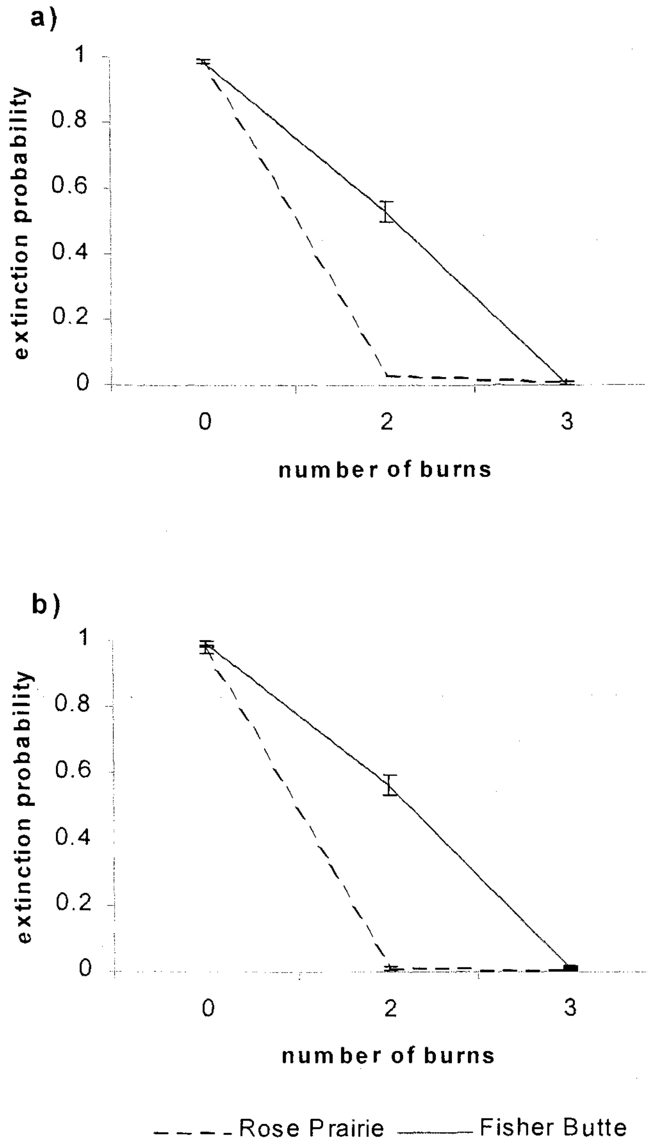

Figure 2.3. Extinction probability in burned and unburned stochastic environments calculated through a) element selection (calculated with RAMAS/stage) and b) matrix selection (POPPROJ2). All runs were 100-yr simulations iterated 1,000 times. Initial population sizes were 800 plants, and extinction was defined as falling below 10 individuals. Vertical lines are 95% confidence intervals

Extinction probability

In the absence of fire, both populations were projected to become extinct in nearly all of the 100 year projections, regardless of our method of modeling environmental stochasticity. At Rose Prairie, burning twice or three times in six years lowered extinction probability nearly to 0 (Figure 3). Extinction probability at Fisher Butte also declined from near certainty without fire to near 0 in prairies burned three times. In the two-burn treatment at Fisher Butte extinction probability was 57% under element selection and 53% by matrix selection (Figure 3).

Elasticities

The effect of fire on elasticities differed between sites. At Rose Prairie, the most important transition in the unburned environment was one-umbel plants staying the same size (elasticity=0.202), while stasis of two-umbel plants had the greatest effect on lambda in habitats burned twice and three times (0.141 and 0.120, respectively) (Table 2.4). Elasticity at Fisher Butte shifted in importance from constancy of three-leaved vegetative plants (0.170) in the unburned treatment to stasis of three-umbel plants in burned areas (0.129 and 0.123). For elasticities summed by stage, most confidence intervals overlapped within a site and treatment combination, but burning appeared to decrease the importance of mid-sized plants and increase the elasticity of small plants (Figure 4). These effects differed from site to site, however. The elasticity of one-umbel plants, for example, decreased in burned environments at Rose Prairie, while seedlings and small vegetative plants increased in importance. At

Table 2.4. Elasticities for weighted mean matrices (1988-93) for each site and burning treatment. Values for fertility are displayed on top rows. Stasis values are found on the diagonals, growth below the diagonals, and regression above (excluding fertilities). The transition with the highest elasticity is shown in bold for each matrix, and the bottom row is the sum (Σ) of the upper rows for each column.

Stage at time *t*+1	Stage at time *t*											
	S	V2	V3	R1	R2	R3	S	V2	V3	R1	R2	R3
	Rose Prairie						**Fisher Butte**					
no burns												
S	0	0	0	0.013	0.041	0.004	0	0	0	0.015	0.040	0.032
V2	0.015	0.012	0.005	0	0	0	0.043	0.019	0.009	0.004	0.001	0
V3	0.028	0.019	0.108	0.071	0.011	0	0.034	0.039	**0.171**	0.044	0.016	0.003
R1	0.016	0	0.103	**0.202**	0.098	0	0.009	0.011	0.078	0.098	0.048	0.002
R2	0	0	0.020	0.134	0.060	0.014	0	0.007	0.043	0.073	0.056	0.010
R3	0	0	0	0	0.018	0.011	0	0	0.005	0.013	0.028	0.051
total Σ	0.058	0.032	0.236	0.418	0.228	0.029	0.086	0.076	0.306	0.246	0.189	0.097
two burns (1988 & 91)												
S	0	0	0	0.016	0.104	0.024	0	0	0	0.004	0.042	0.052
V2	0.083	0.047	0.006	0.005	0.002	0.001	0.051	0.033	0.013	0.004	0.002	0
V3	0.043	0.054	0.041	0.016	0.020	0.001	0.044	0.047	0.068	0.021	0.012	0
R1	0.018	0.013	0.053	0.046	0.033	0.003	0.003	0.017	0.055	0.049	0.046	0.002
R2	0	0.020	0.075	0.077	**0.141**	0.010	0	0.006	0.051	0.077	0.089	0.015
R3	0	0.009	0	0.006	0.024	0.013	0	0	0.005	0.018	0.047	**0.129**
total Σ	0.143	0.142	0.175	0.166	0.323	0.051	0.098	0.103	0.191	0.171	0.238	0.199
three burns (1988, 89, & 91)												
S	0	0	0	0.018	0.106	0.020	0	0	0	0.004	0.034	0.060
V2	0.092	0.044	0.002	0	0.001	0	0.055	0.018	0.013	0.002	0.001	0
V3	0.027	0.036	0.049	0.029	0.007	0.002	0.038	0.044	0.087	0.018	0.007	0.001
R1	0.016	0.032	0.051	0.062	0.061	0.000	0.005	0.015	0.055	0.057	0.034	0.008
R2	0.008	0.010	0.048	0.114	**0.120**	0.005	0	0.012	0.029	0.067	0.100	0.022
R3	0	0.016	0	0	0.010	0.015	0	0	0.011	0.026	0.055	**0.123**
total Σ	0.143	0.139	0.150	0.222	0.305	0.041	0.098	0.089	0.194	0.174	0.230	0.214

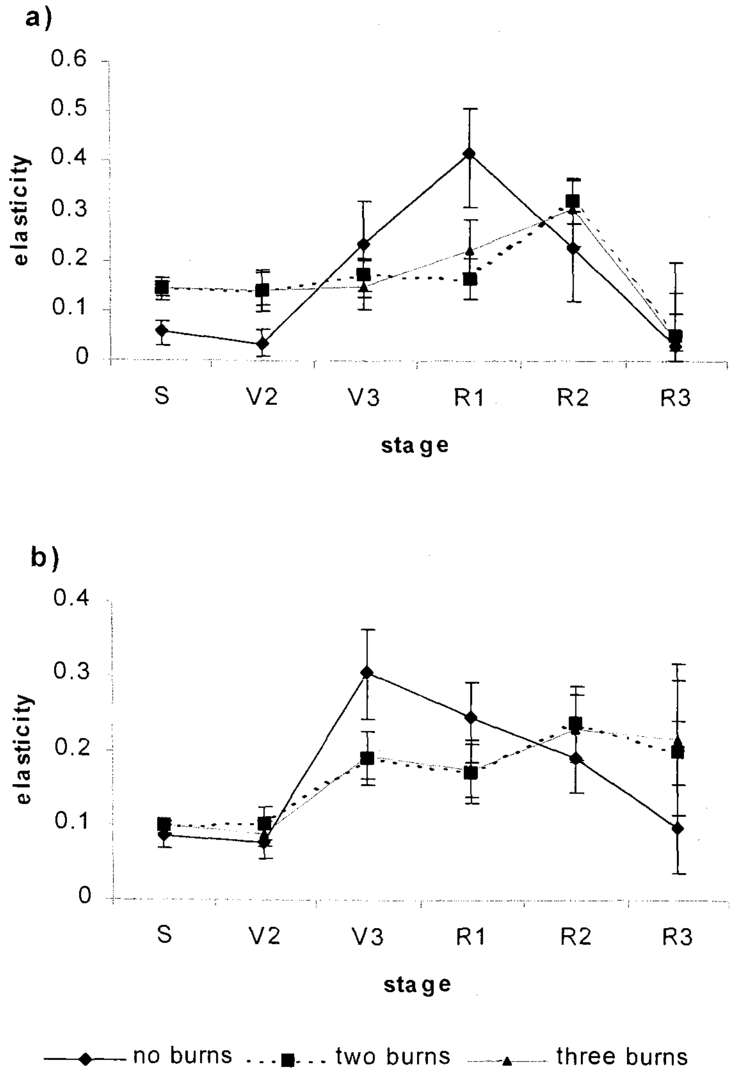

Figure 2.4. Stage-summed elasticities for populations in burned and unburned environments at a) Rose Prairie and b) Fisher Butte based on weighted mean matrices from six years of observations. Error bars represent bootstrapped 95% confidence intervals.

Fisher Butte, the elasticity of large vegetative (V3) plants decreased in burned environments, but the impact of seedlings and small vegetatives (V2) on population growth rate was unaffected by fire.

Seed bank analysis

No viable seeds were encountered in sieved-soil samples from four *Lomatium bradshawii* populations. Fewer than one fruit per sample was detected at all sites, and no fruits were encountered at Fisher Butte (Table 2.5). Some fruits were discovered intact, but these either contained no embryo or the embryo was not viable. The remaining fruits (0-67%) were decayed and/or broken and contained incomplete embryo tissue, if any.

DISCUSSION

In the absence of fire, *Lomatium bradshawii* did not maintain populations with projected long-term viability. Unburned populations of *L. bradshawii* at two locations had individual vital rates dominated by stasis and regression to smaller stages. Stochastic projections estimated growth rates below 1.0 and very high probabilities of extinction (97%-100%). Fall burning, in contrast, had several positive effects despite considerable environmental stochasticity. For example, stasis and growth to larger stage classes dominated vital rates in burned populations, and seedling survival

Table 2.5. Fruits encountered in soil samples from four *Lomatium bradshawii* populations. Samples (N) were taken after seedling emergence and before fruit dispersal to detect a persistent soil seed bank.

		Mean (1 SE) number fruits		Intact	Decayed	Viable
Site	N	per sample	per m^2	(%)	(%)	(%)
Fisher Butte	20	0.00 (0.00)	0.00 (0.00)	0	0	0
Rose Prairie	18	0.06 (0.05)	1.50 (1.25)	100	0	0
Long Tom	15	0.13 (0.09)	3.25 (2.25)	100	0	0
Buford Park	20	0.60 (0.22)	15.0(5.5)	33	67	0

increased relative to unburned plots. Stochastic population growth rates increased, especially in the treatment with highest fire frequency (three burns in six years). Burning twice in six years was sufficient to raise growth rates over 1.0 at Rose Prairie but not Fisher Butte. At the latter site, stable to positive growth rates were observed only in plots with three-burns in six years. Extinction probability declined in burned plots, dropping to near 0 at Rose Prairie in both burn treatments. At Fisher Butte, the population burned twice in six years had a 53%-57% chance of extinction (depending on our method of modeling environmental stochasticity), while the population that was burned three times had almost zero extinction risk in 100-yr simulations.

Regardless of which method was used to incorporate stochasticity, population growth rates consistently increased in burned vs. unburned habitats (Figure 2) and extinction risk declined in these treatments (Figure 3), with the estimates of these values becoming nearly identical between methods in most cases. Apparently, any within-population correlation structure between matrix elements that these populations had was not sufficient to alter results relative to models that allowed the elements to vary independently. This may not always be the case, and an earlier comparison of the two methods using RAMAS/stage and POPPROJ with data from another rare plant species showed substantial differences in extinction estimates with 25-yr projections (Greenlee and Kaye 1997). Additional comparisons of these techniques and assessments of matrix element correlation are needed to evaluate the widely held concerns of population modelers that such correlation structure is common and affects the results of stochastic matrix model simulations (Caswell 2000, Menges 2000).

The risks of extinction determined here for *Lomatium bradshawii* are comparable to results obtained for other plant species with similar population growth rates and environmental stochasticities. Menges (1992b) applied various levels of environmental stochasticity to published transition matrices for eight plant species, and concluded that a 'moderate' level of environmental stochasticity (mean to variance ratio$\approx$0.01) was sufficient to limit growth of populations with $\lambda < 1.05$, but populations with $\lambda > 1.12$ were not restrained by even "extreme" levels of stochasticity (ratio$\approx$0.3). The observed environmental stochasticities for *L. bradshawii* are in the range that Menges considered "moderate" to "strong." Our estimates of extinction probability were high (53%-100%) for populations with $\lambda < 1.05$, and low (0%-1%) for those with $\lambda > 1.12$, as might be expected from Menges' results, suggesting that lambda and environmental stochasticity interact to control extinction probability in predictable ways (Tuljapurkar and Orzack 1980, Lande and Orzack 1988, Lande 1993).

Density dependence was not incorporated into our models of *Lomatium bradshawii* population dynamics. It is possible that our low estimates of extinction probability for burned populations with positive growth rates were overly optimistic because high densities would eventually reduce plant survival and fecundity and thus limit population growth. Under this scenario populations would be kept relatively small and vulnerable to stochastic declines. Our pilot tests with population ceilings, however, suggested that limiting population size did not increase extinction risk. On the other hand, declining populations could experience both positive and negative effects of density dependence. For example, as densities declined survival could have increased, but fecundity could have either increased due to lowered intraspecific competition or decreased due to Alee effects. Since the relative strengths of these forces are unknown for *L. bradshawii*, their effects on extinction probability are also uncertain. However, our observations of this species suggest that as density declines the gaps created by missing plants are filled by aggressive interspecific competitors, thus lessening benefits of lowered intraspecific density. Reduced fecundity and progeny fitness at low densities could occur in this species, and this would tend to increase extinction risk over the estimates presented here.

Attempts to validate transition matrix models of plant population dynamics are few and have yielded mixed results. A stochastic model based on random selection between two matrices failed to predict population size fifteen years later (Bierzychudek 1999), but an element selection model from four years of observation estimated population size very well after seven years (Kephart and Paladino 1997). No validations of long term (e.g., 100-yr) projections from matrix models have been attempted, for obvious reasons. Beissinger and Westphal (1998) suggest that qualitative conclusions should be emphasized over the quantitative results of population viability analyses, and we concur. Without validation and inclusion of population processes like density dependence and demographic stochasticity, the relative predictions of our models, i.e., burning improves population growth rate and lowers extinction risk, should be emphasized over the absolute estimates of these parameters.

Elasticities

Fire appeared to shift stage-specific contributions to population growth rate, but these effects differed from site to site. At Rose Prairie, fire appeared to decrease the importance of seedlings and small vegetative plants and increase the contribution of one-umbel reproductive plants (Table 2.4 and Figure 2.4). Burning at Fisher Butte, on the other hand, decreased the importance of large vegetative plants. In terms of demographic functions, burning at Rose Prairie increased the importance of fertility and growth, and lowered the elasticities for regression and stasis, but had little effect on these processes at Fisher Butte. The observed site-differences in response to burning shown by *Lomatium bradshawii* are not surprising, given the spatial variability in demographic processes observed in many other herbaceous species that have been modeled with transition matrices (e.g., Sarukhan and Gadgil 1974, Bierzychudek 1982, Meagher 1982, de Kroon et al. 1987, van Groenendael and Slim 1988, Menges 1990, Gregg 1991, Horvitz and Schemske 1995, Silvertown et al. 1996, Oostermeijer et al.

1996, Kephart and Paladino 1997). What is noteworthy in this case, however, is that the effect of fire on individual stages and demographic processes differed somewhat among locations, but the trend toward improved population viability did not.

Silvertown et al. (1993) analyzed elasticities from 45 herbaceous species and 21 woody plants, and concluded that these two life-history strategies are significantly different in terms of the importance of growth, survival, and fecundity to population growth. The elasticities of *Lomatium bradshawii* for these processes are well within the ranges observed for herbaceous species, and are typical of herbaceous plants of open habitats (Silvertown et al. 1993). In addition, the relative importance of growth and survival may be typical of species with life-spans similar to *Lomatium bradshawii*. In a review of five tree species, Caswell (1986) suggested that survival may be most important for long-lived, slow-growing species in general, and Silva et al. (1991) argued that growth may be most important in short-lived, fast-growing species, such as annuals, biennials, and short-lived perennials. Indeed, the relative importance of growth and survival appear to be related to individual longevity (Enright et al. 1995). For *L. bradshawii*, survival and growth had nearly equal elasticities at Fisher Butte, while at Rose Prairie, growth was more important than stasis (but only in burned plots); fire had no consistent effect on these parameters. Therefore, we suggest that for intermediate life-spans and growth rates (such as many iteroperous herbs), neither growth nor survival are consistently more significant to population growth. This concurs with the observation of Silvertown et al. (1993) that, on average, elasticities for growth (0.439±0.183) and survival (0.398±0.256) are nearly equal for herbs.

Elasticities identify individual transitions and stages where small errors in transition rate estimates will cause relatively large changes in projected population growth. In some of our matrices, large reproductive (R3) plants had high elasticities, and their transition rates were calculated from observations of relatively few plants (resulting in large bootstrapped confidence intervals for that stage; see Figure 4). Therefore, larger sample sizes for this stage could lower measurement error and might alter our results.

Elasticities also have important implications for conservation and management because they identify crucial life-history stages where scarce management resources may be targeted for maximum benefit. For example, if fire could not be applied to a particular population because of the risk of burning adjacent property, elasticities from unburned sites suggest that focusing on large vegetative (V3) or small reproductive (R1) plants to improve conditions for those stages (e.g., removing interspecific competitors) would yield a faster growing population than equal improvements to other stages. Recent studies suggest that this type of assessment from a mean transition matrix should be treated with caution, however (Benton and Grant 2000; Heppell et al. 2000). For example, Wisdom et al. (2000) showed that the relative rank of individual elasticities may be unstable when demographic uncertainty, variation, and covariation are incorporated into matrix simulations. Our elasticities are bounded by boot-strapped confidence intervals (Figure 4), which provide a measure of uncertainty for their estimate, but they do not account for factors like covariation among vital rates.

Seed bank

Our data indicate that *Lomatium bradshawii* does not maintain a persistent soil seed bank. Even though some fruits survived at least one year in the soil, the seeds within them were not viable (Table 2.5). Absence of a soil seed bank may be typical for other *Lomatium* species, as well. For example, 98.5% of all *L. dissectum* seeds distributed in artificial piles were either removed by postdispersal seed predators, died of other causes, or germinated within 43 weeks of dispersal (Thompson 1985). Similar seed losses were observed for *L. triternatum* in a different component of the same study, and the author concluded that seed survival for more than one year was unlikely for these species. Although it is possible that larger sample sizes in our study might have detected some viable *L. bradshawii* seeds, our sample strategy maximized the likelihood of detecting seeds by sampling in close proximity to reproductive plants following a year of relatively high seed production (T.N. Kaye, unpublished data). Even if some viable seeds persist for more than one year, they apparently do so in such low numbers as to be of little significance to the population. Therefore, modeling *L. bradshawii* population dynamics without a soil seed bank seems reasonable.

Ecological and conservation implications

Prior to Euro-American settlement, Willamette Valley prairies were probably burnt annually in the fall by Kalapuya Indians to promote food plants and game (Boyd 1986, 1999). Very little information is available to document the extent or patchiness of individual past fires, but these burns were apparently very large, covering several hundred ha (Douglas, 1914). Open dry prairies may have burned almost every year, and wetland prairies and canyons on north slopes were probably exposed to somewhat less frequent blazes. In the absence of fire, native prairies in western Oregon are invaded by shrubs and forest vegetation dominated by *Quercus garryana, Pseudotsuga menziesii, Pinus ponderosa, Abies grandis*, or *Fraxinus latifolia* (Franklin and Dyrness 1988, Streatfield and Frenkel 1997). The historic dependence of prairie habitat on burning suggests that the distribution and evolution of *Lomatium bradshawii* is related, at least in part, to long-term Native American cultural practices, and the decline of this species has been aggravated by habitat loss and fire suppression by post-settlement residents. Therefore, even populations that occur in protected areas, such as wildlife refuges and habitat preserves, are vulnerable unless woody vegetation is controlled and fire or some other management technique is used to enhance population growth. In some cases, more aggressive methods than fire may be required to remove woody vegetation, such as at Long Tom ACEC, where hardwood trees (*Fraxinus latifolia*) shade the herbaceous vegetation and *L. bradshawii* is projected to decline despite frequent burning (Kaye et al. 1994).

Burning may have several effects on prairie communities, any of which could contribute to the positive changes observed for *Lomatium bradshawii*. Burning is widely believed to deliver a pulse of nutrients to soil and plants (Bond and van Wilgen 1996), at least in the first 1-2 years after a fire (Kucera and Ehrenrich 1962, Old 1969, Ojima et al. 1994). Pendergrass et al. (1998) suggest that burning Willamette Valley prairies consumes thatch and standing biomass, creating bare areas suitable for plant growth and establishment. Voles, which can be significant herbivores of *Lomatium bradshawii* (Kaye, personal observation; A. Drew, Oregon State University, unpublished data), are negatively affected by prairie fires through short-term reduction in food-plants and hiding-cover making them vulnerable to predators (e.g., Vacanti and Geluso 1985). In addition, heat and smoke from burns can stimulate seed germination in many fire-adapted species (Keeley and Fotheringham 1997), although the effect of fire on *L. bradshawii* seeds is unknown. These factors and others, either alone or more likely in combination, may drive the positive effects of fire observed in this study.

The value of controlled burns as a management tool for native vegetation and individual plant species in Willamette Valley prairies has already been described (Pendergrass 1995, Pendergrass et al. 1998, Streatfield and Frenkel 1997, Maret and Wilson 2000). Crown-size, umbel number, and seed production of *L. bradshawii* plants increases significantly in areas subjected to fire compared to plants in unburned areas (Pendergrass et al. 1999, Finley and Kauffman 1992). Our analyses with matrix models drawn from six years of population observations demonstrate that controlled fires may enhance the population viability of this species, not just individual plant size characteristics.

These results were qualitatively consistent among two locations with similar hydrology and soils, but the applicability of these results to other populations of *Lomatium bradshawii* is unknown, and our models have not been validated for them. Differences in the relative abundance of each stage, plant community composition, past management, seasonal precipitation, soil depth, hydrology, and fire behavior could affect the response of specific populations to controlled burns. Pendergrass et al. (1998) reported that the 1988 burns produced greater heat per unit area and consumed more total biomass at Fisher Butte than Rose Prairie, while the 1989 burns were similar at the two locations but were more spotty than the year before. Also, although a *Deschampsia cespitosa* community-type was widespread at both sites, a *Vaccinium cespitosum* type was present only at Rose Prairie and a *Rosa nutkana/Juncus nevadensis* community occurred only at Fisher Butte (Pendergrass 1995). These patterns and other site dissimilarities may account for some of the quantitative differences in fire response between the study populations, such as higher λ_s at Rose Prairie after burns, differences in fecundities and elasticities, and opposite changes in some transition rates between the two sites (e.g., the R2 to R3 transition probability decreased with burning at Rose Prairie but increased after fires at Fisher Butte [Table 2.3]). It is likely that other populations of *L. bradshawii* would also exhibit variations in population-level responses due to variation in fire behavior and other site differences.

Fire may not be the only disturbance with positive effects on this species. The presence of populations in areas like Rose Prairie and Fisher Butte, where fires have been suppressed for many years yet the populations are still extant, suggests that other disturbances may have occurred in these areas to keep the habitat suitable for *Lomatium bradshawii*. Mowing, livestock grazing, floods, and other actions could conceivably benefit the species' population growth and should be explored as alternatives to controlled burning for managing western Oregon prairie remnants, especially in areas with fire-adapted weeds.

Conclusion

Fire and location had significant effects on stage-specific transitions, and stochastic projection models indicated that burning had a positive effect on the population viability of *Lomatium bradshawii*. Transition matrix models derived from field experiments with fire in *L. bradshawii* habitat indicated that populations of this species will decline in the absence of burning, and may grow if burnt two or three times in six years, depending on the location. Further, extinction probability in 100-yr simulations declined from near certainty without fire to very low odds under these burning frequencies. These results contribute to our ability to manage western Oregon prairies, their constituent species, and *L. bradshawii* in particular. They serve as one of a few available examples of stochastic matrix modeling used to compare management treatments for promoting rare plant populations (Oostermeijer 1996, Lesica 1997, Gross et al. 1998, Menges and Dolan 1998). This approach has widespread applicability for assessing management actions for rare species, especially when proposed habitat alterations can be tested for two to several years prior to large-scale implementation.

LITERATURE CITED

Alverson, E.R. 1989. Use of a county soil survey to locate remnants of native grassland in the Willamette Valley, Oregon. Pages 107-112 in R.S. Mitchell, C.J. Sheviak, and D.J. Leopold, editors. Ecosystem management: Rare Species and Significant Habitats. Proceedings 15th Annual Natural Areas Conference, New York State Museum Bulletin, pp. 107-112.

Alverson, E.R. 1990. A survey for native grassland remnants in the mid-Willamette Valley, Oregon. Oregon Department of Agriculture, Salem, Oregon.

Aplet, G.H., R.D. Laven, and R.B. Shaw. 1994. Application of transition matrix models to the recovery of the rare Hawaiian shrub, *Tetramalopium arenarium* (Asteraceae). Natural Areas Journal 14:99-106.

Barker, N.G. and G.B. Williamson. 1988. Effect of winter fire on *Sarracenia alata* and *S. psittacina*. American Journal of Botany 75:138-143.

Beissinger, S.R. and M.I. Westphal. 1998. On the use of demographic models of population viability in endangered species management. Journal of Wildlife Management 62:821-841.

Benton, T.G. and A. Grant. 2000. Elasticity analysis as an important tool in evolutionary and population ecology. Trends in Ecology and Evolution 14:467-471.

Bierzychudek, P. 1982. The demography of jack-in-the-pulpit, a forest perennial that changes sex. Ecological Monographs 52:335-351.

Bierzychudek, P. 1999. Looking backwards: assessing the projections of a transition matrix model. Ecological Applications 9:1278–1287.

Bond, W.J., and B.W. van Wilgen. 1996. Fire and plants. Chapman and Hall, London.

Borchert, M. 1989. Post fire demography of *Thermopsis macrophylla* H.A. var. angina J.T. Howell (Fabaceae), a rare perennial herb in chaparral. American Midland Naturalist 122:120-132.

Boyd, R. 1986. Strategies of Indian burning in the Willamette Valley. Canadian Journal of Anthropology 5:65-86.

Boyd, R. 1999. Strategies of Indian burning in the Willamette Valley. Pages 94-138 in R. Boyd, editor. Indians, fire and the land. Oregon State University Press, Corvallis, Oregon.

Boyd, R.S. and L.L. Serafini. 1992. Reproductive attrition of the rare chaparral shrub *Fremontodendron decumbens* Lloyd (Sterculiaceae). American Journal of Botany 79:1264-1272.

Burgman, M.A., S. Ferson, and H.R. Ackakaya. 1993. Risk assessment in conservation biology. Chapman and Hall, London.

Campbell, J.J., D.D. Taylor, M.E. Medley, and A.C. Risk. 1991. Floristic and historical evidence of fire-maintained, grassy pine-oak barrens before settlement in southeastern Kentucky. Pages 359-375 in S.C. Nodvin and T.A. Waldrop, editors. Fire and the environment: ecological and cultural perspectives. Southeastern Forest Experiment Station, Asheville, N.C.

Carlson, P.R., G.W. Tanner, J.M. Wood, and S.R. Humphrey. 1993. Fire in key deer habitat improves browse, prevents succession and preserves endemic herbs. Journal of Wildlife Management 57:914-928.

Caswell, H. 1986. Life cycle models for plants. Lectures on Mathematics in the Life Sciences. 18:171-233.

Caswell, H. 2000. Prospective and retrospective perturbation analyses: their roles in conservation biology. Ecology 81:619-627.

Caswell, H. 2001. Matrix population models. Second edition. Sinauer Associates, Inc., Sunderland, Massachusetts.

Caswell, H. and T.N. Kaye. In press. Stochastic demography and conservation of *Lomatium bradshawii* in a dynamic fire regime. Advances in Ecological Research.

Currier, P.J. 1984. Response of prairie fringed orchid to fire and reduction in grazing. Restoration and Management Notes 2:28.

de Kroon, H., A. Plaiser, and J. van Groenendael. 1987. Density dependent simulation of the population dynamics of a perennial grassland species, *Hypochaeris radicata*. Oikos 50:3-12.

de Kroon, H., A. Plaiser, J. van Groenendael, and H. Caswell. 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. Ecology 67:1427-1431.

Douglas, D. 1914. Journal kept by David Douglas during his travels in North America 1823-1827. William Wesley and Son, London. Published under the direction of the Royal Horticultural Society.

Dunwiddie, P.W. 1990. Rare plants in coastal heathlands: observations on *Corema conradii* and *Helianthemum dumosum*. Rhodora 92:22-26.

Enright, N., M. Franco, and J. Silvertown. 1995. Comparing plant life histories using elasticity analysis: the importance of life span and the number of life-cycle stages. Oecologia 104:79-84.

Ferson, S. 1991. RAMAS/stage: Generalized stage-based modeling for population dynamics (version 1.4). Applied Biomathematics, Setauket, New York.

Fiedler, P.L. 1987. Life history and population dynamics of rare and common mariposa lilies (*Calochortus* Pursh: Liliaceae). Journal of Ecology 75:977-995.

Fingleton, B. 1984. Models of category counts. Cambridge University Press, Cambridge, U.K.

Finley, K.K. 1994. Hydrology and related soil features of three Willamette Valley wetland prairies. M.Sc. thesis, Oregon State University, Corvallis.

Finley, K.K. and J.B. Kauffman. 1992. Soils and hydrology of Willamette Valley wetland prairies and ecological response of *Lomatium bradshawii* and *Erigeron decumbens* var. *decumbens* to prescribed fire. A progress report to the U.S. Army Corps of Engineers and the Bureau of Land Management, Eugene, Oregon.

Folkerts, G.W. 1977. Endangered and threatened carnivorous plants of North America. Pages 301-313 in G.T. Prance and T.S. Elias, editors. Extinction is forever: threatened and endangered species of plants in the Americas and their significance in ecosystems today and in the future. New York Botanical Garden, Bronx, N.Y.

Franklin, J.F., and C.T. Dyrness. 1988. Natural Vegetation of Oregon and Washington. Oregon State University Press, Corvallis, Oregon.

Gankin, R. and J. Major. 1964. *Arctostaphylos myrtifolia*, its biology and relationship to the problem of endemism. Ecology 45:792-808.

Greenlee, J. and T.N. Kaye. 1997. Stochastic matrix projections: a comparison of the effect of element and matrix selection methods on quasi-extinction risk for *Haplopappus radiatus* (Asteraceae). Pages 66-71 in Kaye, T.N., A. Liston, R.M. Love, D. Luoma, R.J. Meinke, and M.V. Wilson, editors. Conservation and Management of Native Plants and Fungi. Native Plant Society of Oregon, Corvallis, Oregon.

Gregg, K.B. 1991. Variation in behaviour of four populations of the orchid Cleistes divaricata, an assessment using transition matrix models. Pages 139-159 in

T.C.E. Wells and J.H. Willems, editors. Population ecology of terrestrial orchids. Academic Publishing, The Hague, The Netherlands.

Gross, K., J.R. Lockwood III, C.C. Frost, and W.F. Morris. 1998. Modeling controlled burning and trampling reduction for conservation of *Hudsonia montana*. Conservation Biology 12:1291-1301.

Habeck, J.R. 1961. The original vegetation of the mid-Willamette Valley, Oregon. Northwest Sci. 35:65-77.

Hardin, D.E. and D.L. White. 1992. Rare vascular plant taxa associated with wiregrass (*Aristida stricta*) in the southeastern United States. Natural Areas Journal 9:234-245.

Hartnett, D.C. and D.R. Richardson. 1989. Population biology of *Bonomia grandiflora* (Convolvulaceae): effects of fire on plant and seed bank dynamics. American Journal of Botany 73:361-369.

Hawkes, C.V. and E.S. Menges. 1995. Density and seed production of a Florida endemic, *Polygonella basiramia*, in relation to time since fire and open sand. The American Midland Naturalist 133:138-145.

Heppell, S., C. Pfister, and H. de Kroon. 2000. Elasticity analysis in population biology: methods and applications. Ecology 81:605-606.

Hessl, A. and S. Spackman. 1995. Effects of fire on threatened and endangered plants: an annotated bibliography. U.S. Department of the Interior, National Biological Service, Washington, D.C.

Heydecker, W. 1973. Seed ecology. The Pennsylvania State University Press, London.

Horvitz, C.C. and D.W. Schemske. 1995. Spatiotemporal variation in demographic transitions of a tropical understory herb: projection matrix analysis. Ecological Monographs 65:155-192.

Horvitz, C.C., D.W. Schemske and H. Caswell. The relative "importance" of life-history stages to population growth: prospective and retrospective studies. Pages 248–271 in S. Tuljapurkar and H. Caswell, editors. Structured-population models in marine, terrestrial and freshwater systems. Chapman and Hall, New York, New York.

Jacobs, J. 1993. New hope for the Peter's Mountain Mallow. Endangered Species Technical Bulletin 18(3):13-14.

Jacobson, G.L., H. Almquist-Jacobson, and J.C. Winne. 1991. Conservation of rare plant habitat: insights from the recent history of vegetation and fire at Crystal Fen, northern Maine, USA. Biological Conservation 57:287-314.

Johannessen, C.L., W.A. Davenport, A. Millet, and S. McWilliams. 1971. The vegetation of the Willamette Valley. Annals of the Association of American Geography 61:286-302.

Johnson, A.F. and W.G. Abrahamson. 1990. A note on the fire responses of species in rosemary scrubs on the southern Florida Lake Wales Ridge. Florida Scientist 53:138-143.

Johnson, A.F. and A. Blyth. 1988. Re-discovery of *Calamovilfa curtissii* (Graminae) in Florida Panhandle. Sida 13:137-140.

Kagan, J.S. 1980. The biology of *Lomatium bradshawii* (Apiaceae), a rare plant of Oregon. M.S. thesis, University of Oregon, Eugene.

Kaye, T.N. 1992. Bradshaw's desert-parsley: population monitoring and pollination biology. Kalmiopsis 2:1-4.

Kaye, T.N., K. Pendergrass, and K.K. Finley. 1994. Population biology of *Lomatium bradshawii*. I. Population viability analysis under three prairie burning treatments. Oregon Department of Agriculture, Salem, Oregon.

Keeley, J.E. and C.J. Fotheringham. 1997. Trace gas emissions and smoke-induced seed germination. Science 276:1248-1250.

Kephart, S.R. and C. Paladino. 1997. Demographic change and microhabitat variability in a grassland endemic, *Silene douglasii* var. *oraria* (Caryophyllaceae). American Journal of Botany 84:179-189.

Kucera, C.L. and J.H. Ehrenreich. 1962. Some effects of annual burning on central Missouri prairie. Ecology 43:334-336.

Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. The American Naturalist 142:911-927.

Lande, R., and S.H. Orzack. 1988. Extinction dynamics of age-structured populations in a fluctuating environment. Proceedings of the National Academy Science 85:7418-7421.

Lefkovitch, L.P. 1965. The study of population growth in organisms grouped by stages. Biometrics 21:1-18.

Lesica, P. 1997. Demography of the endangered plant, *Silene spaldingii* (Caryophyllaceae) in northwest Montana. Madroño 44: 347–358.

Lesica, P. 1999. Effects of fire on the demography of the endangered, geophytic herb *Silene spaldingii* (Caryophyllaceae). American Journal of Botany 86: 996-1002..

Lindsey, A.H. 1982. Floral phenology patterns and breeding systems in *Thaspium* and *Zizia* (Apiaceae). Systematic Botany 7:1-12.

Lindsey, A.H. and C.R. Bell. 1985. Reproductive biology of Apiaceae. II. Cryptic specialization and floral evolution in *Thaspium* and *Zizia*. American Journal of Botany 72:231-237.

MacRoberts, M.H. and B.R. MacRoberts. 1990. Notes on the occurrence of *Platanthera integra* (Nutt.) A. Gray ex Beck (Orchidaceae) in West Central Louisiana. Phytologia 69:378-381.

Manders, P.T. 1987. A transition matrix model of the population dynamics of the Clanwilliam cedar (Widdringtonia cedarbergensis) in natural stands subject to fire. Forest Ecology and Management 20:171-186.

Maret, M.P. and M.V. Wilson. 2000. Fire and seedling population dynamics in western Oregon prairies. Journal of Vegetation Science 11:307-314.

Maschinski, J., R. Frye, and S. Rutman. 1997. Demography and population viability of an endangered plant species before and after protection from trampling. Conservation Biology 11:990-999.

McClaren, M.P. and P.C. Sundt. 1992. Population dynamics of rare orchid *Spiranthes delitescens*. Southwestern Naturalist 37:299-333.

Meagher, T.R. 1982. The population biology of *Chamaelirium luteum*, a dioecious member of the lily family: two sex population projections and stable population structure. Ecology 63:1701-1711.

Menges, E.S. 1986. Predicting the future of rare plant populations: demographic monitoring and modeling. Natural Areas Journal 6:13-25.

Menges, E.S. 1990. Population viability analysis for an endangered plant. Conservation Biology 4:52-62.

Menges, E.S. 1992a. Habitat preferences and response to disturbance for *Dicerandra frutescens*, a rare Lake Wales Ridge (Florida) endemic plant. Bulletin of the Torrey Botanical Club 119:308-313.

Menges, E.S. 1992b. Stochastic modeling of extinction in plant populations. Pages 253-275 in P.L. Fiedler and S.K. Jain, editors. Conservation biology: the theory and practice of nature conservation, preservation, and management. Chapman and Hall, New York.

Menges, E.S. 1995. Factors limiting fecundity and germination in small populations of *Silene regia* (Caryophyllaceae), a rare hummingbird-pollinated prairie forb. American Midland Naturalist 133:242-255.

Menges, E.S. 2000. Population viability analyses in plants: challenges and opportunities. Trends in Ecology and Evolution 15:51-56.

Menges, E.S. and R.W. Dolan. 1998. Demographic viability of populations of *Silene regia* in midwestern prairies: relationships with fire management, genetic variation, geographic location, population size and isolation. Journal of Ecology 86:63-78.

Menges, E.S. and J. Kimmich. 1996. Microhabitat and time-since-fire: Effects on demography of *Eryngium cuneifolium* (Apiaceae), a Florida scrub endemic. American Journal of Botany 83:185-191.

Moir, W.H. and P. Mika. 1976. Prairie vegetation of the Willamette Valley, Benton, Co., Oregon. Unpublished report, Research Work Unit 125, U.S.D.A. Forest Science Lab, Corvallis, Oregon.

Moloney, K.A. 1986. A generalized algorithm for determining category size. Oecologia 69:176-180.

Myers, R.L. 1989. Condominiums, trailer parks and high intensity fires: the future of sand pine scrub preserves in Florida. Proceedings of the 17th Tall Timbers Fire Ecology Conference, Tallahassee Florida.

Noble, I.R. and R.O. Slatyer. 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. Vegetatio 43:5-21.

Ojima, D.D., D.S. Schimel, W.J. Parton, and C.E. Owensby. 1994. Long- and short-term effects of fire on nitrogen cycling in tallgrass prairie. Biogeochemistry 24:67-84.

Oostermeijer, G. 1996. Population viability of the rare *Gentiana pneumonanthe*. The relative importance of demography, genetics, and reproductive biology. Ph.D. dissertation. Institute for Systematics and Population Biology, University of Amsterdam, The Netherlands.

Oostermeijer, G., M.L. Brugman, E.R. de Boer, and H.C.M. den Nijs. 1996. Temporal and spatial variation in the demography of *Gentiana pneumonanthe*, a rare perennial herb. Journal of Ecology 84:153-166.

Oregon Natural Heritage Program.2001. Rare, threatened and endangered plants and animals of Oregon. Oregon Natural Heritage Program, Portland, Oregon.

Owen, W.R. and R. Rosentreter. 1992. Monitoring rare perennial plants: techniques for demographic studies. Natural Areas Journal 12:32-39.

Parenti, R.L., A.F. Robinson, and J.S. Kagan. 1993. Bradshaw's lomatium recovery plan. U.S. Fish and Wildlife Service, Portland, OR.

Pendergrass, K.L. 1995. Vegetation composition and response to fire of native Willamette Valley wetland prairies. M.Sc. Thesis, Oregon State University, Corvallis, OR. 241 pp.

Pendergrass, K.L., P.M. Miller, and J.B. Kauffman. 1998. Prescribed fire and the response of woody species in Willamette Valley wetland prairies. Restoration Ecology 6:303-311.

Pendergrass, K.L., P.M. Miller, J.B. Kauffman, and T.N. Kaye. 1999. The role of prescribed burning in maintenance of an endangered plant species, *Lomatium bradshawii*. Ecological Applications 9:1420–1429.

Phillips, B.G., H. Green, S. Dudley, and R. Galeano-Popp. 1992. Prescribed fire research on Flagstaff pennyroyal (*Hedeoma diffusum* Greene). Pages 162-169 in R. Sivinski and K. Lightfoot, editors. Proceedings of the Southwestern rare and endangered plant conference. New Mexico Forestry Resources and Conservation Division, Santa Fe, New Mexico.

Sarukhan, J. and M. Gadgil. 1974. Studies on plant demography: *Ranunculus repens* L., *R. bulbosus* L., and *R. acris* L. III. A mathematical model incorporating multiple modes of reproduction. Journal of Ecology 62:921-936.

Schemske, D.W., B.C. Husband, M.H. Ruckelshaus, C. Goodwillie, I.M. Parker, and J.G. Bishop. 1994. Evaluating approaches to the conservation of rare and endangered plants. Ecology 75:584-606.

Schlessman, M.A. 1978. Systematics and reproductive biology of *Lomatium farinosum* (Geyer ex Hooker) Coulter & Rose (Umbelliferae). Madrono 25:1-9.

Shaw, R.G. 1987. Density-dependence in *Salvia lyrata*: Experimental alteration of densities of established plants. Journal of Ecology 75:1049-1063.

Silva, J.F., J. Raventos, and H. Caswell. 1990. Fire and fire exclusion effects on the growth and survival of two savanna grasses. Acta Œcologica 11:783-800.

Silva, J.F., J. Raventos, H. Caswell, and M.C. Trevisan. 1991. Population responses to fire in a tropical savanna grass, *Andropogon semiberbis*: a matrix model approach. Journal of Ecology 79:345-356.

Silvertown, J., M. Franco, and E.S. Menges. 1996. Interpretation of elasticity matrices as an aid to the management of plant populations for conservation. Conservation Biology 10:591-597.

Silvertown, J., M. Franco, I. Pisanty, and A. Mendoza. 1993. Comparative plant demography: relative importance of demographic components to the finite rate of increase in perennial plants. Journal of Ecology 81:465-476.

Steel, R.G.D., J.H. Torrie, and D.A. Dickey. 1997. Principles and procedures of statistics, a biometrical approach. Third edition. The McGraw-Hill Companies, Inc. New York.

Stone, C.P. and J.M. Scott. 1985. Hawaii's terrestrial ecosystems: preservation and management. Cooperative National Park Resources and Studies Unit, University of Hawaii, Manoa, Hawaii.

Streatfield, R. and R.E. Frenkel. 1997. Ecological survey and interpretation of the Willamette Valley Floodplain Research Natural Area, W.L. Finley National Wildlife Refuge, Oregon, USA. Natural Areas Journal 17:346-354.

Thompson, J.N. 1985. Postdispersal seed predation in *Lomatium* spp. (Umbelliferae): variation among individuals and species. Ecology 66:1608-1616.

Tuljapurkar, S.D. 1990. Population dynamics in variable environments. Springer-Verlag, New York.

Tuljapurkar, S.D. and S.H. Orzack. 1980. Population dynamics in variable environments. I. Long-run growth rates and extinction. Theoretical Population Biology 18:314-342.

Usher, M.B. 1976. Extensions to models, used in renewable resource management, which incorporate an arbitrary structure. Journal of Environmental Management 4:123-140.

Vacanti, P.L. and K.N. Geluso. 1985. Recolonization of a burned prairie by meadow voles (*Microtus pennsylvanicus*). Prairie Naturalist 17:15-22.

van Groenendael, J.M. and P. Slim. 1988. The contrasting dynamics of two populations of *Plantago lanceolata* classified by age and size. Journal of Ecology 77:162-181.

Vandermeer, J. 1978. Choosing category size in a stage projection matrix. Oecologia 32:79-84.

Warren, P.L., R.J. Frye, D. Gori, and A. Laurenzi. 1992. Population biology of *Pediocactus paradinei*, a rare cactus from northern Arizona. Pages 132-143 in R. Sivinski and K. Lightfoot, editors. Proceedings of the Southwestern Rare and Endangered Plant Conference. New Mexico Forestry Resources and Conservation Division, Santa Fe, New Mexico.

Wilson, M.V., E.R. Alverson, D.L. Clark, R.H. Hayes, C.A. Ingersoll, and M.B. Naughton. 1995. The Willamette Valley Natural Areas Network: Promoting restoration through science and stewardship. Restoration and Management Notes 13:26-28.

Wisdom, M.J., L.S. Mills, and D.F. Doak. 2000. Life stage simulation analysis: estimating vital-rate effects on population growth for conservation. Ecology 81:628-641.

Chapter 3

The Effect of Stochastic Technique on Estimates of Population Viability from Transition Matrix Models

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For submission to *Ecology*

INTRODUCTION

Population models are important tools for conservationists and represent applications of population biology theory. As key components of population viability analyses (PVA), they are widely applied to rare and endangered species. Conservationists and managers use population models to assess population health and trends, set priorities, and evaluate management options (Burgman et al. 1993). Different approaches to PVA, however, can lead to different conclusions, even with the same original data (Lindenmeyer et al. 1995, Mills et al. 1996, Pascual et al. 1997, Brook et al. 1999), and these differences can contribute to controversy and unstable priorities for management of imperiled species and the public lands on which they exist (Noon and McKelvey 1996). One common approach to PVA is to assemble field observations of survival and recruitment into a stage- or age-based transition matrix. Schemske et al. (1994) suggested that matrix models could be widely effective in setting recovery objectives and evaluating management proposals for endangered plants. Partly because of its flexibility, the technique has been widely applied to rare and common species with diverse life-histories. Even among matrix models, however, differences in implementation may produce divergent results.

Transition matrices can generate estimates of deterministic parameters such as population growth rate, sensitivities and elasticities, equilibrium population structure, and reproductive values. Often of greater concern to the conservationist are probabilistic measures of population health, such as extinction risk, time to extinction, and stochastic growth rate. These measures of population viability can be estimated when demographic and/or environmental stochasticity are incorporated into the model (Menges 2000, Caswell 2001). Inclusion of environmental stochasticity into matrix models has generally been accomplished through one of two mechanisms, matrix or element selection. For both methods of modeling environmental stochasticity, repeated estimates of annual recruitment, growth and survival must be available or temporal variability must be somehow assumed. Matrix selection involves shuffling whole observed matrices at random at each time step of a simulation, while element selection requires drawing each component of the matrix at random from some statistical distribution. However, the two methods do not always give the same results (Greenlee and Kaye 1997, Kaye et al. 2001). In addition, for implementation of the element selection method, too few data are usually available for a formal assessment of goodness of fit, so a statistical distribution is often assumed and the distribution is fit to the data at hand. In some cases, even if a reliable test of fit is possible, the statistically best distribution may be rejected on the basis of biological or theoretical reasons, or because of modeling convenience. Unfortunately, different statistical distributions of such input variables may change assessments of population viability (Nakoaka 1997), and information on actual temporal variation in demographic parameters is sparse (Menges 1992). The overall implications of which stochastic method is chosen remain unclear.

Another issue that must be addressed when stochastic stage-based models are implemented with the element selection method is that overall survival per stage should be limited to $\leq 100\%$. When individual transitions (elements) are selected at random, the cumulative survival (the sum of all transitions in a matrix column) for a given stage can (but should not) exceed 100%. It is important to constrain survival so that it is never greater than 100%, or the model will create individuals from nothing (Caswell 2001) and produce an overly optimistic estimate of population viability. Some authors of PVAs using stochastic matrix models have either ignored this issue or not mentioned it in their papers, and those that acknowledge the problem have used a variety of techniques to resolve it (e.g., Menges 1992, Gross et al. 1998, Kaye et al. 2001). To date, no empirical comparisons of survival constraint methods have been conducted. This problem does not exist for age-based models since only one transition (survival to the next age) is selected at random for each age-class, nor for matrix selection methods because survival never exceeds 100% in an observed matrix.

No comparisons of different methods of limiting survival to 100% are available, only a few papers compare techniques of incorporating stochasticity, and those that do explore the results from a single species (Greenlee and Kaye 1997, Nakoaka 1997, Kaye et al. 2001). In this paper, we compare seven methods of stochastic matrix simulation (matrix selection and six statistical distributions of element selection) and two methods of constraining survival to $\leq 100\%$. We evaluate the results with a measure of population viability (stochastic growth rate) derived from multiple species and several populations. Our primary objectives are to 1) test for an effect of stochastic method on population viability estimate, 2) test for an effect of survival constraint method, 3) investigate why different methods yield divergent results, and 4) measure the correlation between estimates.

METHODS

Study species and data sets

Data from five plant species were included in this analysis: *Astragalus tyghensis* Peck (Fabaceae), *Cimicifuga elata* Nutt. (Ranunculaceae), *Haplopappus radiatus* Nutt. (Cronq.) (Asteraceae), *Lomatium bradshawii* Rose (Math. & Const.) (Apiaceae), and *L. cookii* Kagan (Apiaceae). All of these taxa are herbaceous perennials and rare or endangered in the western United States (Oregon Natural Heritage Program 2001). Data were collected from multiple populations of each species over a period of five to ten years (Table 3.1); the number of observed transition matrices for each population was one less than the number of years of observation, except for *L. bradshawii* because one year of sampling was skipped resulting in only seven matrices from nine years of observation. In total, multi-year data from 27 populations were used. We included species from a variety of habitats and ecoregions in Oregon. In all cases, individual plants were followed through time as mapped and/or tagged individuals, and recruitment of seedlings (first year plants) was monitored annually. Stage-specific fecundity was estimated based on per capita seed production in year t and seedling recruitment in year $t+1$ (as in Kaye et al. 2001; "anonymous reproduction" of Caswell [2001:173-174]), or, if only one reproductive stage was recognized, based on seedlings

Table 3.1. Study species included in this analysis, number of populations and years observed, number of observed matrices and stage categories, habitat, and ecoregion. All species are herbaceous perennial plants.

species	number of populations	years of observation	number of observed matrices	number of stages	habitat	ecoregion[†]
Astragalus tyghensis	5	10 (1991-2000)	9	5 (seedling plus small, medium, large and very large size classes)	arid rangeland	Columbia Basin
Cimicifuga elata	3	5 (1992-96), or 6 (1992-97)	4-5	5 (seedling, small and large vegetative, reproductive, dormant)	mesic forest	Western Cascade Range
Haplopappus radiatus	10	10 (1991-2000)	9	4 (seedling, small and large vegetative, reproductive)	arid rangeland	Blue Mountains/ Owyhee Upland
Lomatium bradshawii	7	9 (1988-94, 1996-97)	7	5 (seedling, small and large vegetative, small and large reproductive)	wetland prairie	Willamette Valley
L. cookii	2	6 (1994-99)	5	6 (seedling; small and large vegetative; small, medium and large reproductive)	serpentine wetland	Klamath Mountains

[†]Based on map in Oregon Natural Heritage Program (2001).

observed in year $t+1$ per reproductive plant in year t. No seed bank stage was included in our models because biological evidence from studies of these species suggests that their seeds may not persist in the soil or have delayed germination. For example, no viable seeds more than one-year-old have been detected in field studies of *Lomatium* species (Thompson 1985), including *L. bradshawii* (Kaye et al. 2001), or *H. radiatus* (Kaye unpublished data). Seeds of *C. elata* stored under dry, room-temperature conditions do not remain viable for greater than one year, and field sown seeds of *A. tyghensis* emerge in the following spring only (Kaye unpublished data). Information on each species, including field sampling techniques, individual matrix construction methods, and the annual matrices, is available in the Appendix.

Stochastic population growth rate

We focused on stochastic population growth rate (λ_s) as a measure of population viability for this analysis. Stochastic growth rate was chosen over the more conventional extinction probability because it is not tied to a particular time horizon. Most estimates of extinction probability are based on simulations for a particular period of time, such as 100 years, and this time period may be selected to resolve differences between populations or treatments (i.e., if all populations go extinct after 100 year projections, the time window may be shortened until at least some populations have a chance of persisting). However, this variability in time span makes it difficult to compare results across studies (Menges 2000), and we found it difficult to identify a single time horizon appropriate to all 27 data sets included in this study. Any one period of simulation resulted in several populations with extinction probabilities of either 0 or 1. This resulted in an inability to resolve differences in these populations, and created many constant values inappropriate for evaluation with analysis of variance (ANOVA). Unlike the deterministic growth rate (λ), λ_s incorporates environmental variability and does not assume a stable (equilibrium) population structure (Tuljapurkar 1990). Further, as stochasticity increases, λ_s declines, and is always less than the average growth rate (which estimates λ) (Caswell 2001). Populations with λ_s greater than 1.0 are projected to grow, while those with λ_s less than 1.0 are projected to decline, making λ_s a convenient measure of population viability in stochastic environments.

To calculate λ_s, we followed the numerical simulation method outlined in Caswell (2001:396). When the log of population growth is averaged over a very large number of time steps, it converges to a fixed value determined by vital rates and environmental processes (Caswell 2001, Tuljapurkar 1990). For each type of simulation, we ran the models described below for 10,000 time steps (discarding the first 500 to omit transient effects) to calculate the stochastic growth rate. All stochastic modeling described in this paper was implemented in MATLAB 5 (The Mathworks 1998).

Modeling environmental stochasticity

Environmental stochasticity was modeled in two main ways, through matrix selection and element selection. To incorporate stochasticity via matrix selection, the observed matrices were assumed to be independently and identically distributed (iid). At each time step of a simulation, one matrix was selected at random and post-multiplied by the vector of individual abundances (e.g., Bierzychudek 1982, Lennartsson 2000). The initial stage distribution was the average observed distribution for each population. In element selection, a statistical distribution was first fit to the observed data for each transition matrix element, then random values were drawn from the distribution to create a new matrix at each time step. This matrix was then post-multiplied by the abundance vector to iterate the model, as above.

We used six different statistical distributions to compare the effect of input distribution shape on λ_s. Each of these distributions has been used in prior stochastic modeling studies (Table 3.2) or has been recommended for examination. They included the beta, truncated normal, truncated gamma, triangular, uniform, and observed/discontinuous (see Figure 3.1 for examples). Transition probabilities must be bounded by 0 and 1. Therefore, the fitted distributions must also be constrained to prevent transition probabilities less than zero or greater than 100% from being selected at random, a modeling error that is biologically unsound. Therefore, the beta distribution is a good candidate, since it is bounded by 0 and 1 by definition. The beta is also very flexible, capable of fitting to an extremely wide variety of distribution shapes (Evans et al. 2000). The normal distribution, on the other hand, must be truncated to 0 and 1, and in our implementation this was accomplished by omitting values outside <0 and >1 and resampling until an appropriate value was obtained. The gamma distribution is bounded by 0 on the left tail, but was truncated to 1 on the

Table 3.2. Examples of stochastic models, their use of statistical distributions for varying transition elements, and methods of constraining survivals to 100%.

distribution	species or study	survival constraint	citation
beta	*Hudsonia montana*	transitions contingent on survival	Gross et al. 1998
beta	Desert tortoise	none required	Doak et al. 1994
normal	comparative study	none	Guerrant 1996
truncated normal	*Totoaba macdonaldi*	none required	Cisneros-Mata et al. 1997.
truncated normal	various, comparative	resampled	Menges 1992
truncated normal	*Lomatium bradshawii*	if survival >100%, rescaled to 100%	Kaye et al. 2001
truncated normal and lognormal	*Yoldia notabilis*	none required	Nakoaka 1997
truncated lognormal	giant kelp	not indicated (none?)	Burgman and Gerard 1990
perfect positive correlation	lognormal (truncated for survivals)	northern spotted owl	Akçakaya and Raphael 1998
gamma	Chinook salmon	none required	Ratner et al. 1997.
uniform	*Pediocactus paradinei*	not indicated (none?)	Frye 1998
uniform	*Astragalus cremnophylax*	not indicated (none?)	Maschinski et al. 1997.
uniform	*Euphorbia clivicola*	not indicated (none?)	Pfab and Witkowski 2000
observed/ discontinuous	red-cockaded woodpecker	none required	Maguire et al. 1995

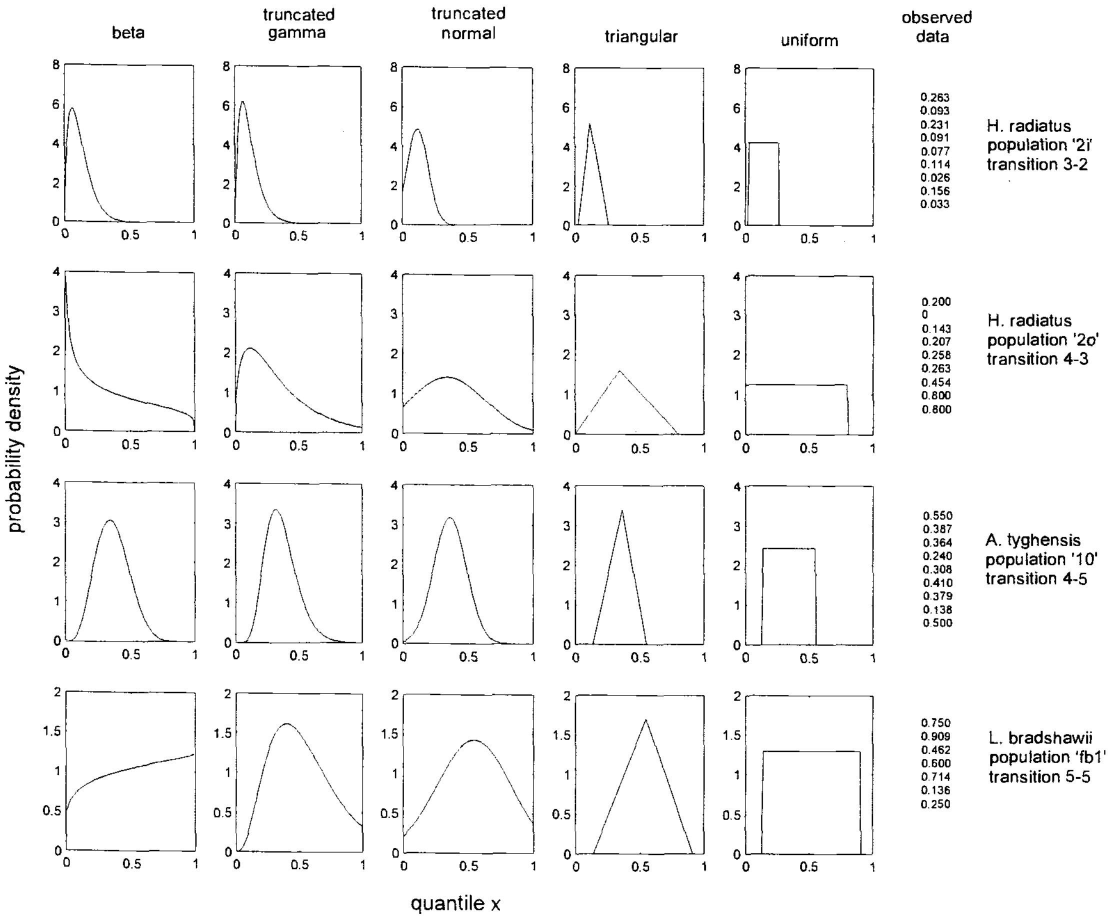

Figure 3.1. Probability densities of some statistical distributions fit to examples of observed values of transition rates recorded over several years of observation. Each column illustrates a different distribution (beta, truncated gamma, truncated normal, triangular, and uniform) and each row represents the fit of these distributions to the data listed at the right, which are selections from among the data sets used in this paper. These data represent the observed values for a particular transition, as indicated in the notes at the far right. Note that the truncated normal distribution is truncated at both tails and the truncated gamma is truncated only on the right, and the degree of truncation differs substantially among observed data sets.

right by omitting values > 1 and resampling. The triangular distribution may be appropriate when only minimum and maximum values are known (Caswell 2001), although a most likely value must be specified. We fit this model to our observed data by finding the minimum and maximum values, and using the mean as the most likely value. For the uniform distribution (also known as the rectangular distribution), we determined only the minimum and maximum values from our data sets. Finally, the observed/discontinuous distribution was defined here as the set of observed values for each transition, and these were drawn at random with equal probability (iid).

The method of matching moments was used to fit the beta and gamma distributions to our data because the observed values contained zeros and ones in some cases. An alternative would have been to use maximum likelihood estimation techniques, but this would have forced us to drop observed values equal to 0 or 1. However, dropping values would necessitate dropping whole matrices if we were to compare element selection with matrix selection methods, and we wanted to emphasize the empirical basis of our data sets while maximizing the available sample sizes. Frey and Burmaster (1999) have shown that, for the beta distribution at least, although the method of matching moments produces less efficient statistical parameter estimates than maximum likelihood methods, matching moment estimates are less sensitive to extreme values. Therefore, we used matching moment estimators because they appear to be adequately robust and because they tolerated the occasional zeros and ones among our observed values. For all our simulations, stochasticity was applied only to the transition elements; recruitment parameters were held constant.

Constraining survival

We examined two methods of constraining overall survival to 100%. In the first method, if the sum of transition probabilities for a given stage exceeded 100%, the entire set for that stage was resampled until it did not exceed 100% (a method employed by Menges 1992). We refer to this method as resampling. Our second method was to temporarily include mortality in our observed fates, draw a set of transition probabilities (including mortality) for each stage, rescale all probabilities to sum to 100%, then omit the mortality values in the final matrix. In this process, rescaling was applied at every time step to every stage, forcing the sum of all fates (including mortality) to equal 100% (which they always do in the real world). We refer to this method as rescaling and believe it has not been employed previously.

Analysis

Testing for effects of input distributions, survival constraint, and study species. We tested for effects of input distribution, survival constraint method, species, and interactions among these factors using SAS proc mixed (SAS Institute, Inc. 1990). Use of raw estimates of λ_s as a response variable posed a difficulty because survival constraint methods were applied only to the element selection procedures, not the matrix selection procedure, making our design unbalanced. Therefore, we chose a response variable that compared the relative response of each element selection procedure to matrix selection estimates of λ_s. Specifically, for each population, we calculated the proportional difference in λ_s between the matrix selection procedure and the procedures using various element selection distributions and survival constraint methods (i.e., [λ_s element−λ_s matrix]/λ_s matrix). This step was appropriate given that we are interested in the relative effects of these methods more than their actual estimates of mean stochastic growth rate. We considered this response variable to be structured in a split plot design, with species as the whole plot. Species was included as a fixed effect to test for differences among taxa in their PVA sensitivity to model assumptions, and for interactions with the other factors.

Detecting bias in mean and variability. To explore the fit of each simulation technique to the observed data, we compared the mean and variability of each transition element from the observed data sets with results from each of the element selection and survival constraint techniques. First, we used each of the element selection methods to generate 1000 random matrices from each population using each of the survival constraint methods. Second, we calculated the mean and standard deviation (STD) for each transition element (excluding recruitment) from these simulated data sets. Third, we calculated the relative difference in mean and STD between those estimated from the observed values and those calculated from the simulated matrices. We defined bias broadly to include the combined differences between observed and simulated means and STDs due to survival constraint method and distribution shape. We then tested for correlations between mean estimates of relative bias and mean relative differences in λ_s, using multiple regression, to determine how much of the simulation technique effects were due to these biases.

This process was repeated using estimates of mean relative bias weighted by the elasticity of each element, so that bias in elements of relatively low importance to growth rate were down-weighted and those with high influence were weighted more strongly. Although stochastic elasticities may be estimated as measures of the importance of individual transitions on λ_s (Tuljapurkar 1990a, Caswell 2001:402-408), we used elasticities calculated from mean observed matrices because they are easier to calculate and they are excellent predictors of stochastic elasticities, even though the deterministic and stochastic growth rates may be quite different (Caswell 2001, Caswell and Kaye in press).

Correlation among techniques. Even if the various techniques for incorporating stochasticity result in different estimates of λ_s, we would like to know if they yield similar results on a relative basis. That is, if one population has a higher λ_s than another as measured by one stochastic method, is it also higher as measured by a different method? To measure their degree of association, we tested for correlations between estimates of λ_s from each method of including temporal variability using the Pearson product moment (R), and this procedure was repeated for each method of constraining survival.

RESULTS

Effects of input distributions, survival constraint, and study species

Model procedures had substantial effects on estimates of stochastic population growth rates. The choice of input distributions and survival constraint methods both had significant effects on mean proportional differences in λ_s relative to the matrix selection method (Table 3.3), and there was a significant two-way interaction between these factors ($P \leq 0.0001$). That is, the resampling method of constraining stage-specific survival to ≤ 100% yielded mean estimates of λ_s consistently lower than the rescaling procedure, but the magnitude of this reduction differed among stochastic element selection methods (Figure 3.2). Study species did not affect these results ($P=0.804$), and there were no two- or three-way interactions with taxon ($P \geq 0.333$). Estimates of λ_s spanned from 0.658 to 1.173, making the results applicable to a wide range of population behavior.

When the resampling survival-constraint method was applied, most element-selection distributions yielded estimates of λ_s equal or lower than estimates derived by matrix selection. The beta distribution yielded the lowest relative estimate of λ_s (14% lower than the matrix shuffle method), while the truncated gamma and observed/discontinuous distributions were only slightly (but significantly) closer to the matrix shuffle estimates (Figure 3.2). Both the truncated normal and uniform distributions produced mean λ_s estimates indistinguishable from matrix selection. The mean estimate from the triangular distribution was intermediate between these two

Table 3.3. Split-plot ANOVA for the effects of species, statistical distribution of input variables, and survival constraint method on the proportional change in λ_s relative to the matrix selection procedure (NDF and DDF are numerator and denominator degrees of freedom).

Source	NDF	DDF	Type III *F*	Pr > *F*
whole plot effects				
species	4	22	0.4	0.8044
subplot effects				
survival constraint method	1	242	686.17	0.0001
stochastic method	5	242	53.79	0.0001
interactions				
stochastic method × constraint method	5	242	24.91	0.0001
species × constraint method	4	242	0.94	0.4434
species × stochastic method	20	242	1.12	0.3326
species × stochastic method × constraint method	20	242	0.46	0.9788

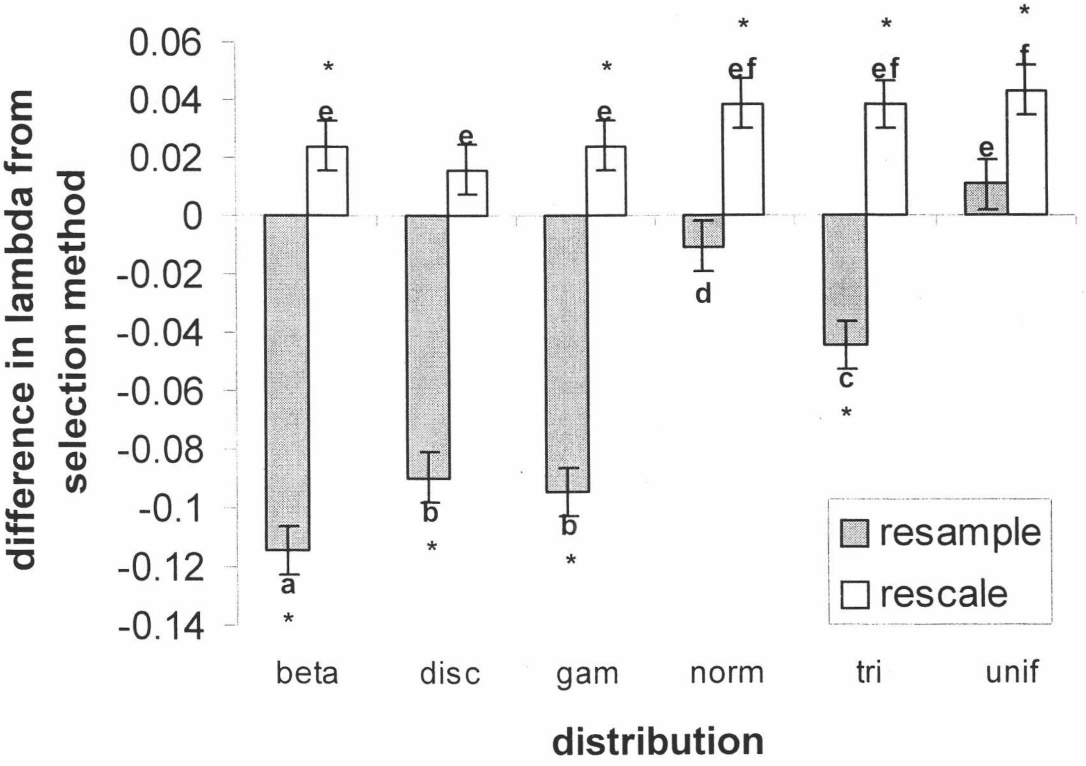

Figure 3.2. Mean proportional difference (±1 SE) in stochastic population growth rate (λ_s) between matrix selection and the element selection procedures. Six statistical distributions were used for the element selection method: beta, observed/discontinuous (disc), truncated gamma (gam), truncated normal (norm), triangular (tri), and uniform (unif). Two survival constraint methods, resample and rescale, were also compared. Bars with the same letter did not differ at the 0.05 level (Fisher's protected LSD). Asterisks (*) indicate a significant difference (0.05 level) between the stochastic growth rate calculated via matrix selection and each element selection method.

groups of procedures. In contrast, under the resampling procedure, most λ_s estimates were higher than those from matrix selection. Estimates from the uniform distribution were highest (about 4% higher than estimates from matrix selection) and those from the beta, truncated gamma, and observed/discontinuous were lowest (Figure 3.2). Those from the truncated normal and triangular distributions were intermediate. Estimates from the observed/discontinuous distribution did not differ significantly from the matrix selection method (Figure 3.2).

Evaluation of bias in mean and variability

Unweighted mean and STD. Bias was detected in the unweighted mean and STD of several element selection methods and both survival constraint techniques. Compared to the observed values, mean transition element values were reduced by 12-15% by the beta, truncated gamma, and observed discontinuous distributions when the resample constraint method was used. When the rescale technique was employed, however, these distributions had no detectable bias on transition means (Figure 3.3, top left). In contrast, the truncated normal, triangular, and uniform distributions consistently increased the mean over the observed values by 6-31%, regardless of survival constraint method. Standard deviations were also altered by the different methods. In all cases, STDs were depressed relative to the observed values. Values derived from the beta, truncated gamma, and observed/discontinuous showed the least bias (6-21% lower than observed), while those from the triangular had the greatest reduction (64-83%), depending on the method of constraining survival (Figure 3.3, middle left).

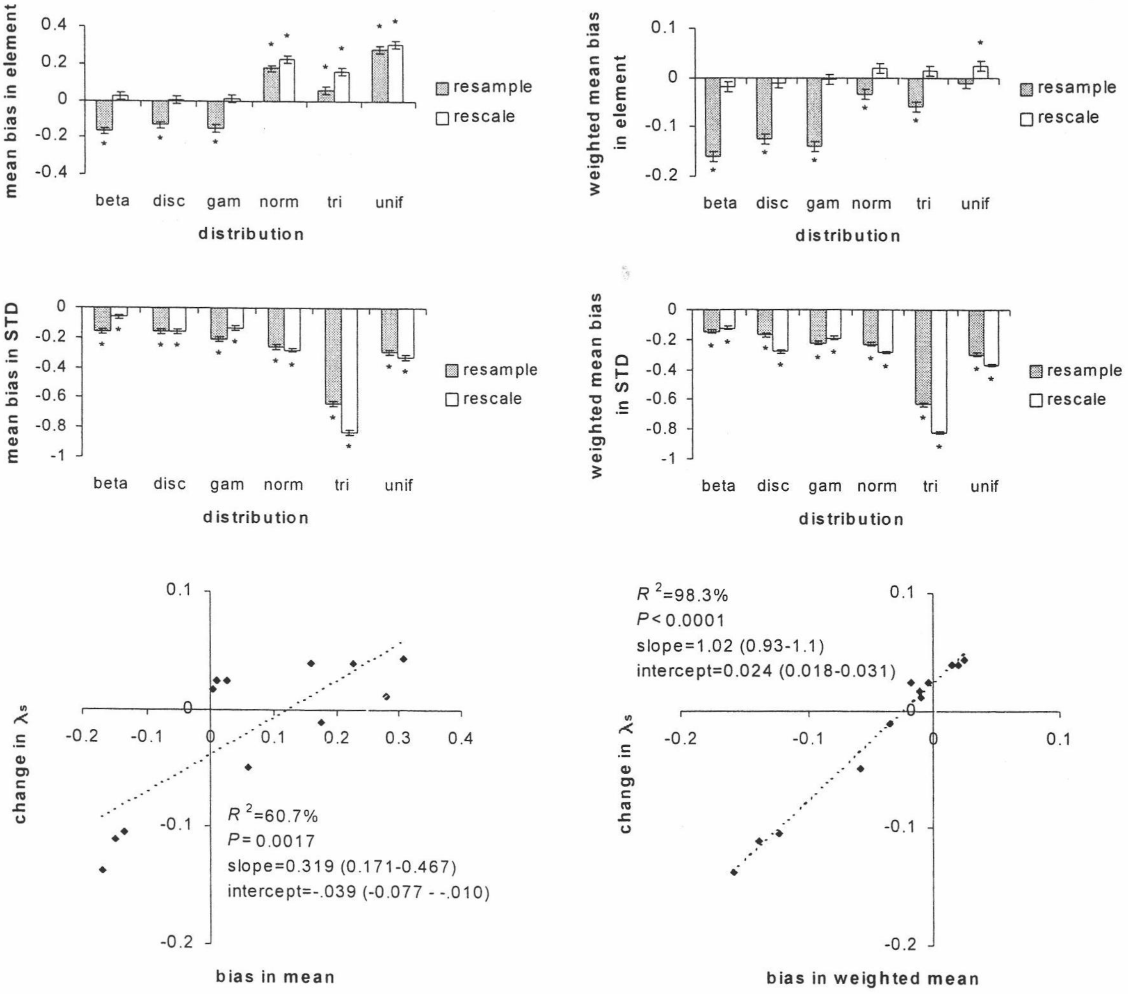

Figure 3.3. Evaluation of relative bias in transition means (top panels) and standard deviations (middle panels) relative to observed values. The correlation between change in λ_s and bias in element means is shown (bottom panels) along with the linear models. Mean bias in standard deviation was omitted from the models because it was not significant in the multiple regressions (P=0.10-0.66). Left panels use unweighted means and right panels use means weighted by elasticities. Asterisks indicate significant difference from zero at the 0.05 level of probability.

There were no consistent differences in bias to the standard deviation caused by the two survival constraint procedures. Multiple linear regression indicated that bias in the mean had a significant effect on proportional difference in λ_s ($P=0.0017$), while reductions in STD did not ($P=0.6603$). Bias in the mean explained 60.7% of the variability in λ_s estimates (Figure 3.3, bottom left).

Weighted mean and STD. When bias in mean transition elements was weighted by elasticity, a somewhat different picture emerged. The resampling procedure resulted in varying degrees of negative bias, depending on the statistical distribution used to incorporate stochasticity. For example, the beta, truncated gamma, and observed/discontinuous distributions resulted in reductions in the weighted means of 12-16% (similar to the unweighted case), but the truncated normal and triangular biased the weighted mean downward by 3 and 6%, respectively (Figure 3.3, top right). The uniform distribution had no effect on the weighted means. The rescaling procedure resulted in no detectable bias on the weighted mean transition rates for all stochastic methods except the uniform, which increased the mean by about 2% (Figure 3.3, top right). Overall, weighted STD biases differed little from the non-weighted cases (Figure 3.3, middle right).

As in the unweighted case, multiple regression indicated a significant linear correlation between differences in λ_s and bias in the weighted mean ($P<0.0001$), but not STD ($P=0.1038$). Bias in the weighted mean explained 98.3% of the variability in proportional differences in lambda between element selection techniques and matrix selection. The slope of this relationship was indistinguishable from 1 (95% CI 0.93-1.1), and the intercept was close to, but slightly higher than, 0 (95% CI 0.018-0.031). Thus, variation in λ_s estimates derived through element selection relative to matrix selection were due almost entirely to biases in the weighted mean transition rates.

Correlation among techniques

Most methods of incorporating stochasticity into matrix models produced estimates of λ_s that were highly correlated. For both methods of survival-constraint, resampling and rescaling, the lowest correlation was between estimates via the beta and observed/discontinuous distributions (R=0.862 and 0.849, respectively) and the highest was between the truncated gamma and uniform (R=0.992 and 0.992, respectively) (Table 3.4). Regardless of which survival-constraint technique was used, at least 16 of the 21 possible correlations were $\geq$0.9.

DISCUSSION

Effects of stochastic methods and survival constraints

Different methods of incorporating stochasticity into matrix models resulted in substantial variation in estimates of population viability. The species from which the observed data were collected, however, had no effect, and estimates of λ_s spanned a wide range, suggesting that these results may be broadly applicable. In element selection, the distribution shape for sampling transition probabilities had significant

Table 3.4. Pearson correlation coefficients (*R*) for each of seven methods of incorporating environmental variability to calculate stochastic population growth rate (λ_s). Correlations with λ_s calculated using the resample survival constraint method are above the diagonal, while those derived via the rescale method are below ($P \leq 0.0001$ in each case).

Stochastic method	matrix selection	observed/ discontinuou	uniform	truncated normal	truncated gamma	triangular	beta
matrix selection	--	0.869	0.928	0.877	0.926	0.915	0.905
observed/ discontinuous	0.916	--	0.877	0.970	0.913	0.977	0.862
uniform	0.976	0.893	--	0.920	0.991	0.930	0.986
truncated normal	0.955	0.975	0.945	--	0.943	0.959	0.895
truncated gamma	0.962	0.900	0.992	0.954	--	0.949	0.988
triangular	0.951	0.989	0.942	0.991	0.948	--	0.908
beta	0.947	0.849	0.984	0.906	0.973	0.903	--

effects on estimates of stochastic lambda, but the magnitude and direction of this effect depended on which method was used to constrain stage-specific survival to $\leq 100\%$ (Figure 3.2). For example, when resampling was used to constrain survivals, the beta, observed/discontinuous, truncated gamma, and triangular distributions resulted in λ_s estimates significantly lower than those derived from matrix selection. But when survivals were constrained through rescaling, all distributions, except the observed/discontinuous, exceeded matrix selection estimates of λ_s. Overall, combining the resampling method with the beta distribution resulted in the lowest mean estimates of λ_s (13.8% below the average matrix selection estimates), while rescaling with the uniform distribution produced the highest (4.3% greater than matrix selection estimates). Despite variation in estimates of λ_s, the different stochastic methods produced highly correlated results (R=0.849-0.992, Table 3.4), suggesting that although their quantitative estimates of population viability may have differed, their relative ranking of populations did not.

Concerns that choice of a stochastic method and distribution shape might influence the results of risk assessment models are not new (Bukowski et al. 1995, Nakoaka 1996, Hamed and Bedient 1997, Menges 2000, Caswell 2001). Past comparisons of matrix and element selection procedures have found both large and small differences in estimates of population viability. For example, a comparison from *H. radiatus* found that element selection from a truncated normal distribution resulted in much lower estimates of extinction risk than matrix selection (Greenlee and Kaye 1997). Kaye et al. (2001) found estimates of λ_s derived for *L. bradshawii* from element selection (truncated normal distribution) to be identical to, or moderately higher than, estimates from matrix selection. Extinction probability estimates were either identical or slightly lower than from matrix selection. These patterns are consistent with those reported here, which should be expected because both examples used earlier portions of the same data sets used in this analysis. Even so, Greenlee and Kaye (1997) incorporated only four years of data and Kaye et al. (2001) used six, and both studies used a different approach to survival constraint than those conducted here (see below). Although stochastic growth rate has been recommended as a measure of population viability suitable for comparisons across studies (Menges 2000), differences among stochastic methods make many comparisons dangerous. This problem can be avoided, however, if the same methods are used among studies (which seldom may be the case; see Table 3.2), or if the estimates of stochastic growth rate are first adjusted by the cumulative bias of the specific survival constraint methods and probability distributions. In general, comparisons across viability studies should strive to standardize as many model assumptions as possible, a practice that may find much agreement among techniques (Brook et al. 2000a and 2000b).

Among element selection methods, skewness has been identified as an important aspect of a distribution with potential effects on estimates of population growth rate (Slade and Levinson 1984), and the selection of a statistical distribution can, in theory, substantially affect the results of a risk assessment (Bukowski 1995). The effects of different distributions have been much more thoroughly reviewed for randomly varying recruitment (Tallie et al. 1995) than transition probabilities. Nakoaka (1997), for example, estimated λ_s for two populations of a marine clam by allowing recruitment to vary according to both lognormal and truncated normal distributions (one-tailed truncation was necessary because recruitment must be bounded by zero on the left). Relative to the truncated normal, the lognormal decreased λ_s at one site but increased it at the second. In our analyses, recruitment was held invariant and stochasticity was applied only to the transition probabilities. If we had allowed recruitment to vary as well, our results may have differed and/or there may have been an interaction between choice of recruitment and transition distributions. Since both types of vital rates are often varied in stochastic matrix models, this area deserves further research.

Resampling to constrain survival to $\leq 100\%$ always reduced λ_s relative to rescaling by introducing negative bias into weighted mean vital rates (Figure 3.3). The rescaling method, on the other hand, did not introduce measurable bias (except for the uniform distribution, which was slightly positively biased). Although researchers have used various techniques to constrain stage-specific survivals to $<100\%$, or ignored the problem (Table 3.2), we found the choice of survival constraint technique to have a strong effect on our results. Results from the rescaling technique were fairly consistent among element selection distributions, with the only significant differences being between the uniform distribution and the beta, discontinuous/observed, and truncated gamma (which were indistinguishable from each other, Figure 3.2). Relative to estimates from matrix selection, λ_ss were higher by only 1.7% (discontinuous/observed) to 4.3% (uniform). Other methods used by previous authors of stage-based stochastic matrix models include a different form of rescaling used when survivals sum to greater than 100% (without regard to mortality, e.g., Kaye et al. [2001]) and making transitions contingent on underlying vital processes (e.g., Gross et al. 1998).

One reason for the similarity in results among the element selection methods compared here with rescaling (in the relative absence of bias) may be that some of their important differences are in their tails — their chance of extreme events — and these tails were either bounded to fall between zero and one, or were truncated to do so. In an examination of the tail behavior of the lognormal, Weibull, gamma, and inverse gaussian distributions in Monte Carlo simulations, Haas (1997) found that even at relatively high standard deviations, the important differences among them were in the extreme (upper) tails. Since the distributions with long tails included in our implementations (i.e., normal and gamma) were truncated, these differences were, at least in part, reduced. For example, the triangular and truncated normal distributions have identical peak values, but substantial portions of both tails of the normal may be cut off (Figure 3.1), thus increasing the similarity of the two distributions. Haas (1997) further showed that identifying the correct distribution from small data sets may be difficult or impossible (our samples numbered only 4-9, depending on the species), but the differences will be primarily in the tails. Again, if the tails are truncated, these differences may be partly mitigated.

Although truncation may help explain some of the similarities among the element selection methods evaluated here, it is not necessarily a recommended practice. Especially in cases where only one tail is truncated, omitting chance events in this way from a distribution will change the mean and reduce variance, as illustrated here by negative bias in STD estimates (Figure 3.3). Truncation of transition probabilities drawn from a normal distribution, especially those near 1, lowered the mean and increased extinction probability in viability models of the fish, *Totoaba macdonaldi* (Cisneros-Mata et al. 1997). In the case of Nakoaka's (1997) marine clam, truncation of the lower tail in the normal distribution was required to generate random numbers for modeling variation in recruitment. This one-tailed truncation increased the mean by about 25% and decreased the variance by 35% at one site (as discussed in Caswell 2001:412), destroying the fit of the distribution to the data. It may be that in many of our cases with observed data, substantial portions of the normal and gamma probability density functions were within 0-1, which would explain why truncating them produced little or no effect on the weighted mean and only "typical" reductions (Figure 3.3) in standard deviation. Of course, the effect of truncation will be stronger as the mean approaches 0 or 1 (depending on the distribution), because a larger proportion of the probability density function will be truncated. For example, if a gamma distribution is fitted to a group of observed transition probabilities close to 1, the upper tail will extend substantially past 1 and truncation will remove a significant portion of the probability density function. If this is a concern, a clever procedure (Burgman and Gerard 1990) that will reduce its effect is to transform the observed probabilities (p) to $q = 1-p$, fit the distribution, draw a random sample, then back transform the value to $1-q$, thus avoiding most truncations.

Selecting a distribution that does not require truncation may be preferred. The endpoints of the uniform and triangular distribution were defined by the observed data, so they never fell beyond 0-1 in our samples. However, their shapes are simplistic and they did not capture variance well, resulting in relatively low STDs (28-83% below observed values). Even so, they may be appropriate in cases where few data are available. For example, the triangular distribution may be an efficient substitute for the beta in some cases (McCrimmon and Ryavec 1964). The beta distribution, in contrast, is bounded by 0 and 1 and has a flexible shape within those bounds, traits that make it useful for modeling transition probabilities. It is perhaps the first distribution that should be explored when developing a stochastic matrix model with element selection. The observed/discontinuous distribution did not allow transition elements to vary outside the observed limits, and it did not allow selection of values other than those observed. Depending on the model, this may or may not be a desirable trait. When combined with the rescale survival constraint method, it produced results indistinguishable from those derived with the beta distribution or matrix selection. Other distributions that have received little attention but that stochastic matrix modelers should explore include the S-distribution, which is based on differential equations and is well suited to probabilities (Voit and Schwake 2000), and the beta-binomial, which is appropriate for distributions based on probabilities derived from counts (Griffiths 1973, Tamura and Young 1987, Kahn and Raftery 1996). The beta-binomial may be especially useful and appropriate for stochastic matrix models because it can separate demographic variability from estimates of environmental stochasticity (Kendall 1998).

Matrix vs. element selection

Both approaches for incorporating stochasticity, element selection and matrix selection, have advantages and disadvantages as modeling techniques. For example, because element selection can sample from parametric distributions of transition probabilities, the possible trajectories that a population size can follow are limited only by the distribution shape. In contrast, matrix selection limits the number of pathways a population can follow in a stochastic simulation because, at each time step, one of a finite number of matrices must be selected. Through parametric element selection, a greater number of possible paths can be explored, especially those that occur with lower frequency (the tails in a distribution). These rare events may be important for assessing chance events like extinction (Burgman et al. 1993). Element selection may also accommodate missing data more efficiently than matrix selection by fitting a distribution to the vital rates for which data are available. In matrix selection, individual missing vital rates must be estimated or replaced with pooled data from the other individual matrices. However, matrix selection is not confronted with the problem of constraining stage-specific survivals to ≤100%, while element selection in most stage-structured models is. Finally, element selection may be a better choice when stochasticity must be applied to individual vital rates through a functional relationship with an environmental factor, such as precipitation (e.g., Gross et al. 1998).

One weakness of standard element selection methods is that transition probabilities may not be explicitly correlated with one another, even though a "good" year for one vital rate, such as survival of reproductive plants, is often a good year for another, such as fecundity. Therefore, a matrix could be constructed from random elements that has a mixture of "good" and "bad" vital rates — a condition that may not occur in nature. Matrix selection is not usually faced with this problem since all of the elements in an individual matrix usually come from the same year and represent observed vital rates. Correlation among vital rates is believed to be widespread (Horvitz and Schemske 1995, Oostermeijer et al. 1996, Horvitz et al. 1997, Gross et al. 1998, Caswell 2000, Menges 2000, Caswell 2001) and may tend to reduce population viability (Ferson and Burgman 1995, Cisneros-Mata et al. 1997, Pfab and Witkowski 2000). In the current study, differences in estimates of λ_s were largely explained ($R^2 = 98.4\%$) by degree of bias in mean transition rates (after weighting with elasticities), and the slope of the regression line for this linear correlation did not differ from 1.0 (Figure 3.3). The intercept of this line was slightly higher (2.4%) than expected, however, and this may be due, in part, to increases in λ_s (relative to matrix selection) through omission of correlation structure during element selection. Unfortunately, tools for multivariate random number generation are not widely available (Caswell 2001) for distributions other than the normal, but recent advances in statistical methods (e.g., Ferson and Burgman 1995, Haas 1999, Fackler 1999) may make their application more accessible for stochastic matrix models (see Chapter 4).

Conclusion

For many observed data sets, it may be difficult to test the fit of a particular distribution, partly because of limited samples (Karian and Dudewicz 2000:90-96). Sorribas et al. (2000) demonstrated that even with 160 random samples from known distributions, a best-fit screening algorithm failed to identify the source distribution in a majority of cases. Despite this uncertainty, most stochastic modelers select a distribution that seems reasonable, fit it to their available data, and execute the model. We have shown that distribution choice for transition probabilities may have a strong influence on stage-structured matrix model outcomes, and this effect is consistent across a variety of plant species. Although the effect can cause differences in viability estimates, it was largely explained by degree of bias induced by the different survival constraint methods we employed. Little previous attention has been given to the survival constraint problem, which applies only to stage-structured models in which individuals can make more than one transition, but choice of this procedure can be at least as important as element selection technique. To avoid bias in influential transitions, we recommend use of the rescaling procedure used here. Also, our estimates of λ_s were strongly correlated among the various stochastic methods, indicating that the relative values of λ_s estimates were generally consistent.

The wide range of population viability estimates possible from a single data set analyzed by slightly different methods is cause for concern; one technique might indicate a robust population while another could project a rapid decline. We agree with Beissinger and Westphal (1998) and Menges (2000) that the strength of viability analysis rests in its use as a comparative tool rather than a means of assessing the health of individual populations. Especially in the face of uncertainty due to measurement error, which can create very wide confidence intervals on estimates of extinction probability (Ludwig 1999, Fieberg and Ellner 2000), the use of viability analyses to assess the relative vigor of a group of populations or the impact of a habitat alteration should be emphasized over quantitative estimates of viability. Fortunately, the relative ranking of populations appears to be fairly robust to differences in stochastic methods. It may also be sound practice to compare several methods when making management recommendations for endangered species (e.g., Pascual et al. 1997 and Fisher et al. 2000).

Although stochastic growth rate has been recommended as a measure of population viability suitable for comparisons across studies (Menges 2000), differences among stochastic methods make such comparisons dangerous. This problem can be avoided, however, if the same methods are used among studies (which is seldom the case, see Table 3.2), or if the estimates of stochastic growth rate are first adjusted by the cumulative bias of the specific survival constraint methods and probability distributions.

LITERATURE CITED

Akçakaya, H.R. and M.G. Raphael. 1998. Assessing human impact despite uncertainty: viability of the northern spotted owl metapopulation in the northwestern USA. Biodiversity and Conservation 7:875-894.

Beissinger, S.R. and M.I. Westphal. 1998. On the use of demographic models of population viability in endangered species management. Journal of Wildlife Management 62:821-841.

Bierzychudek, P. 1982. The demography of jack-in-the-pulpit, a forest perennial that changes sex. Ecological Monographs 52:335-351.

Brook, B.W., J.R. Cannon, R.C. Lacey, C. Mirande, and R. Frankham. 1999. A comparison of the population viability analysis packages GAPSS, INMAT, RAMAS, and VORTEX for the Whooping Crane (*Grus americana*). Animal Conservation 2:23-31.

Brook, B.W., M.A. Burgman, and R. Frankham. 2000a. Differences and congruencies between PVA packages: the importance of sex ratio for predictions of extinction risk. Conservation Ecology 4:4. [online] URL: http://www.consecol.org/vol4/iss1/art6.

Brook, B.W., J.J. O'Grady, A.P. Chapman, M.A. Burgman, H.R. Akçakaya, and R. Frankham. 2000b. Predictive accuracy of population viability analysis in conservation biology. Nature 404:385-387.

Bukowski, J., L. Korn, and D. Wartenberg. 1995. Correlated inputs in quantitative risk assessment: the effects of distributional shape. Risk Analysis 15:215-219.

Burgman, M.A., S. Ferson, and H.R. Akçakaya. 1993. Risk assessment in conservation biology. Chapman and Hall, London.

Burgman, M.A. and V.A. Gerard. 1990. A stage-structured, stochastic population model for the giant kelp *Macrocystis pyrifera*. Marine Biology 105:15-23.

Caswell, H. 2000. Prospective and retrospective perturbation analyses: their roles in conservation biology. Ecology 81:619-627.

Caswell, H. 2001. Matrix population models. Second edition. Sinauer Associates Inc., Sunderland, Massachusetts.

Caswell, H. and T.N. Kaye. In press. Stochastic demography and conservation of *Lomatium bradshawii* in a dynamic fire regime. Advances in Ecological Research.

Cisneros-Mata, M.A., L.W. Botsford, and J.F. Quinn. 1997. Projecting viability of *Totoaba macdonaldi*, a population with unknown age-dependent variability. Ecological Applications 7:968-980.

Doak, D., P. Kareiva, and B. Klepetka. 1994. Modeling population viability for the desert tortoise in the western Mojave Desert. Ecological Applications 4:446-460.

Evans, M., N. Hastings and B. Peacock. 2000. Statistical Distributions. Third edition. John Wiley and Sons, New York.

Fackler, P. 1999. Generating correlated multidimensional variates. [online] URL: http://www4.ncsu.edu/unity/users/p/pfackler/www/#WorkingPapers.

Ferson, S. and M.A. Burgman. 1995. Correlations, dependency bounds and extinction risks. Biological Conservation 73:101-105.

Ferson, S., L.R. Ginzburg and H. R. Akçakaya. In press. Whereof one cannot speak: when input distributions are unknown. Risk Analysis.

Fieberg, J. and S.P. Ellner. 2000. When is it meaningful to estimate an extinction probability? Ecology 81:2040-2047.

Fisher, D.O., S.D. Hoyle, and S.P. Bloomberg. 2000. Population dynamics and survival of an endangered wallaby: a comparison of four methods. Ecological Applications 10:901-910.

Frey, H.C. and D.E. Burmaster. 1999. Methods of characterizing variability and uncertainty: comparison of bootstrap simulations and likelihood-based approaches. Risk Analysis 19:109-130.

Frye, R.J. 1998. Population viability analysis of *Pediocactus paradinei*. Pages 39-46 in J. Maschinski, H.D. Hammond and L. Holter, editors. Southwestern Rare and Endangered Plants: Proceedings of the Second Conference. General Technical Report RM-GTR-283. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

Greenlee, J. and T.N. Kaye. 1997. Stochastic matrix projections: a comparison of the effect of element and matrix selection methods on quasi-extinction risk for *Haplopappus radiatus* (Asteraceae). Pages 66-71 in T.N. Kaye, A. Liston, R.M. Love, D. Luoma, R.J. Meinke, and M.V. Wilson, editors. Conservation and Management of Native Plants and Fungi. Native Plant Society of Oregon, Corvallis, Oregon.

Griffiths, D.A. 1973. Maximum likelihood estimation for the beta-binomial distribution and an application to the household distribution of the total number of cases of disease. Biometrics 29:637-648.

Gross, K., J.R. Lockwood III, C.C. Frost, and W.F. Morris. 1998. Modeling controlled burning and trampling reduction for conservation of *Hudsonia montana*. Conservation Biology 12:1291-1301.

Guerrant, E.O. 1996. Designing populations: demographic, genetic, and horticultural dimensions. Pages 171-207 in D.A. Falk, C.I. Millar, and M. Olwell, editors. Restoring Diversity. Island Press, Washington D.C. .

Haas, C.N. 1997. Importance of distributional form in characterizing inputs to Monte Carlo risk assessments. Risk Analysis 17:107-113.

Haas, C.N. 1999. On modeling correlated random variables in risk assessment. Risk Analysis 19:1205-1214.

Hamed, M.M. and P.B. Bedient. 1997. On the effect of probability distributions of input variables in public health risk assessment. Risk Analysis 17:97-105.

Horvitz, C.C. and D.W. Schemske. 1995. Spatiotemporal variation in demographic transitions of a tropical understory herb: projection matrix analysis. Ecological Monographs 65:155-192.

Horvitz, C.C., D.W. Schemske and H. Caswell. 1997. The relative "importance" of life-history stages to population growth: prospective and retrospective studies. Pages 248–271 in S. Tuljapurkar and H. Caswell, editors. Structured-population models in marine, terrestrial and freshwater systems. Chapman and Hall, New York, New York.

Kahn, M.J. and A.E. Raftery. 1996. Discharge rates of Medicare stroke patients to skilled nursing facilities: Baysian logistic regression with observed heterogeneity. Journal of the American Statistical Association — Applications and Case Studies 91:29-41.

Karian, Z.A. and E.J. Dudewicz. 2000. Fitting Statistical Distributions. CRC Press, Boca Raton, Florida.

Kaye, T.N., K.L. Pendergrass, K. Finley, and J.B. Kauffman. 2001. The effect of fire on the population viability of an endangered prairie plant. Ecological Applications, in press.

Kendall, B.E. 1998. Estimating the magnitude of environmental stochasticity in survivorship data. Ecological Applications 8:184-193.

Kephart S.R. and C. Paladino. 1997. Demographic change and microhabitat variability in a grassland endemic, *Silene douglasii* var. *oraria* (Caryophyllaceae). American Journal of Botany 84:179-189.

Lennartsson, T. 2000. Management and population viability of the pasture plant *Gentiana campestris*: the role of interactions between habitat factors. Ecological Bulletin 48:111-121.

Lindenmeyer, D.B., M.A. Burgman, H.R. Akçakaya, R.C. Lacy, and H.P. Possingham. 1995. A review of the generic computer programs ALEX, RAMAS/space and VORTEX for modelling the viability of wildlife populations. Ecological Modelling 82:161-174.

Ludwig, D. 1999. Is it meaningful to estimate a probability of extinction? Ecology 80:298-310.

Maguire, L.A., G.F. Wilhere, and Q. Dong. 1995. Population viability analysis for red-cockaded woodpeckers in the Georgia Piedmont. Journal of Wildlife Management 59:533-542.

Maschinski, J., R. Frye, and S. Rutman. 1997. Demography and population viability of an endangered plant species before and after protection from trampling. Conservation Biology 11:990-999.

Mathworks, The. 1998. Matlab, version 5. The Mathworks, Inc., Natick, Massachusetts.

McCrimmon, K.R. and C.A. Ryavec. 1964. An analytical study of PERT assumptions. Operations Research 12:113-124.

Menges, E.S. 1990. Population viability analysis for an endangered plant. Conservation Biology 4:52-62.

Menges, E.S. 1992. Stochastic modeling of extinction in plant populations Pages 253-275 in P.L. Fiedler and S.K. Jain, editors. Conservation biology: the theory and practice of nature conservation, preservation, and management. Chapman and Hall, New York.

Menges, E.S. 2000. Population viability analyses in plants: challenges and opportunities. Trends in Ecology and Evolution 15:51-56.

Menges, E.S. and R.W. Dolan. 1998. Demographic viability of populations of *Silene regia* in midwestern prairies: relationships with fire management, genetic variation, geographic location, and population size. Journal of Ecology 86:63-78.

Mills, L.S., S.G. Hayes, C. Baldwin, M.J. Wisdom, J. Citta, D.J. Mattson, and K. Murphy. 1996. Factors leading to different viability predictions for a grizzly bear data set. Conservation Biology 10:863-873.

Nakoaka, M. 1996. Dynamics of age- and size-structured populations in fluctuating environments: applications of stochastic matrix models to natural populations. Researches in Population Ecology 38:141-152.

Nakoaka, M. 1997. Demography of the marine bivalve *Yoldia notabilis* in fluctuating environments: an analysis using a stochastic matrix model. Oikos 79:59-68.

Noon, B.R. and K.S. McKelvey. 1996. Management fo the spotted owl: A case history in conservation biology. Annual Review of Ecology and Systematics 27:135-162.

Oostermeijer, G., M.L. Brugman, E.R. de Boer, and H.C.M. den Nijs. 1996. Temporal and spatial variation in the demography of *Gentiana pneumonanthe*, a rare perennial herb. Journal of Ecology 84:153-166.

Oregon Natural Heritage Program, 2001. Rare, threatened and endangered plants and animals of Oregon. Oregon Natural Heritage Program, Portland, Oregon.

Pascual, M.A., P. Kareiva, and R. Hilborn. 1997. The influence of model structure on conclusions about the viability of harvesting of Serengeti wildebeest. Conservation Biology 11:966-976.

Pfab, M.F. and E.T.F. Witkowski. 2000. A simple population viability analysis of the critically endangered *Euphorbia clivicola* R.A. Dyer under four management scenarios. Biological Conservation 96:263-270.

Ratner, S., R. Lande and B.B. Roper. 1997. Population viability analysis of spring Chinook salmon in the South Umpqua River, Oregon. Conservation Biology 11:879-889.

SAS Institute, Inc. 1990. SAS/STAT User's Guide, version 6. Fourth edition, volume 2. SAS Institute, Inc., Cary, North Carolina.

Slade, N.A. and H. Levinson. 1984. The effects of skewed distributions of vital statistics on growth of age-structured populations. Theoretical Population Biology 26:361-366.

Schemske, D.W., B.C. Husband, M.H. Ruckleshaus, C. Goodwillie, I.M. Parker, and J.H. Bishop. 1994. Evaluating approaches to the conservation of rare and endangered plants. Ecology 75:584-606.

Sorribas, A., J. March, and E.O. Voit. 2000. Estimating age-related trends in cross-sectional studies using S-distributions. Statistics in Medicine 19:697-713.

Tallie, C., G.P. Patil, and R.C. Hennemuth. 1995. Modelling and analysis of recruitment distributions. Environmental and Ecological Statistics 2:315-329.

Tamura, R.N. and S.S. Young. 1987. A stabilized moment estimator for the beta-binomial distribution. Biometrics 43:813-824.

Thompson, J.N. 1985. Postdispersal seed predation in *Lomatium* spp. (Umbelliferae): variation among individuals and species. Ecology 66:1608-1616.

Tuljapurkar, S.D. 1990. Population dynamics in variable environments. Springer-Verlag, New York.

Voit, E.O. and L.H. Schwake. 2000. Random number generation from right-skewed, symmetric, and left skewed distributions. Risk analysis 20:59-71.

Chapter 4

Does Correlation among Vital Rates Matter? The Effect of Correlation Structure, Vital Rate Distribution, and Species On Estimates of Population Viability

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For submission to *Ecological Applications*

INTRODUCTION

Population viability analysis (PVA) is a central tool in conservation biology (Soulé 1987). The use of population models in this context represents an application of ecological theory to real world problems, often in an attempt to develop management practices that minimize the risk of extinction of protected species (Burgman et al. 1993). Transition matrix models are a widely used method for PVA (Menges 1990, 2000). The technique involves pooling information on many aspects of a species' life-cycle, including recruitment, survival, and growth, into a single structured model (Caswell 2001). The method has been promoted as a powerful tool for PVA and for understanding the basic life-history of species targeted for conservation, partly because of its flexibility in accommodating different species and the variety of useful demographic parameters it can estimate (Schemske et al. 1994). However, differences in implementation of PVA models can lead to alternative, even conflicting, conclusions, even when the same source data are used (Lindenmeyer et al. 1995, Mills et al. 1996, Pascual et al. 1997, Brook et al. 1999), and this is true for matrix models as well (Nakoaka 1996, Chapter 3).

Correlation among vital rates may affect the outcome of risk assessments in general (Bukowski et al. 1995) and stochastic matrix models in particular (Tuljapurkar 1982, Caswell 2001). Positive correlations are possible when different stages respond in similar ways to their environment. For example, if rainfall in a given year promotes growth of both small and large individuals to the next higher size class, these growth probabilities will likely be correlated over time. Positive correlations among vital rates have been shown to increase variability in estimates of average growth rate and extinction risk (Doak et al. 1994). There is ample evidence that demographic parameters are correlated across years and environments (Horvitz and Schemske 1995, Horvitz et al. 1997, Caswell 2000, Oostermeijer et al. 1996), and inclusion of this correlation structure in stochastic models may be necessary to avoid overly optimistic estimates of population viability (Nakoaka 1996). However, negative correlations among vital rates are also possible (Oostermeijer et al. 1996), and these tend to counteract the effects of positive correlations (Tuljapurkar 1982, Ferson and Burgman 1995, Orzack 1997). Therefore, the effect of correlation structure on population viability estimates may depend on the nature of the correlations among vital rates, which, in turn, may differ among species and environments.

Transition matrices can generate estimates of deterministic parameters such as population growth rate, sensitivities and elasticities, equilibrium population structure, and reproductive values. Often of greater concern to the conservationist are probabilistic measures of population health, such as extinction risk, time to extinction, and stochastic growth rate. These measures of population viability can be estimated when demographic and/or environmental stochasticity are incorporated into a model (Menges 2000, Caswell 2001). Inclusion of environmental stochasticity into matrix models has generally been accomplished through one of two mechanisms, matrix or element selection. For both methods, repeated estimates of annual recruitment, growth and survival must be available (e.g., Bierzychudeck 1982) or temporal variability must be somehow assumed (e.g., Menges 1992). Matrix selection involves shuffling whole observed matrices at random at each time step of a simulation, while element selection requires drawing each component of the matrix at random from some statistical distribution. However, the two methods do not always give the same results (Greenlee and Kaye 1997, Kaye et al. 2001, see also Chapter 3). In addition, for implementation of the element selection method, too few data are usually available for a formal assessment of goodness of fit, so a statistical distribution is often assumed and the distribution is fit to the data at hand. In some cases, even if a reliable test of fit is possible, the statistically best distribution may be rejected on the basis of biological or theoretical reasons, or because of modeling convenience. Unfortunately, different statistical distributions of such input variables may change assessments of population viability (Nakoaka 1997), and information on temporal variation in demographic parameters is sparse (Menges 1992). The overall implications of which stochastic method is chosen remain unclear.

Few examples of incorporating correlation structure into stochastic matrix models are available, and these tend to emphasize positive correlations and single species. Comparisons of different methods of incorporating stochasticity are also infrequent, especially those that examine the effects of various statistical distributions for element selection (Chapter 3). One reason correlation structure is seldom included is that multivariate random number generators are not widely available (Caswell 2001) and implementation is generally complex. In this paper, we compare the effects of correlation among vital rates on population viability using five methods of stochastic matrix simulation (bootstrap, beta, truncated normal, truncated gamma, and uniform distributions). We evaluate the results with a measure of population viability (stochastic growth rate) derived from observed data for multiple species and several populations. Our primary objectives are to 1) assess the effects of correlations among vital rates on population viability estimates and determine if these effects differ among species and stochastic methods, 2) explore factors that influence the effects of these correlations, and 3) measure the correlation of viability estimates derived through different methods.

METHODS

Study species and data sets

Data from five plant species were included in this analysis: *Astragalus tyghensis* Peck (Fabaceae), *Cimicifuga elata* Nutt. (Ranunculaceae), *Haplopappus radiatus* Nutt. (Cronq.) (Asteraceae), *Lomatium bradshawii* Rose (Math. & Const.) (Apiaceae), and *L. cookii* Kagan (Apiaceae). All of these taxa are herbaceous perennials and rare or endangered in the western United States (Oregon Natural Heritage Program 2001). Data were collected from multiple populations of each species over a period of five to ten years (Table 4.1); the number of observed transition matrices for each population was one less than the number of years of observation, except for *L. bradshawii* because one year of sampling was skipped resulting in only seven matrices from nine years of

Table 4.1. Study species included in this analysis, number of populations and years observed, number of observed matrices and stage categories, habitat, and ecoregion. All species are herbaceous perennial plants.

species	number of populations	years of observation	number of observed matrices	number of stages	habitat	ecoregion[†]
Astragalus tyghensis	5	10 (1991-2000)	9	5 (seedling plus small, medium, large and very large size classes)	arid rangeland	Columbia Basin
Cimicifuga elata	3	5-6 (1992-96)	4-5	5 (seedling, small and large vegetative, reproductive, dormant)	mesic forest	Western Cascade Range
Haplopappus radiatus	10	10 (1991-2000)	9	4 (seedling, small and large vegetative, reproductive)	arid rangeland	Blue Mountains/ Owyhee Upland
Lomatium bradshawii	7	9 (1988-94, 1996-97)	7	5 (seedling, small and large vegetative, small and large reproductive)	wetland prairie	Willamette Valley
L. cookii	2	6 (1994-99)	5	6 (seedling; small and large vegetative; small, medium and large reproductive)	serpentine wetland	Klamath Mountains

[†] Based on map in Oregon Natural Heritage Program (2001).

observation. In total, multi-year data from 27 populations were used. We included species from a variety of habitats and ecoregions in Oregon. In all cases, individual plants were followed through time as mapped and/or tagged individuals, and recruitment of seedlings (first year plants) was monitored annually. Stage-specific fecundity was estimated based on per capita seed production in year *t* and seedling recruitment in year $t+1$ (as in Kaye et al. 2001; "anonymous reproduction" of Caswell [2001:173-174]), or, if only one reproductive stage was recognized, based on seedlings observed in year $t+1$ per reproductive plant in year *t*. No seed bank stage was included in our models because biological evidence from studies of these species suggests that their seeds may not persist in the soil or have delayed germination. For example, no viable seeds more than one year old have been detected in field studies of *Lomatium* species (Thompson 1985), including *L. bradshawii* (Kaye et al. 2001), or *H. radiatus* (Kaye unpublished data). Seeds of *C. elata* stored under dry, room-temperature conditions do not remain viable for greater than one year, and field sown seeds of *A. tyghensis* emerge in the following spring only (Kaye unpublished data). Information on each species, including field sampling techniques, individual matrix construction methods, and the annual matrices, is available in the Appendix.

Stochastic population growth rate

We focused on stochastic population growth rate (λ_s) as a measure of population viability for this analysis. Stochastic growth rate was chosen over the more conventional extinction probability because it is not tied to a particular time horizon.

Most estimates of extinction probability are based on simulations for a particular period of time, such as 100 years, and this time period may be selected to resolve differences between populations or treatments (i.e., if all populations go extinct after 100 year projections, the time window may be shortened until at least some populations have a chance of persisting). However, this variability in time span makes it difficult to compare results across studies (Menges 2000), and we found it difficult to identify a single time horizon appropriate to all 27 data sets included in this study. Any one period of simulation either resulted in several populations with extinction probabilities of 0 or 1. This resulted in an inability to resolve differences in these populations, and created many constant values inappropriate for evaluation with analysis of variance (ANOVA). Unlike the deterministic growth rate (λ), λ_s incorporates environmental variability and does not assume a stable (equilibrium) population structure (Tuljapurkar 1990). Further, as stochasticity increases, λ_s declines, and is always less than the average growth rate (which estimates λ) (Caswell 2001). Populations with λ_s greater than 1.0 are projected to grow, while those with λ_s less than 1.0 are projected to decline, making λ_s a convenient measure of population viability in stochastic environments.

To calculate λ_s, we followed the numerical simulation method outlined in Caswell (2001:396). When the log of population growth is averaged over a very large number of time steps, it converges to a fixed value determined by vital rates and environmental processes (Caswell 2001, Tuljapurkar 1990). For each type of simulation, we ran the models for 10,000 time steps (discarding the first 500 to omit transient effects) to calculate λ_s. All stochastic modeling described in this paper was implemented in MATLAB 5 (The Mathworks 1998).

Modeling environmental stochasticity

Environmental stochasticity was modeled by randomly selecting transition matrix elements from either observed values (a bootstrap approach) or parametric distributions fit to the observed values. We compared these approaches to evaluate the effect of distribution shape on the importance of correlation to estimates of λ_s. The observed values represented the temporal variability known for each population of each species. At each time step of a simulation, a matrix was constructed at random and post-multiplied by the vector of individual abundances to obtain a new vector of individual stage abundances. The initial stage distribution was the average observed distribution over all years of observation for each population. For the bootstrap method, stage specific recruitment (the top row of the transition matrices) was allowed to vary through time by randomly selecting from among the observed recruitment rates. For each of the parametric methods described below, recruitment varied according to a gamma distribution, which has been shown to work well for fecundities (Tallie et al. 1995). When individual transitions (elements) are selected at random, the cumulative survival (the sum of all transitions in a matrix column excluding recruitment) for a given stage can, but should not, exceed 100%. It is important to constrain stage-specific survival so that it is never greater than 100%, or the model will create individuals from nothing (Caswell 2001) and produce an overly optimistic estimate of population viability. We constrained survival with the rescaling method of Chapter 3, which rescales each transition rate (including mortality) so that the sum of all rates of a given stage always sums to 100% while minimizing bias to the element means.

Distributions of vital rates. We compared five methods of randomly varying transition elements. These were the bootstrap and four parametric distributions: beta, truncated gamma, truncated normal, and uniform. To incorporate stochasticity via the bootstrap, the observed values were assumed to be independently and identically distributed (iid) (the observed/discontinuous distribution of Chapter 3). For the parametric approaches, a statistical distribution was first fit to the observed data for each transition element, then random values were drawn from the distribution to create a new matrix at each time step. Each of these distributions has been used in previous stochastic modeling studies (Table 4.2). Because transition probabilities must be bounded by 0 and 1, the fitted distributions must also be constrained or transition probabilities less than zero or greater than 1 might be selected at random, a modeling error that is biologically unsound. Therefore, the beta distribution is a good candidate, since it is bounded by 0 and 1 by definition. The beta is also very flexible, capable of fitting to an extremely wide variety of distribution shapes (Evans et al. 2000). The normal distribution, on the other hand, must be truncated to 0 and 1. The gamma distribution is bounded by 0 on the left tail, but was truncated to 1 on the right in our simulations. For the uniform distribution (also known as the rectangular distribution), we determined only the minimum and maximum values from our data sets.

Table 4.2. Examples of stochastic models, their inclusion of correlation structure, and use of statistical distributions for varying transition elements.

correlation among vital rates	distribution	species or study	citation
none	normal	comparative study	Guerrant 1996
none	truncated lognormal	giant kelp	Burgman and Gerard 1990
none	truncated normal	various, comparative	Menges 1992
none	truncated normal	*Lomatium bradshawii*	Kaye et al. 2001
none	truncated normal and lognormal	*Yoldia notabilis*	Nakoaka 1997
none	gamma	Chinook salmon	Ratner et al. 1997.
none	uniform	*Pediocactus paradinei*	Frye 1998
none	uniform	*Astragalus cremnophylax*	Maschinski et al. 1997.
none	observed/ discontinuous	red-cockaded woodpecker	Maguire et al. 1995
perfect positive correlation	lognormal (truncated for survivals)	spotted owl	Akçakaya and Raphael 1998
perfect positive correlation	truncated normal	*Totoaba macdonaldi*	Cisneros-Mata et al. 1997.
perfect positive correlation	uniform	*Euphorbia clivicola*	Pfab and Witkowski 2000
as observed	beta	Desert tortoise	Doak et al. 1994
as observed	beta	*Hudsonia montana*	Gross et al. 1998
retained within whole matrices	bootstrap (matrix selection)	jack-in-the-pulpit	Bierzychudeck 1982
retained within whole matrices	bootstrap (matrix selection)	*Gentianella campestris*	Lennartsson 2000

The method of matching moments was used to fit the beta and gamma distributions to our data because observed values contained zeros and ones in for some transitions. An alternative would have been to use maximum likelihood estimation techniques, but this would have forced us to drop observed values equal to 0 or 1. However, dropping these values would necessitate dropping entire matrices if we were to compare element selection with bootstrapping of observed whole matrices, and we wanted to emphasize the empirical basis of our data sets while maximizing the available sample sizes. Frey and Burmaster (1999) have shown that, for the beta distribution at least, although the method of matching moments produces less efficient statistical parameter estimates than maximum likelihood methods, matching moment estimates are less sensitive to extreme values. Therefore, we used matching moment estimators because they appear to be adequately robust and because they tolerated the occasional zeros and ones among our observed values.

Correlation among vital rates. For all distributions except the bootstrap, we used the method of Fackler (1999) to generate dependent random variables (e.g., matrix elements such as recruitment, vegetative plant growth, stasis of reproductive individuals, etc.) with the marginal distributions we selected. The pairwise dependence of the variables was specified by an observed correlation matrix for each population. Even though our sample sizes were relatively low (4-9) for estimating correlations, they were typical (if not large) for demographic studies of rare species. The key to this technique is to specify the correlation matrix using a non-parametric correlation measure that is not sensitive to monotonic transformations of the variables (Fackler 1999). This method is equivalent to the normal copula (Fackler, personal communication), and appears to be similar to that proposed by Iman and Conover (1982) and reviewed in Haas (1999). It does not seem to have been implemented previously in the context of stochastic matrix models. Copulas are functions that describe the relationship between variables based on their joint dependencies and marginal distributions (the reader is referred to Genest and MacKay 1986 and Nelson 1999 for introductions to copulas). We used Spearman rank correlation coefficients (R_s) (which, for the joint normal distribution, are associated with the Pearson fractile correlations [C] by $C=2\times\sin[\pi/6\times R_s]$), because they are not sensitive to non-linear transformations of the variables, while Pearson product moment correlations are. This method involves generating a set of correlated normal variates, through use of the Cholesky decomposition of C, which are then transformed to have uniform marginals. The desired inverse probability transform is then applied to each variate individually, thus retaining the fractile correlation structure. One convenient feature of this approach is that individual variates may be transformed to different marginal distributions and still maintain the specified correlation structure, which accommodates our use of the gamma distribution for recruitment and the same or other distributions for transition probabilities. Use of the Cholesky function requires that the correlation matrix be positive semidefinite, which was not always the case in our data sets (possibly because some correlations could be derived from linear combinations of others). Therefore, we applied a ridge correction to the correlation matrices prior to their use by adding a value equal to the minimum eigenvalue of each matrix. In all cases, this value was extremely small ($\leq 10^{-16}$), and resulted in no detectable corruption of the realized marginals or correlations.

Maintaining correlation structure for the bootstrap method was treated as a special case. Instead of selecting correlated variates using Fackler's (1999) method, we selected whole observed matrices from among the observed data sets. This technique of incorporating environmental stochasticity is also known as matrix selection (Chapters 2 and 3), and preserves the observed association of matrix elements (Greenlee and Kaye 1997, Menges 2000, Kaye et al. 2001).

Analysis

Tests for effects of correlation, input distributions, and study species. We tested for effects of correlation among vital rates, input distributions, species, and interactions among these factors using SAS proc mixed (SAS Institute, Inc. 1990). Use of raw estimates of λ_s as a response variable posed a difficulty because we were likely to detect species effects simply because some species may have had stronger or weaker population growth rates. Further, we were interested in the relative effects of these methods more than their actual estimates of mean λ_s. Therefore, we chose as a response variable the proportional change in λ_s when correlation among elements was included. We considered this response variable to be structured in a split plot design, with species as the whole plot.

***Detecting bias in mean* $\mathbf{R}_s$.** Our procedure of constraining survival to $\leq 100\%$ was applied to each column of a matrix independent of the other columns after random values were drawn. This procedure introduced the possibility of altering the correlation among the transition elements in unpredicted ways. To test for bias to the Spearman rank correlation coefficients, we compared the mean R_s of each transition element in the observed data sets with simulated results for each species. First, we used the distributions and correlation method described above to generate 1000 random matrices from each population. Second, we calculated the mean R_s for each of these sets. Third, we calculated the difference between the mean observed R_s and the simulated R_s as an estimate of bias. Mean estimates of bias for each species were then evaluated for significant difference from zero and from one another using ANOVA.

***Explaining variation in effects of correlation*.** The magnitude and direction of correlations are both important aspects of the overall correlation structure among the vital rates in a transition matrix. In theory, as the correlation among elements increases, so to will its effect on population dynamics. This effect, however, will be controlled, at least in part, by the sign of the correlations, with positive and negative correlations cancelling each other out. From the observed correlation matrices for each of our study populations, we calculated 1) the mean absolute value of R_s ($|R_s|$), 2) the difference between the absolute value of the mean positive and negative R_ss ($\bar{x}_{\mathrm{pos}R\mathrm{s}} - |\bar{x}_{\mathrm{neg}R\mathrm{s}}|$), and 3) the ratio of the number of positive to negative correlations. The first is a measure of overall correlation strength, such that as the magnitude of correlations increase, average $|R_s|$ increases as well, regardless of correlation sign. The other two are indices of the balance between positive and negative correlations. For example, if the strength of positive correlations is exactly matched by negative correlations, their difference will be zero. But if negative correlations are stronger than the positives, the difference will be less than zero (and vice versa). Similarly, if negative R_s outnumber positive R_s, their ratio will be less than one (and vice versa). We performed a stepwise multiple regression with mean proportional change in λ_s due to correlation for each species as the dependent variable, and mean $|R_s|$, difference between mean positive and negative R_s, and ratio of positive to negative R_s as the potential explanatory variables.

Correlation between techniques. Even if combining dependencies among transition elements with the various techniques for incorporating stochasticity results in different estimates of λ_s, we would like to know if the various methods yield relatively similar results. That is, if one population has a higher estimated λ_s than another as measured by one stochastic method in combination with correlation among vital rates, is it also higher as measured by a different method? Does this relationship change if correlation structured is omitted? To measure their degree of association, we correlated estimates of λ_s from each method of including temporal variability using the Pearson product moment (R), and this procedure was repeated for estimates with and without correlation among vital rates.

RESULTS

Effects of correlation, input distributions, and study species

The effect of including correlation among vital rates on estimates of λ_s differed between study species ($P=0.0101$) but not among the various statistical distributions and methods used to incorporate stochasticity ($P=0.1209$), and there was no interaction between these terms ($P=0.1147$) in a split-plot ANOVA (Table 4.3). The significant effect of species in this model can be interpreted as an interaction between species and correlation effects on estimated λ_s. Estimates of λ_s were significantly lower when correlation was included than when it was omitted from the stochastic models for two of the five species examined here (Figure 4.1, note asterisks). Including observed correlation among transition elements reduced estimates of λ_s by 1.7% on average for *A. tyghensis* and 3.0% for *L. bradshawii*, but there was no detectable effect in three other species. The magnitude of this effect was greatest in *L. bradshawii* and least in *C. elata* and *H. radiatus*, and intermediate in *A. tyghensis* and *L. cookii*.

Bias in R_s

A small, but significant, positive bias was detected among the correlation coefficients in our simulated matrices relative to the observed R_s. The strength of this bias differed among species, ranging from an average of 0.012 in *H. radiatus* to 0.047 in *C. elata*, and was significantly different from zero ($P\leq 0.0001$) in each case (Figure 4.2).

Table 4.3. Split-plot ANOVA for the effects of statistical distribution of input variables and species on the proportional change in λ_s when correlations among vital rates are included (NDF and DDF are numerator and denominator degrees of freedom).

source	NDF	DDF	Type III *F*	*P*
whole plot				
species	4	22	4.3	0.0101
subplot				
distribution	4	88	1.88	0.1209
interaction				
species × distribution	16	88	1.51	0.1147

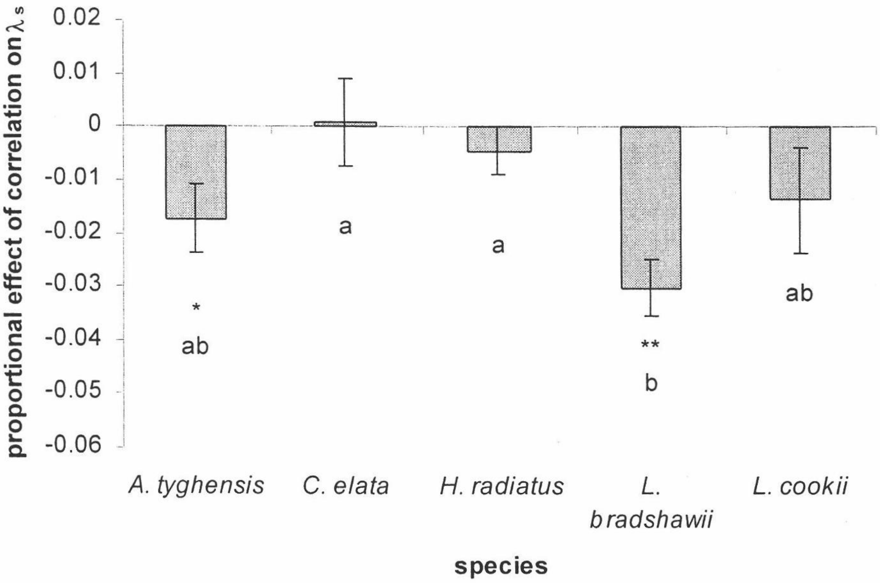

Figure 4.1. Mean (±1 SE) proportional effect of correlation on stochastic growth rate (λ_s) for five plant species. Bars with the same letter do not differ at the 0.05 level of probability (Fisher's protected LSD) and asterisks indicate significant difference from zero ($*0.05 > P \geq 0.01$, $**P \leq 0.0001$).

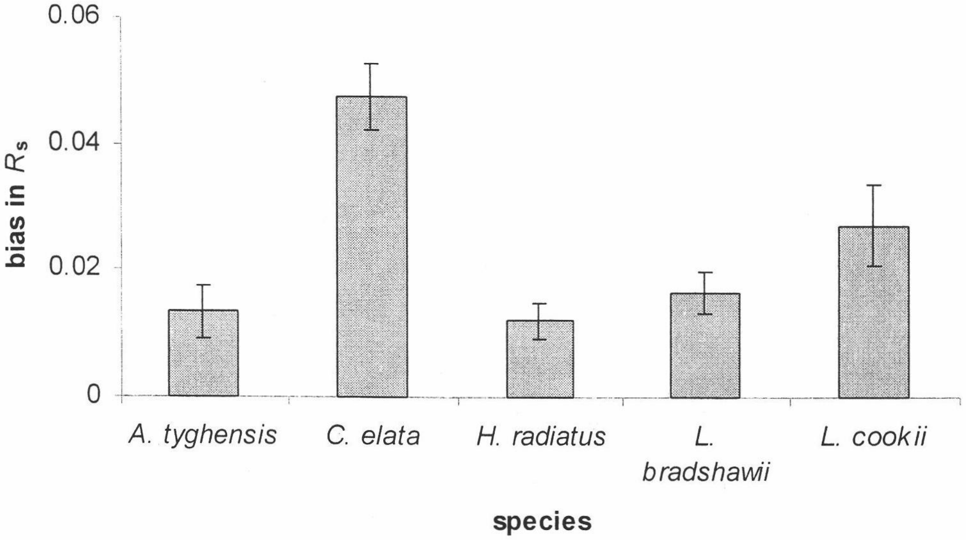

Figure 4.2. Mean (±1 SE) bias in Spearman rank correlation coefficients (R_s) for each of five plant species examined. Bias was defined here as the average difference between mean observed and simulated R_s.

Effects of correlation strength and sign on stochastic growth rate

The average absolute value of R_s ranged from 0.35 in *H. radiatus* to 0.51 in *L. cookii* (Figure 4.3, top), while the average difference between mean positive and negative R_s was closest to zero in *L. bradshawii* (0.001) and most negative in *H. radiatus* (-0.044) (Figure 4.3, center). Negative R_s outnumbered positive R_s by a ratio of 0.930 in *L. bradshawii* to 0.858 in *H. radiatus* (Figure 4.3, bottom). In stepwise multiple regression with proportional effect of correlation on λ_s as the dependent variable, the only factor in the final model was the ratio of the number of positive to negative R_s (Figure 4.4). The final model explained 95.6% of the variability in correlation effect ($P=0.0026$), and took the form:

$$\text{proportional effect of correlation on } \lambda_s = 0.392 \times [\text{no. positive:negative } R_s] - 0.335$$

In separate regressions, the proportional effect of vital rate correlations on λ_s was also associated with the difference between mean positive and negative R_s at ($R=0.84$, $P=0.075$), but the linear association of this factor with the ratio of positive to negative R_s ($R=0.89$, $P=0.044$) prevented it from entering the stepwise regression model. There was no significant association between effect of correlation on λ_s and mean $|R_s|$ either alone ($R=0.22$, $P=0.73$), or as part of a larger regression model.

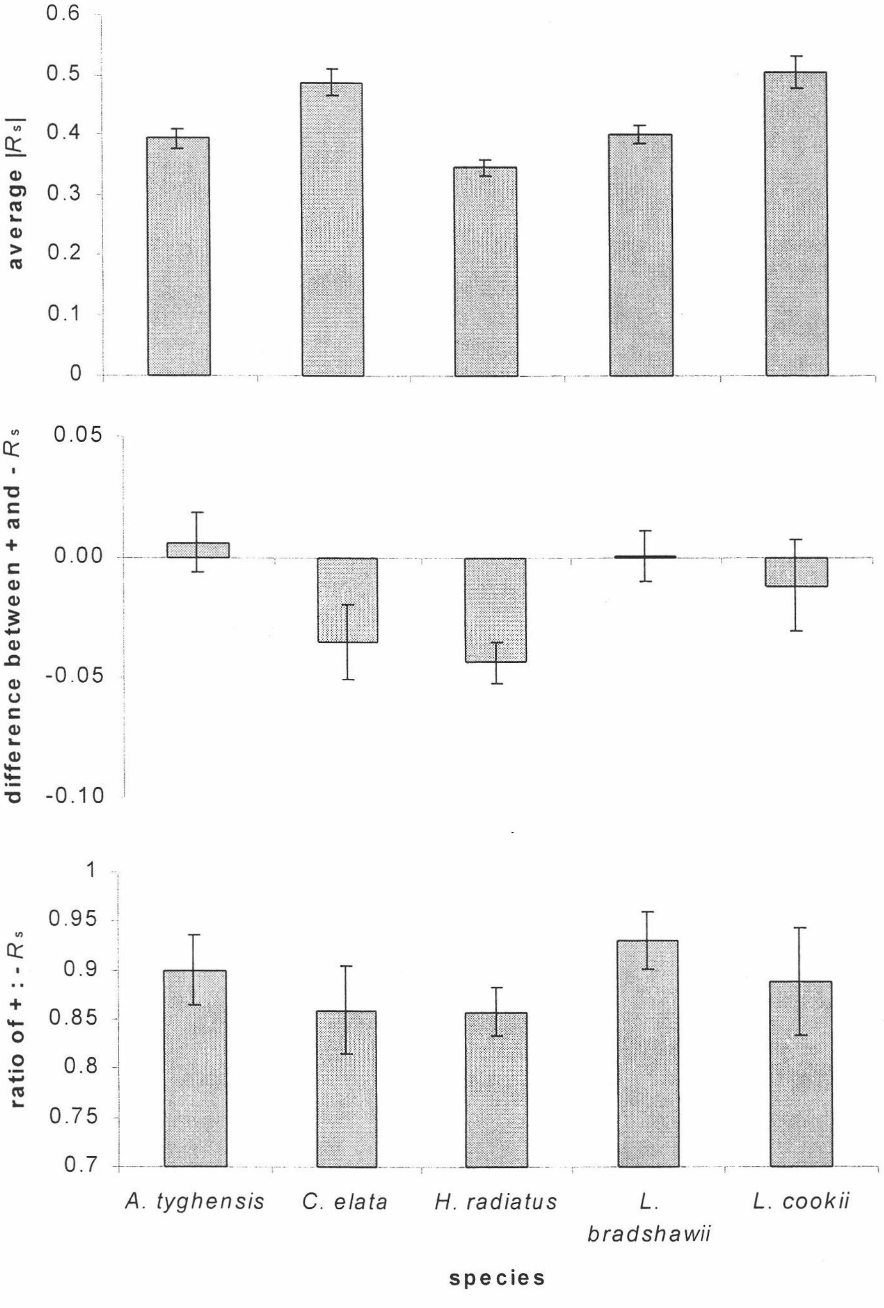

Figure 4.3. Mean (±1 SE) absolute value of observed correlation coefficients (|R_s|, top), difference between mean positive and negative R_s values (middle) and ratio of number of positive to negative R_s (bottom) for each of five species included in this study. For the ratios, when negative correlations outnumber positives, the value is less than 1.

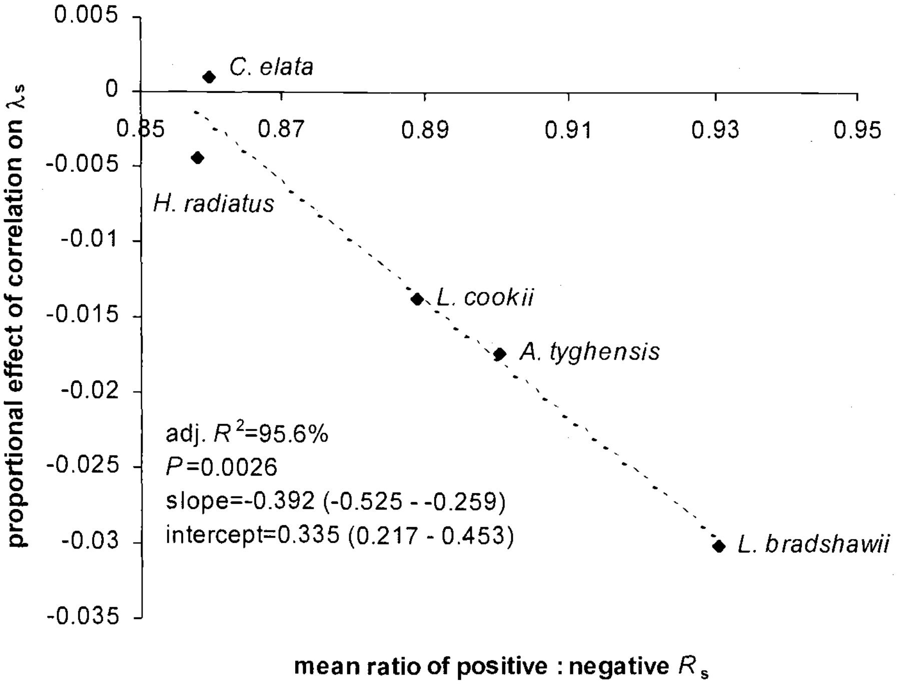

Figure 4.4. Mean ratio of positive to negative R_s values vs. proportional effect of including correlation structure on estimates of stochastic growth rate (λ_s). Ratios less than 1.0 indicate that negative correlations outnumber positive values. The fitted linear regression line (dashed) and model parameters are also shown.

Correlation among techniques

Most estimates of λ_s were highly and significantly correlated. When correlation among vital rates was included in the models, the various statistical distributions yielded estimates of λ_s that were correlated between $R=0.847$ (uniform vs. beta) and $R=0.993$ (bootstrap vs. truncated gamma) (Table 4.4, above diagonal, all $P\leq0.0001$). When correlation among elements was excluded (Table 4.4, below diagonal), association among estimates of λ_s from the various techniques ranged from $R= 0.843$ to $R=0.980$ ($P\leq0.0001$), except for correlations involving the bootstrap method, which were much lower ($R=0.579$ to 0.703, $P\leq0.0016$). Within each statistical distribution, estimates of λ_s derived with and without correlation structure were also highly correlated ($R=0.973$-0.988) (Table 4.4, diagonal).

DISCUSSION

Correlations among vital rates

Including correlation among vital rates in stochastic matrix models significantly reduced estimates of population viability in two plant species, but no effect was detected in three others examined here. Adding correlation to the models resulted in an average 1.7% decline in estimated λ_s in *A. tyghensis* and a 3% reduction in *L. bradshawii* (Figure 4.1). Effects of correlation were not significant in *C. elata, L. cookii*, or *H. radiatus*. Our modeling correlation structure resulted in very little bias to the correlations (Figure 4.2). Although published comparisons of stochastic models

Table 4.4. Pearson correlation coefficients (*R*) for estimates of stochastic population growth rate (λ_s) derived from five methods of incorporating environmental stochasticity. Correlations with λ_s calculated by including correlation structure are above the diagonal ($P \leq 0.0001$), while those estimated without correlation structure are below ($P \leq 0.0016$). Values on the diagonal (in bold) are correlations between λ_s estimates with and without correlation structure ($P \leq 0.0001$ in all cases).

Stochastic method	bootstrap	uniform	truncated normal	truncated gamma	beta
bootstrap	**0.973**	0.884	0.991	0.993	0.975
uniform	0.579	**0.985**	0.920	0.874	0.847
truncated normal	0.626	0.974	**0.986**	0.990	0.964
truncated gamma	0.703	0.884	0.944	**0.988**	0.978
beta	0.638	0.843	0.904	0.980	**0.980**

with and without cross-correlations among transition elements are few, their conclusions are in general agreement with ours. For example, population simulations with *Totoaba macdonaldi* using both a diffusion approximation approach and Monte Carlo methods found that inclusion of correlations among vital rates tended to increase extinction risk (Cisneros-Mata et al. 1997). In that study, the authors assumed perfect positive correlations in their comparisons. For most species in natural stochastic environments, however, correlations among matrix elements may include many negative values and are rarely, if ever, perfect, as in herbaceous plants such as *Calathea ovandensis* of Mexican rainforests (Horvitz and Schemske 1995) and *Gentiana pneumonanthe* of Scandinavian heathlands (Oostermeijer et al. 1996). Doak et al. (1994) found that adding observed correlations (which included both positive and negative values) to their desert tortoise model increased variability in mean growth rate and population size estimates after 25-50 years. Presumably this increase in variability would translate into a reduction in estimates of population viability, although they did not test this explicitly.

Our analysis suggests that the effect of correlations among vital rates on stochastic matrix model outcomes depends on the nature and type of correlations present, and this differs among species. The average ratio of the number of positive to negative correlations among vital rates was an excellent predictor (adj. $R^2=95.6\%$) of the proportional change in stochastic growth rate among species due to inclusion of these correlations (Figure 4.4). This measure of correlation structure is simple to calculate and represents the relative distribution of positive and negative correlations across all vital processes. There was an indication that the relative strength of positive vs. negative correlations ($\bar{x}_{\mathrm{pos}Rs} - |\bar{x}_{\mathrm{neg}Rs}|$) was also important in explaining this variation, but its function was weaker (adj. $R^2=60.1\%$, $P=0.075$) and it was not included in the regression model after a stepwise procedure. We were surprised that the average strength of correlations was not a significant factor in explaining variation among species in mean λ_s, because stronger correlations should, in theory, result in a greater effect (Tuljapurkar 1982). It may be that inclusion of a greater number of species could elucidate these relationships by encompassing life histories with a greater range in absolute and relative correlation strengths. Even so, it is clear that the relative mix of positive and negative correlations among model parameters is an important aspect of correlation structure. Ferson and Burgman (1995), using various hypothetical correlation structures in a stochastic model for Leadbeater's possum, found that estimates of extinction probability increased or decreased depending on whether correlations were positive, negative, or mixed, and whether dependencies were linear or non-linear. The simplistic assumption of complete positive correlation used in some models (e.g., Table 4.2) may yield overly pessimistic estimates of population viability. We suggest that if inclusion of correlation structure is desired, empirically derived correlations should be incorporated over hypothetical structures.

Correlation structure is clearly a complex factor in population models (Tuljapurkar 1982), and its effect on model results will differ among species and life histories (Orzack 1993, 1997). Although omitting correlation structure, as many authors of population viability models have done (e.g., Table 4.2), may appear to be a hazardous assumption, it may have little effect on results of PVAs in some species due to the balancing effect of positive and negative correlations. Even in our most extreme case, *L. bradshawii*, in which the average 3% decline was statistically significant, its biological significance was less obvious, and conservationists will have to decide for themselves what magnitude of effect on viability is important. Within a given technique for incorporating environmental stochasticity, estimates of λ_s derived with and without cross-correlation among elements were strongly correlated ($R \geq 0.973$), suggesting that for purposes of assessing the relative differences among populations or management actions, inclusion of correlation structure may be of little significance.

Input distributions

The effects of correlation structure did not depend on which method we used to incorporate stochasticity into the transition matrix models (Table 4.3). Including correlation structure had the same effect on estimates of λ_s for each species regardless of whether stochasticity was driven by a bootstrap method, or parametric distributions such as the beta, truncated gamma, truncated normal, or uniform. Some authors (e.g., Menges 2000) have noted that the bootstrap method of shuffling whole observed matrices (matrix selection) could exaggerate correlations among vital rates, but we found no evidence that stochastic method altered the effects of correlation.

Even though stochastic method did not alter the effects of correlation structure, different input distributions can have significant effects on estimates of population viability. For example, we found (in Chapter 3) significant differences in estimates of

λ_s among bootstrap, beta, truncated gamma, truncated normal, uniform and triangular distributions of transition rates for incorporating stochasticity. In the present study, we found a close association (R=0.847-0.993) in estimates of λ_s among various input distributions when correlation among vital rates was included. However, in the absence of correlation structure, associations between the bootstrap method and each parametric method were weaker (R=0.579-0.703). These correlations are lower than those observed in Chapter 3 (R=0.849-0.990) with the same data sets and similar modeling procedures. The primary difference between methods in these two studies was that, in the current case, we allowed recruitment to vary (via the bootstrap or gamma distribution) while it was held constant in the previous study. Apparently, stochasticity in recruitment can have a substantial effect on estimates of λ_s, possibly interacting with the choice of distribution shape used to model transition probabilities. Nakoaka (1997), for example, found that lognormal and truncated normal distributions for varying recruitment in clam population models yielded estimates of λ_s that differed significantly. Our results suggest that if correlation is included among all vital rates, and transitions and recruitment vary stochastically, then estimates of population viability may differ among stochastic methods but their relative rankings will not.

This is relevant because conservationists have expressed concern that viability analyses yield results so sensitive to model parameters that any conclusions are uncertain, if not misleading. We agree with Beissinger and Westphal (1998) and Menges (2000) that the strength of viability analysis lies in its use as comparative tool rather than a means of precisely assessing the health of individual populations.

Especially in the face of uncertainty due to measurement error, which can create very wide confidence intervals on estimates of extinction probability (Ludwig 1999, Fieberg and Ellner 2000), the use of viability analysis to assess the relative vigor of a group of populations or the impact of a habitat alteration should be emphasized over quantitative estimates of viability. Fortunately, the relative ranking of populations appears to be fairly robust to differences in stochastic methods, especially when correlation structure is included.

Conclusion

Temporal correlation among vital rates in our stochastic matrix models altered estimates of population viability, but this effect differed among species and was generally weak. The magnitude of change in estimated λ_s for each species examined here was largely explained by the ratio of positive to negative cross-correlations of transition matrix elements; as the relative number of negative correlations decreased, the impact of correlation structure increased. When deciding whether or not to include such correlation structure in viability models, conservationists may want to examine the correlations in their species as a means of assessing their anticipated effect, and we have provided a tentative linear regression model for doing so. Examples of stochastic matrix approaches that incorporate correlations are few, but we hope our illustration of a straightforward method based on rank correlations will encourage others to include this aspect of stochastic population dynamics in future models where correlation is deemed important. Our implementation, which was based on an approach described by

Fackler (1999), is only one of a variety of methods that may be useful for this purpose, and the extent to which correlation technique affects model results deserves further attention. The use of copulas in functions for generating multivariate random numbers may be particularly fruitful (Haas 1999, Frees and Valdez 1998), especially because of their ability to accommodate non-linear dependencies (Embrechts et al. 1999 and in press) and a mixture of statistical distributions for different vital rates.

We found no interaction between inclusion of correlation structure and various distribution shapes for incorporating stochasticity. Stochastic method may, however, have significant effects on estimates of λ_s, which can lead to differing conclusions regarding the health of a given population. When correlation structure is maintained in stochastic models, the estimates of λ_s are generally highly correlated, suggesting that PVA should stress comparisons between populations over quantitative estimates of population health. Incorporating stochasticity into matrix models through bootstrapping whole observed matrices (matrix selection) may be preferable in many cases because the method appears to be relatively conservative and does not bias transition elements (Chapter 3). In addition, it does not bias correlation structure and its results do not appear to differ substantially from other methods of including correlation.

LITERATURE CITED

Akçakaya, H.R. and M.G. Raphael. 1998. Assessing human impact despite uncertainty: viability of the northern spotted owl metapopulation in the northwestern USA. Biodiversity and Conservation 7:875-894.

Beissinger, S.R. and M.I. Westphal. 1998. On the use of demographic models of population viability in endangered species management. Journal of Wildlife Management 62:821-841.

Bierzychudek, P. 1982. The demography of jack-in-the-pulpit, a forest perennial that changes sex. Ecological Monographs 52:335-351.

Brook, B.W., J.R. Cannon, R.C. Lacey, C. Mirande, and R. Frankham. 1999. A comparison of the population viability analysis packages GAPSS, INMAT, RAMAS, and VORTEX for the Whooping Crane (*Grus americana*). Animal Conservation 2:23-31.

Bukowski, J., L. Korn, and D. Wartenberg. 1995. Correlated inputs in quantitative risk assessment: the effects of distributional shape. Risk Analysis 15:215-219.

Burgman, M.A., S. Ferson, and H.R. Ackakaya. 1993. Risk assessment in conservation biology. Chapman and Hall, London.

Burgman, M.A. and V.A. Gerard. 1990. A stage-structured, stochastic population model for the giant kelp *Macrocystis pyrifera*. Marine Biology 105:15-23.

Caswell, H. 2000. Prospective and retrospective perturbation analyses: their roles in conservation biology. Ecology 81:619-627.

Caswell, H. 2001. Matrix population models. Second edition. Sinauer Associates Inc., Sunderland, Massachusetts.

Cisneros-Mata, M.A., L.W. Botsford, and J.F. Quinn. 1997. Projecting viability of *Totoaba macdonaldi*, a population with unknown age-dependent variability. Ecological Applications 7:968-980.

Doak, D., P. Kareiva, and B. Klepetka. 1994. Modeling population viability for the desert tortoise in the western Mojave Desert. Ecological Applications 4:446-460.

Embrechts, P., A. McNeil, and D. Straumann. 1999. Correlation: pitfalls and alternatives. Risk 12:69-71.

Embrechts, P., A. McNeil, and D. Straumann. In press. Correlation and dependence in risk management: properties and pitfalls. In M. Dempster, editor. Risk Management: Value at Risk and Beyond. Cambridge University Press, Cambridge (2001).

Evans, M., N. Hastings and B. Peacock. 2000. Statistical Distributions. Third edition. John Wiley and Sons, New York.

Fackler, P. 1999. Generating correlated multidimensional variates. [online] URL: http://www4.ncsu.edu/unity/users/p/pfackler/www/#WorkingPapers.

Ferson, S. and M.A. Burgman. 1995. Correlations, dependency bounds and extinction risks. Biological Conservation 73:101-105.

Fieberg, J. and S.P. Ellner. 2000. When is it meaningful to estimate an extinction probability? Ecology 81:2040-2047.

Frees, E.W. and E.A. Valdez. 1998. Understanding relationships using copulas. North American Actuarial Journal 2:1-25.

Frey, H.C. and D.E. Burmaster. 1999. Methods of characterizing variability and uncertainty: comparison of bootstrap simulations and likelihood-based approaches. Risk Analysis 19:109-130.

Frye, R.J. 1998. Population viability analysis of *Pediocactus paradinei*. Pages 39-46 in J. Maschinski, H.D. Hammond and L. Holte, editors. Southwestern Rare and Endangered Plants: Proceedings of the Second Conference. General Technical Report RM-GTR-283. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

Genest, C. and R. MacKay. 1986. The joy of copulas. American Statistician 50:280-283.

Greenlee, J. and T.N. Kaye. 1997. Stochastic matrix projections: a comparison of the effect of element and matrix selection methods on quasi-extinction risk for *Haplopappus radiatus* (Asteraceae). Pages 66-71 in T.N. Kaye, A. Liston, R.M. Love, D. Luoma, R.J. Meinke, and M.V. Wilson, editors. Conservation and Management of Native Plants and Fungi. Native Plant Society of Oregon, Corvallis, Oregon.

Gross, K., J.R. Lockwood III, C.C. Frost, and W.F. Morris. 1998. Modeling controlled burning and trampling reduction for conservation of *Hudsonia montana*. Conservation Biology 12:1291-1301.

Guerrant, E.O. 1996. Designing populations: demographic, genetic, and horticultural dimensions. Pages 171-207 in D.A. Falk, C.I. Millar, and M. Olwell, editors. Restoring Diversity. Island Press, Washington D.C.

Haas, C.N. 1999. On modeling correlated random variables in risk assessment. Risk Analysis 19:1205-1214.

Horvitz, C.C. and D.W. Schemske. 1995. Spatiotemporal variation in demographic transitions of a tropical understory herb: projection matrix analysis. Ecological Monographs 65:155-192.

Horvitz, C.C., D.W. Schemske and H. Caswell. 1997. The relative "importance" of life-history stages to population growth: prospective and retrospective studies. Pages 248–271 in S. Tuljapurkar and H. Caswell, editors. Structured-population models in marine, terrestrial and freshwater systems. Chapman and Hall, New York, New York.

Iman, R.L. and W.J. Conover. 1982. A distribution-free approach to inducing rank correlation among input variables. Communications in Statistics — Simulation and Computation 11:311-334.

Kaye, T.N., K.L. Pendergrass, K. Finley, and J.B. Kauffman. 2001. The effect of fire on the population viability of an endangered prairie plant. Ecological Applications, in press.

Lennartsson, T. 2000. Management and population viability of the pasture plant *Gentiana campestris*: the role of interactions between habitat factors. Ecological Bulletin 48:111-121.

Lindenmeyer, D.B., M.A. Burgman, H.R. Akçakaya, R.C. Lacy, and H.P. Possingham. 1995. A review of the generic computer programs ALEX, RAMAS/space and VORTEX for modelling the viability of wildlife populations. Ecological Modelling 82:161-174.

Ludwig, D. 1999. Is it meaningful to estimate a probability of extinction? Ecology 80:298-310.

Maguire, L.A., G.F. Wilhere, and Q. Dong. 1995. Population viability analysis for red-cockaded woodpeckers in the Georgia Piedmont. Journal of Wildlife Management 59:533-542.

Maschinski, J., R. Frye, and S. Rutman. 1997. Demography and population viability of an endangered plant species before and after protection from trampling. Conservation Biology 11:990-999.

Mathworks, The. 1998. Matlab, version 5. The Mathworks, Inc., Natick, Massachusetts.

Menges, E.S. 1990. Population viability analysis for an endangered plant. Conservation Biology 4:52-62.

Menges, E.S. 1992. Stochastic modeling of extinction in plant populations. Pages 253-275 in P.L. Fiedler and S.K. Jain, editors. Conservation biology: the theory and practice of nature conservation, preservation, and management. Chapman and Hall, New York.

Menges, E.S. 2000. Population viability analyses in plants: challenges and opportunities. Trends in Ecology and Evolution 15:51-56.

Mills, L.S., S.G. Hayes, C. Baldwin, M.J. Wisdom, J. Citta, D.J. Mattson, and K. Murphy. 1996. Factors leading to different viability predictions for a grizzly bear data set. Conservation Biology 10:863-873.

Nakoaka, M. 1996. Dynamics of age- and size-structured populations in fluctuating environments: applications of stochastic matrix models to natural populations. Researches in Population Ecology 38:141-152.

Nakoaka, M. 1997. Demography of the marine bivalve *Yoldia notabilis* in fluctuating environments: an analysis using a stochastic matrix model. Oikos 79:59-68.

Nelson, R.B. 1999. An Introduction to Copulas. Springer, New York.

Oostermeijer, G., M.L. Brugman, E.R. de Boer, and H.C.M. den Nijs. 1996. Temporal and spatial variation in the demography of *Gentiana pneumonanthe*, a rare perennial herb. Journal of Ecology 84:153-166.

Oregon Natural Heritage Program, 2001. Rare, threatened and endangered plants and animals of Oregon. Oregon Natural Heritage Program, Portland, Oregon.

Orzack, S.H. 1993. Life history evolution and population dynamics in variable environments: Some insights from stochastic demography. Pages 63-104 in J. Yoshimura and C.W. Clark, editors. Adaptation in Stochastic Environments. Springer-Verlag, New York.

Orzack, S.H. 1997. Life history evolution and extinction. Pages 273-302 in S. Tuljapurkar and H. Caswell, editors. Structured Population Models in Marine, Terrestrial, and Freshwater Systems. Chapman and Hall, New York.

Pascual, M.A., P. Kareiva, and R. Hilborn. 1997. The influence of model structure on conclusions about the viability of harvesting of Serengeti wildebeest. Conservation Biology 11:966-976.

Pfab, M.F. and E.T.F. Witkowski. 2000. A simple population viability analysis of the critically endangered *Euphorbia clivicola* R.A. Dyer under four management scenarios. Biological Conservation 96:263-270.

Ratner, S., R. Lande and B.B. Roper. 1997. Population viability analysis of spring Chinook salmon in the South Umpqua River, Oregon. Conservation Biology 11:879-889.

SAS Institute, Inc. 1990. SAS/STAT User's Guide, version 6. Fourth edition, volume 2. SAS Institute, Inc., Cary, North Carolina.

Schemske, D.W., B.C. Husband, M.H. Ruckleshaus, C. Goodwillie, I.M. Parker, and J.H. Bishop. 1994. Evaluating approaches to the conservation of rare and endangered plants. Ecology 75:584-606.

Soulé, M.E. 1987. Viable populations for conservation. Cambridge University Press, Cambridge, England.

Tallie, C., G.P. Patil, and R.C. Hennemuth. 1995. Modelling and analysis of recruitment distributions. Environmental and Ecological Statistics 2:315-329.

Thompson, J.N. 1985. Postdispersal seed predation in *Lomatium* spp. (Umbelliferae): variation among individuals and species. Ecology 66:1608-1616.

Tuljapurkar, S.D. 1982. Population dynamics in variable environments. II. Correlated environments, sensitivity analysis and dynamics. Theoretical Population Biology 21:114-140.

Tuljapurkar, S.D. 1990. Population dynamics in variable environments. Springer-Verlag, New York.

Chapter 5. Conclusion

A BRIEF REVIEW OF MATRIX MODEL APPLICATIONS

Transition matrix models have proven to be an enormously versatile application of population biology theory to the study of ecological dynamics. They have been used primarily to describe and forecast the population processes of individual species, including animals and plants. Some notable applications illustrating the diversity of species and life histories the models have been applied to are plants, such as *Pedicularis furbishae* (Menges 1990), giant kelp (Burgman and Gerard 1990), clams (Nakoaka 1997), red cockaded woodpeckers (Maguire et al. 1995), salmon (Ratner et al. 1997), and possums (Ferson and Burgman 1995), including both stage- and age-classified population structures, and even density dependence (Jensen 1995, Ginzburg et al. 1990).

But ecologists have recently taken these structured models beyond description of species dynamics to a wide range of applications, such as theoretical (Chau 2000) and applied harvest scenarios for wildlife (Kokko and Lindstrom 1998), medicinal plants (Nantel et al. 1996), and economically useful palms (Olmsted and Alvarez-Buylla 1995); effects of disturbance on plant species (Giho and Seno 1997, Seno and Nakamijo 1999, Chapter 2); invasion dynamics of exotic species (Parker 2000) and impacts of biocontrol agents (Shea and Kelly 1998, McEvoy and Coombs 1999); metapopulation dynamics (e.g., Akçakaya and Raphael 1998); and description of host-pathogen (Yang et al. 1997) and predator-prey systems (Kittlein 1997). The scale of applications has ranged from the dynamics of individual plant parts, such as demography of buds on birch trees (Maillette 1982), to dynamics of moss communities on decaying wood (Kimmerer 1993), forest tree succession (Osho 1996, Lin and Buongiorno 1997, Kolbe et al. 1999, Logofet 2000), and vegetation dynamics in general (Balzter 2000). Recent novel uses of matrix models in conservation biology have included developing recovery (Aplet et al. 1994) and reintroduction (Guerrant and Pavlik 1998) strategies for rare plants and animals (Heppell et al. 1996) and inclusion of genetic factors such as inbreeding depression (Oostermeijer 2000, Menges and Dolan 1998). Elasticity analysis, a type of sensitivity analysis possible with matrix models, has been of great value in population management and studies of life history evolution (e.g., Heppell et al. 2000).

GOALS AND CONCLUSIONS OF THIS DISSERTATION

The addition of stochasticity to matrix models makes possible the assessment of probabilistic events, such as extinction, and this has made transition matrices one of the most important tools available for population viability analysis. Even so, many unanswered questions about the application of matrix models to field-collected demographicdata have remained. For example, do different methods of including stochasticity in matrix models affect estimates of extinction probability and stochastic population growth rate? Do different methods of constraining stage-specific survival to

≤100%, a seemingly trivial but surprisingly important problem, affect these results? Does the inclusion of correlation among vital rates, such as recruitment, stasis, and growth, affect estimates of population viability? If so, what aspects of correlation structure are important? And finally, if these methods yield divergent estimates of population viability, do they at least result in similar rankings of populations or treatments?

In this dissertation, I have attempted to demonstrate the usefulness of the matrix model technique and answer these questions through a case study and comparative analyses of stochastic methods. These analyses have emphasized the use of empirical observations at every step, so that the results will have the greatest utility to those interested in applied population and ecological models. I have also intentionally avoided extensive use of mathematical notation in hopes that the material presented will be as accessible as possible to ecologists with little formal mathematical training, but who desire to organize their field observations into a synthetic ecological model.

Use of a stochastic modeling approach showed that the effect of fire on the population viability of *Lomatium bradshawii* was clearly positive, and this effect was consistent across two study sites, two response variables, and through two different stochastic methods (Chapter 2). Increasing fire frequency reduced extinction risk and increased stochastic population growth rate, both measures of population viability, at both Rose Prairie and Fisher Butte. Precise estimates of these response variables differed slightly in some cases, but their relative ranking among fire treatments remained the same.

These conclusions set the stage for in-depth evaluations of the effects of stochastic techniques on estimates of population viability. Using field observations from 27 populations of five species, *Astragalus tyghensis*, *Cimicifuga elata*, *Haplopappus radiatus*, *L. bradshawii*, and *L. cookii*, collected over a period of five to ten years, I performed a series of comparisons of methods used to incorporate stochasticity into stage-based models for population viability analysis. Different methods of incorporating stochasticity (i.e., matrix selection vs. various statistical distributions for varying transition elements) and constraining stage-specific survival to ≤100% (resample vs. rescaling procedures) yielded substantially divergent estimates of stochastic growth rate, and there was a significant interaction between these methods (Chapter 3). Most of the variation in growth rate estimates was explained by bias in mean transition element values (weighted by their elasticities), such that methods that caused a reduction in average transition rates also reduced estimates of stochastic growth rate. There was no effect of study species on these results, suggesting that the conclusions are widely applicable, at least among perennial plants and possibly across a variety of organisms.

Incorporating correlation among transition elements caused a significant reduction in estimated stochastic growth rate in only two of five species examined (Chapter 4), and the maximum mean reduction (*L. bradshawii*) was only 3%. There was no interaction with stochastic method in this effect. Much of the variation in average response to correlation structure among species was due the relative balance between positive and negative associations among the vital rates. For example, as the number and strength of negative correlations increased, they tended to overwhelm the effects of positive correlations. Positive correlations are known to increase stochasticity and therefore reduce stochastic growth (Tuljapurkar 1982, Orzack 1997), so the presence of so many negative correlations buffer populations from the stochastic effects of positive correlations. Therefore, it may be possible for population modelers to assess the importance of correlation structure in their target species prior to making the substantial effort to include it by evaluating the relative strength and number of positive and negative associations among their observed matrix elements.

In Chapter 2, no correlation structured was modeled in the element selection technique, despite the fact that I later learned correlation may be important in that species. Even so, the relative results of the matrix and element selection methods for estimating extinction probability and stochastic growth rate were qualitatively similar, an important point stressed in each of the chapters of this dissertation.

One question that may be worth pursuing with regard to correlation structure is, do species with different relative amounts of positive and negative correlations differ in their success or vulnerability to stochastic environments? For example, do invasive species have correlation structures with a higher rate of negative associations among vital rates that could buffer them against stochasticity or even give them an advantage over non-invasive species? Similarly, do rare species have more positive correlations among vital rates than their common congeners, and could this help explain their rarity? Could environmental stochasticity interact with the correlation structure of a species to determine its relative success over different portions of its range? To what extent do the correlation structures of species influence the composition of plant communities in habitats of differing degrees of environmental stochasticity? These and questions related to the evolution of correlation among vital processes may deserve further attention.

Perhaps the most important and consistent result of this dissertation is that, although alternative techniques may lead to very strong differences in estimates of population viability (differing by up to 18%), conclusions about the relative ranking of populations or treatments are robust to differences in stochastic methods (Chapters 2, 3 and 4). I observed very high correlations between most stochastic methods and their estimates of stochastic population growth rate. This adds considerable strength to the argument that viability analysis should be used as a comparative tool (as in Chapter 2) rather than a means of assessing the health of individual populations (Beisinger and Westphal 1998, Menges 2000). Quantitative estimates of extinction probability, for example, may be subject to wide margins of error (Ludwig 1999, Fieberg and Ellner 2000), but the qualitative ordering of populations in terms of viability estimates may not.

CONSIDERATIONS FOR STOCHASTIC MATRIX MODELERS

In the future, practitioners of population viability analysis that use transition matrix models should consider the issues raised by this dissertation. In general, if sufficient data are available to implement a stochastic analysis with matrix selection, this technique may be preferred. It has the advantage of requiring no survival constraint correction, no assumptions about the distribution of the matrix elements (aside from the weighting of each matrix, which is generally assumed to be equal), and it includes correlation structure implicitly, as long as each matrix represents observed data from a single population in a single year.

If element selection is necessary, and it may be if there are areas of missing data or observations of various vital processes are pooled from a variety of sources or studies, then more assumptions will be required. For example, survivals will have to be constrained to ≤100% (unless the model is age-based), and I recommend the rescaling procedure described in Chapter 3. Other techniques may either cause substantial bias (such as resampling, Chapter 3) or be excessively cumbersome (as in Gross et al. 1998). Because available data are typically insufficient to test for a fit to a statistical distribution, one must be assumed. If a survival constraint method with low bias is used, the beta and truncated gamma distributions may be good choices of parametric distributions, as might the bootstrap (or observed/discontinuous), because results using these distributions are generally in close agreement with each other and with matrix selection. Finally, including correlations among vital rates may be desirable, but this will depend on the study system. Fortunately, new tools are now available for modeling correlation structure, and modelers can evaluate the likely importance of correlations for their data set simply by counting the number of positive and negative correlations and applying the linear regression model presented in Chapter 4. Careful consideration of these issues and selection of appropriate modeling techniques will improve the quality of population models and their results. Despite these warnings and words of advice, even if the quantitative predictions of stochastic matrix models differ substantially due to differing model assumptions, the qualitative results are very robust to differences in model implementation. Population models are most useful as comparative tools rather than predictors of future conditions.

Bibliography

Akçakaya, H.R. and M.G. Raphael. 1998. Assessing human impact despite uncertainty: viability of the northern spotted owl metapopulation in the northwestern USA. Biodiversity and Conservation 7:875-894.

Alverson, E.R. 1989. Use of a county soil survey to locate remnants of native grassland in the Willamette Valley, Oregon. Pages 107-112 in R.S. Mitchell, C.J. Sheviak, and D.J. Leopold, editors. Ecosystem management: Rare Species and Significant Habitats. Proceedings of the 15th Annual Natural Areas Conference, New York State Museum Bulletin.

Alverson, E.R. 1990. A survey for native grassland remnants in the mid-Willamette Valley, Oregon. Oregon Department of Agriculture, Salem, Oregon.

Aplet, G.H., R.D. Laven, and R.B. Shaw. 1994. Application of transition matrix models to the recovery of the rare Hawaiian shrub, *Tetramalopium arenarium* (Asteraceae). Natural Areas Journal 14:99-106.

Barker, N.G. and G.B. Williamson. 1988. Effect of winter fire on *Sarracenia alata* and *S. pisttacina*. American Journal of Botany 75:138-143.

Beissinger, S.R. and M.I. Westphal. 1998. On the use of demographic models of population viability in endangered species management. Journal of Wildlife Management 62:821-841.

Benton, T.G. and A. Grant. 2000. Elasticity analysis as an important tool in evolutionary and population ecology. Trends in Ecology and Evolution 14:467-471.

Bierzychudek, P. 1982. The demography of jack-in-the-pulpit, a forest perennial that changes sex. Ecological Monographs 52:335-351.

Bierzychudek, P. 1999. Looking backwards: assessing the projections of a transition matrix model. Ecological Applications 9:1278-1287.

Bond, W.J., and B.W. van Wilgen. 1996. Fire and plants. Chapman and Hall, London.

Borchert, M. 1989. Post fire demography of *Thermopsis macrophylla* H.A. var. *angina* J.T. Howell (Fabaceae), a rare perennial herb in chaparral. American Midland Naturalist 122:120-132.

Boyd, R. 1986. Strategies of Indian burning in the Willamette Valley. Canadian Journal of Anthropology 5:65-86.

Boyd, R. 1999. Strategies of Indian burning in the Willamette Valley. Pages 94-138 in R. Boyd, editor. Indians, fire and the land. Oregon State University Press, Corvallis, Oregon.

Boyd, R.S. and L.L. Serafini. 1992. Reproductive attrition of the rare chaparral shrub *Fremontodendron decumbens* Lloyd (Sterculiaceae). American Journal of Botany 79:1264-1272.

Brook, B.W., M.A. Burgman, and R. Frankham. 2000. Differences and congruencies between PVA packages: the importance of sex ratio for predictions of extinction risk. Conservation Ecology 4:4. [online] URL: http://www.consecol.org/vol4/iss1/art6.

Brook, B.W., J.R. Cannon, R.C. Lacey, C. Mirande, and R. Frankham. 1999. A comparison of the population viability analysis packages GAPSS, INMAT, RAMAS, and VORTEX for the Whooping Crane (*Grus americana*). Animal Conservation 2:23-31.

Brook, B.W., J.J. O'Grady, A.P. Chapman, M.A. Burgman, H.R. Akçakaya, and R. Frankham. 2000. Predictive accuracy of population viability analysis in conservation biology. Nature 404:385-387.

Bukowski, J., L. Korn, and D. Wartenberg. 1995. Correlated inputs in quantitative risk assessment: the effects of distributional shape. Risk Analysis 15:215-219.

Burgman, M.A., S. Ferson, and H.R. Akçakaya. 1993. Risk assessment in conservation biology. Chapman and Hall, London.

Burgman, M.A. and V.A. Gerard. 1990. A stage-structured, stochastic population model for the giant kelp Macrocystis pyrifera. Marine Biology 105:15-23.

Burns, B.R. and J. Ogden. 1985. The demography of the temperate mangrove *Avicennia marina* [(Forsk.) Vierh.] at its southern limit in New Zealand. Australian Journal of Ecology 10:125-133.

Campbell, J.J., D.D. Taylor, M.E. Medley, and A.C. Risk. 1991. Floristic and historical evidence of fire-maintained, grassy pine-oak barrens before settlement in southeastern Kentucky. Pages 359-375 in S.C. Nodvin and T.A. Waldrop, editors. Fire and the environment: ecological and cultural perspectives. Southeastern Forest Experiment Station, Asheville, N.C.

Carlson, P.R., G.W. Tanner, J.M. Wood, and S.R. Humphrey. 1993. Fire in key deer habitat improves browse, prevents succession and preserves endemic herbs. Journal of Wildlife Management 57:914-928.

Caswell, H. 1986. Life cycle models for plants. Lectures on Mathematics in the Life Sciences. 18:171-233.

Caswell, H. 2000. Prospective and retrospective perturbation analyses: their roles in conservation biology. Ecology 81:619-627.

Caswell, H. 2001. Matrix population models. Second edition. Sinauer Associates Inc., Sunderland, Massachusetts.

Caswell, H. and T.N. Kaye. In press. Stochastic demography and conservation of Lomatium bradshawii In a dynamic fire regime. Advances In Ecological Research.

Chau, N.P. 2000. Destabilising effect of periodic harvest on population dynamics. Ecological Modelling 127:1 - 9.

Cisneros-Mata, M.A., L.W. Botsford, and J.F. Quinn. 1997. Projecting viability of *Totoaba macdonaldi*, a population with unknown age-dependent variability. Ecological Applications 7:968-980.

Currier, P.J. 1984. Response of prairie fringed orchid to fire and reduction in grazing. Restoration and Management Notes 2:28.

de Kroon, H., A. Plaiser, and J. van Groenendael. 1987. Density dependent simulation of the population dynamics of a perennial grassland species, *Hypochaeris radicata*. Oikos 50:3-12.

de Kroon, H., A. Plaiser, J. van Groenendael, and H. Caswell. 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. Ecology 67:1427-1431.

Doak, D., P. Kareiva, and B. Klepetka. 1994. Modeling population viability for the desert tortoise in the western Mojave Desert. Ecological Applications 4:446-460.

Douglas, D. 1914. Journal kept by David Douglas during his travels in North America 1823-1827. William Wesley and Son, London. Published under the direction of the Royal Horticultural Society.

Dunwiddie, P.W. 1990. Rare plants in coastal heathlands: observations on Corema conradii and Helianthemum dumosum. Rhodora 92:22-26.

Embrechts, P., A. McNeil, and D. Straumann. 1999. Correlation: pitfalls and alternatives. Risk 12:69-71.

Embrechts, P., A. McNeil, and D. Straumann. In press. Correlation and dependence in risk management: properties and pitfalls. In M. Dempster, editor. Risk Management: Value at Risk and Beyond. Cambridge University Press, Cambridge (2001).

Enright, N., M. Franco, and J. Silvertown. 1995. Comparing plant life histories using elasticity analysis: the importance of life span and the number of life-cycle stages. Oecologia 104:79-84.

Enright, N. and J. Ogden. 1979. Applications of transition matrix models in forest dynamics: *Araucaria* in Papua New Guinea and *Nothofagus* in New Zealand. Australian Journal of Ecology 4:3-23.

Evans, M., N. Hastings and B. Peacock. 2000. Statistical Distributions. Third edition. John Wiley and Sons, New York.

Fackler, P. 1999. Generating correlated multidimensional variates. [online] URL: http://www4.ncsu.edu/unity/users/p/pfackler/www/#WorkingPapers.

Ferson, S. 1991. RAMAS/stage: Generalized stage-based modeling for population dynamics (version 1.4). Applied Biomathematics, Setauket, New York.

Ferson, S. and M.A. Burgman. 1995. Correlations, dependency bounds and extinction risks. Biological Conservation 73:101-105.

Ferson, S., L.R. Ginzburg and H. R. Akçakaya. In press. Whereof one cannot speak: when input distributions are unknown. Risk Analysis.

Fieberg, J. and S.P. Ellner. 2000. When is it meaningful to estimate an extinction probability? Ecology 81:2040-2047.

Fiedler, P.L. 1987. Life history and population dynamics of rare and common mariposa lilies (*Calochortus* Pursh: Liliaceae). Journal of Ecology 75:977-995.

Fingleton, B. 1984. Models of category counts. Cambridge University Press, Cambridge, U.K.

Finley, K.K. 1994. Hydrology and related soil features of three Willamette Valley wetland prairies. M.Sc. thesis, Oregon State University, Corvallis.

Finley, K.K. and J.B. Kauffman. 1992. Soils and hydrology of Willamette Valley wetland prairies and ecological response of *Lomatium bradshawii* and *Erigeron decumbens* var. *decumbens* to prescribed fire. A progress report to the U.S. Army Corps of Engineers and the Bureau of Land Management, Eugene, Oregon.

Fisher, D.O., S.D. Hoyle, and S.P. Bloomberg. 2000. Population dynamics and survival of an endangered wallaby: a comparison of four methods. Ecological Applications 10:901-910.

Folkerts, G.W. 1977. Endangered and threatened carnivorous plants of North America. Pages 301-313 in G.T. Prance and T.S. Elias, editors. Extinction is forever: threatened and endangered species of plants in the Americas and their significance in ecosystems today and in the future. New York Botanical Garden, Bronx, N.Y.

Franklin, J.F., and C.T. Dyrness. 1988. Natural Vegetation of Oregon and Washington. Oregon State University Press, Corvallis, Oregon.

Frees, E.W. and E.A. Valdez. 1998. Understanding relationships using copulas. North American Actuarial Journal 2:1-25.

Frey, H.C. and D.E. Burmaster. 1999. Methods of characterizing variability and uncertainty: comparison of bootstrap simulations and likelihood-based approaches. Risk Analysis 19:109-130.

Frye, R.J. 1998. Population viability analysis of Pediocactus paradinei. Pages 39-46 in J. Maschinski, H.D. Hammond and L. Holter, editors. Southwestern Rare and Endangered Plants: Proceedings of the Second Conference. General Technical Report RM-GTR-283. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

Gankin, R. and J. Major. 1964. *Arctostaphylos myrtifolia*, its biology and relationship to the problem of endemism. Ecology 45:792-808.

Genest, C. and R. MacKay. 1986. The joy of copulas. American Statistician 50:280-283.

Giho, H. and H. Seno. 1997. Transition matrix modelling on disturbance-controlled persistence of plant population. Ecological Modelling 94:207-219.

Ginzburg, L.R., S. Ferson, and H.R. Akçakaya. 1990. Reconstructibility of density dependence and the conservative assessment of extinction risk. Conservation Biology 4:63-70.

Greenlee, J. and T.N. Kaye. 1997. Stochastic matrix projections: a comparison of the effect of element and matrix selection methods on quasi-extinction risk for *Haplopappus radiatus* (Asteraceae). Pages 66-71 in Kaye, T.N., A. Liston, R.M. Love, D. Luoma, R.J. Meinke, and M.V. Wilson, editors. Conservation and Management of Native Plants and Fungi. Native Plant Society of Oregon, Corvallis, Oregon.

Gregg, K.B. 1991. Variation in behaviour of four populations of the orchid *Cleistes divaricata*, an assessment using transition matrix models. Pages 139-159 in T.C.E. Wells and J.H. Willems, editors. Population ecology of terrestrial orchids. Academic Publishing, The Hague, The Netherlands.

Griffiths, D.A. 1973. Maximum likelihood estimation for the beta-binomial distribution and an application to the household distribution of the total number of cases of disease. Biometrics 29:637-648.

Gross, K., J.R. Lockwood III, C.C. Frost, and W.F. Morris. 1998. Modeling controlled burning and trampling reduction for conservation of Hudsonia montana. Conservation Biology 12:1291-1301.

Guerrant, E.O. 1996. Designing populations: demographic, genetic, and horticultural dimensions. Pages 171-207 in D.A. Falk, C.I. Millar, and M. Olwell, editors. Restoring Diversity. Island Press, Washington D.C.

Guerrant, E.O. and B.M. Pavlik. 1998. Reintroduction of rare plants: genetics, demography and the role of *ex situ* conservation methods. Pages 80-108 in P.L. Fiedler and P.M. Kareiva, editors. Conservation Biology for the Coming Decade. Second edition. Chapman and Hall, New York.

Haas, C.N. 1997. Importance of distributional form in characterizing inputs to Monte Carlo risk assessments. Risk Analysis 17:107-113.

Haas, C.N. 1999. On modeling correlated random variables in risk assessment. Risk Analysis 19:1205-1214.

Habeck, J.R. 1961. The original vegetation of the mid-Willamette Valley, Oregon. Northwest Sci. 35:65-77.

Hamed, M.M. and P.B. Bedient. 1997. On the effect of probability distributions of input variables in public health risk assessment. Risk Analysis 17:97-105.

Hardin, D.E. and D.L. White. 1992. Rare vascular plant taxa associated with wiregrass (Aristida stricta) in the southeastern United States. Natural Areas Journal 9:234-245.

Hartshorn, G.S. 1975. A matrix model of tree population dynamics. Pages 41-52 in F.B. Golley and E. Medina, editors. Tropical Ecological Systems, Springer-Verlag, New York.

Hartnett, D.C. and D.R. Richardson. 1989. Population biology of *Bonomia grandiflora* (Convolvulaceae): effects of fire on plant and seed bank dynamics. American Journal of Botany 73:361-369.

Hawkes, C.V. and E.S. Menges. 1995. Density and seed production of a Florida endemic, *Polygonella basiramia*, in relation to time since fire and open sand. The American Midland Naturalist 133:138-145.

Heppell, S.S., L.B. Crowder, and D.T. Crouse. 1996. Models to evaluate headstarting as a management tool for long-lived turtles. Ecological Applications 6:556-565.

Heppell, S.S., C. Pfister, and H. de Kroon. 2000. Elasticity analysis in population biology: methods and applications. Ecology 81:605.

Hessl, A. and S. Spackman. 1995. Effects of fire on threatened and endangered plants: an annotated bibliography. U.S. Department of the Interior, National Biological Service, Washington, D.C.

Heydecker, W. 1973. Seed ecology. The Pennsylvania State University Press, London.

Horino, S. and S. Miura. 2000. Population viability analysis of a Japanese black bear population. Population Ecology 42:37-44.

Horvitz, C.C. and D.W. Schemske. 1995. Spatiotemporal variation in demographic transitions of a tropical understory herb: projection matrix analysis. Ecological Monographs 65:155-192.

Horvitz, C.C., D.W. Schemske and H. Caswell. 1997. The relative "importance" of life-history stages to population growth: prospective and retrospective studies. Pages 248-271 in S. Tuljapurkar and H. Caswell, editors. Structured-population models in marine, terrestrial and freshwater systems. Chapman and Hall, New York, New York.

Iman, R.L. and W.J. Conover. 1982. A distribution-free approach to inducing rank correlation among input variables. Communications in Statistics —— Simulation and Computation 11:311-334.

Jacobs, J. 1993. New hope for the Peter's Mountain Mallow. Endangered Species Technical Bulletin 18(3):13-14.

Jacobson, G.L., H. Almquist-Jacobson, and J.C. Winne. 1991. Conservation of rare plant habitat: insights from the recent history of vegetation and fire at Crystal Fen, northern Maine, USA. Biological Conservation 57:287-314.

Jensen, A.L. 1995. Simple density dependent matrix model for population projection. Ecological Modelling 77:43-48.

Johannessen, C.L., W.A. Davenport, A. Millet, and S. McWilliams. 1971. The vegetation of the Willamette Valley. Annals of the Association of American Geographers 61:286-302.

Johnson, A.F. and W.G. Abrahamson. 1990. A note on the fire responses of species in rosemary scrubs on the southern Florida Lake Wales Ridge. Florida Scientist 53:138-143.

Johnson, A.F. and A. Blyth. 1988. Re-discovery of *Calamovilfa curtissii* (Graminae) in Florida Panhandle. Sida 13:137-140.

Kagan, J.S. 1980. The biology of *Lomatium bradshawii* (Apiaceae), a rare plant of Oregon. M.S. thesis, University of Oregon, Eugene.

Kahn, M.J. and A.E. Raftery. 1996. Discharge rates of Medicare stroke patients to skilled nursing facilities: Bayesian logistic regression with observed heterogeneity. Journal of the American Statistical Association — Applications and Case Studies 91:29-41.

Karian, Z.A. and E.J. Dudewicz. 2000. Fitting Statistical Distributions. CRC Press, Boca Raton, Florida.

Kaye, T.N. 1992. Bradshaw's desert-parsley: population monitoring and pollination biology. Kalmiopsis 2:1-4.

Kaye, T.N. 2000. *Lomatium cookii* population monitoring in the Illinois Valley, Josephine County, Oregon. Institute for Applied Ecology, Corvallis, Oregon.

Kaye, T.N. and S. Brady. 1991. *Astragalus tyghensis* monitoring, pollination, and germination. First year project status report. Oregon Department of Agriculture, Salem, Oregon.

Kaye, T.N. and R.J. Meinke. 1992. Population monitoring and pollination biology of Snake River Goldenweed, *Haplopappus radiatus*. Oregon Department of Agriculture, Salem, Oregon.

Kaye, T.N. and M. Kirkland. 1994. *Cimicifuga elata*: Status, habitat analysis, monitoring, inventory, and effects of timber management. Oregon Department of Agriculture, Salem, Oregon.

Kaye, T.N., K. Pendergrass, and K.K. Finley. 1994. Population biology of *Lomatium bradshawii*. I. Population viability analysis under three prairie burning treatments. Oregon Department of Agriculture, Salem, Oregon.

Kaye, T.N., K.L. Pendergrass, K. Finley, and J.B. Kauffman. 2001. The effect of fire on the population viability of an endangered prairie plant. Ecological Applications, in press.

Keeley, J.E. and C.J. Fotheringham. 1997. Trace gas emissions and smoke-induced seed germination. Science 276:1248-1250.

Kendall, B.E. 1998. Estimating the magnitude of environmental stochasticity in survivorship data. Ecological Applications 8:184-193.

Kephart, S.R. and C. Paladino. 1997. Demographic change and microhabitat variability in a grassland endemic, *Silene douglasii* var. *oraria* (Caryophyllaceae). American Journal of Botany 84:179-189.

Kimmerer, R.W. 1993. Disturbance and dominance in *Tetraphis pellucida*: a model of disturbance frequency and reproductive mode. The Bryologist 96(1):73-79.

Kittlein, M.J. 1997. Assessing the impact of owl predation on the growth rate of a rodent prey population. Ecological Modelling 103:123-134.

Kokko, H. and J. Lindstrom. 1998. Seasonal density dependence, timing of mortality, and sustainable harvesting. Ecological Modelling 110:293-304.

Kolbe, A.E., J. Buongiorno, and M. Vasievich. 1999. Geographic extension of an uneven-aged, multi-species matrix growth model for northern hardwood forests. Ecological Modelling 121:235-253.

Kucera, C.L. and J.H. Ehrenreich. 1962. Some effects of annual burning on central Missouri prairie. Ecology 43:334-336.

Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. The American Naturalist 142:911-927.

Lande, R., and S.H. Orzack. 1988. Extinction dynamics of age-structured populations in a fluctuating environment. Proc. Natl. Acad. Sci. 85:7418-7421.

Lefkovitch, L.P. 1965. The study of population growth in organisms grouped by stages. Biometrics 21:1-18.

Lennartsson, T. 2000. Management and population viability of the pasture plant Gentiana campestris: the role of interactions between habitat factors. Ecological Bulletin 48:111-121.

Lesica, P. 1997. Demography of the endangered plant, *Silene spaldingii* (Caryophyllaceae) in northwest Montana. Madroño 44: 347--358.

Lesica, P. 1999. Effects of fire on the demography of the endangered, geophytic herb *Silene spaldingii* (Caryophyllaceae). American Journal of Botany 86: 996-1002.

Lin, C. and J. Buongiorno. 1997. Fixed versus variable-parameter matrix models of forest growth: the case of maple-birch forests. Ecological Modelling 99:263-274.

Lindenmeyer, D.B., M.A. Burgman, H.R. Akçakaya, R.C. Lacy, and H.P. Possingham. 1995. A review of the generic computer programs ALEX, RAMAS/space and VORTEX for modelling the viability of wildlife populations. Ecological Modelling 82:161-174.

Lindsey, A.H. 1982. Floral phenology patterns and breeding systems in *Thaspium* and *Zizia* (Apiaceae). Systematic Botany 7:1-12.

Logofet, D.O. and E.V. Lesnaya. 2000. The mathematics of Markov models: what Markov chains can really predict in forest successions. Ecological Modelling 126: 285-298.

Ludwig, D. 1999. Is it meaningful to estimate a probability of extinction? Ecology 80:298-310.

MacRoberts, M.H. and B.R. MacRoberts. 1990. Notes on the occurrence of *Platanthera integra* (Nutt.) A. Gray ex Beck (Orchidaceae) in West Central Louisiana. Phytologia 69:378-381.

Maguire, L.A., G.F. Wilhere, and Q. Dong. 1995. Population viability analysis for red-cockaded woodpeckers in the Georgia Piedmont. Journal of Wildlife Management 59:533-542.

Maillette, L. 1982. Structural dynamics of silver birch. II. A matrix model of the bud population. Journal of Applied Ecology 19:219-238.

Manders, P.T. 1987. A transition matrix model of the population dynamics of the Clanwilliam cedar (*Widdringtonia cedarbergensis*) in natural stands subject to fire. Forest Ecology and Management 20:171-186.

Maret, M. P. 1997. Effects of fire on seedling establishment in upland prairies of the Willamette Valley, Oregon. M.S. thesis. Department of Botany and Plant Pathology, Oregon State University, Corvallis, OR.

Maschinski, J., R. Frye, and S. Rutman. 1997. Demography and population viability of an endangered plant species before and after protection from trampling. Conservation Biology 11:990-999.

Mathworks, The. 1998. Matlab, version 5. The Mathworks, Inc., Natick, Massachusetts.

McClaren, M.P. and P.C. Sundt. 1992. Population dynamics of rare orchid *Spiranthes delitescens*. Southwestern Naturalist 37:299-333.

McCrimmon, K.R. and C.A. Ryavec. 1964. An analytical study of PERT assumptions. Operations Research 12:113-124.

McEvoy, P.B. and E.M. Coombs. 1999. Biological control of plant invaders: regional patterns, field experiments, and structured population models. Ecological Applications 9:387-401.

Meagher, T.R. 1982. The population biology of *Chamaelirium luteum*, a dioecious member of the lily family: two sex population projections and stable population structure. Ecology 63:1701-1711.

Menges, E.S. 1986. Predicting the future of rare plant populations: demographic monitoring and modeling. Natural Areas Journal 6:13-25.

Menges, E.S. 1990. Population viability analysis for an endangered plant. Conservation Biology 4:52-62.

Menges, E.S. 1992. Habitat preferences and response to disturbance for *Dicerandra frutescens*, a rare Lake Wales Ridge (Florida) endemic plant. Bulletin of the Torrey Botanical Club 119:308-313.

Menges, E.S. 1992. Stochastic modeling of extinction in plant populations. Pages 253-275 in P.L. Fiedler and S.K. Jain, editors. Conservation biology: the theory and practice of nature conservation, preservation, and management. Chapman and Hall, New York.

Menges, E.S. 1995. Factors limiting fecundity and germination in small populations of *Silene regia* (Caryophyllaceae), a rare hummingbird-pollinated prairie forb. American Midland Naturalist 133:242-255.

Menges, E.S. 2000. Population viability analyses in plants: challenges and opportunities. Trends in Ecology and Evolution 15:51-56.

Menges, E.S. and R.W. Dolan. 1998. Demographic viability of populations of *Silene regia* in midwestern prairies: relationships with fire management, genetic variation, geographic location, and population size. Journal of Ecology 86:63-78.

Menges, E.S. and J. Kimich. 1996. Microhabitat and time-since-fire: Effects on demography of *Eryngium cuneifolium* (Apiaceae), a Florida scrub endemic. American Journal of Botany 83:185-191.

Mills, L.S., S.G. Hayes, C. Baldwin, M.J. Wisdom, J. Citta, D.J. Mattson, and K. Murphy. 1996. Factors leading to different viability predictions for a grizzly bear data set. Conservation Biology 10:863-873.

Moir, W.H. and P. Mika. 1976. Prairie vegetation of the Willamette Valley, Benton, Co., Oregon. Unpublished report, Research Work Unit 125, U.S.D.A. Forest Science Lab, Corvallis, Oregon.

Moloney, K.A. 1986. A generalized algorithm for determining category size. Oecologia 69:176-180.

Myers, R.L. 1989. Condominiums, trailer parks and high intensity fires: the future of sand pine scrub preserves in Florida. Proceedings of the 17th Tall Timbers Fire Ecology Conference, Tallahassee Florida.

Nakoaka, M. 1996. Dynamics of age- and size-structured populations in fluctuating environments: applications of stochastic matrix models to natural populations. Researches in Population Ecology 38:141-152.

Nakoaka, M. 1997. Demography of the marine bivalve *Yoldia notabilis* in fluctuating environments: an analysis using a stochastic matrix model. Oikos 79:59-68.

Namkoong, G. and J.H. Roberds. 1974. Extinction probabilities and the changing age structure of Redwood forests. American Naturalist 108:355-368.

Nantel, P., Gagnon, D. and Nault, A. 1996. Population viability analysis of American Ginseng and Wild Leek harvested in stochastic environments. Conservation Biology 10: 608-621.

Nelson, R.B. 1999. An Introduction to Copulas. Springer, New York.

Noble, I.R. and R.O. Slatyer. 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. Vegetatio 43:5-21.

Noon, B.R. and K.S. McKelvey. 1996. Management fo the spotted owl: A case history in conservation biology. Annual Review of Ecology and Systematics 27:135-162.

Ojima, D.D., D.S. Schimel, W.J. Parton, and C.E. Owensby. 1994. Long- and short-term effects of fire on nitrogen cycling in tallgrass prairie. Biogeochemistry 24:67-84.

Olmsted, I. and E.R. Alvarez-Buylla. 1995. Sustainable Harvesting of Tropical Trees: Demography and Matrix Models of Two Palm Species in Mexico. Ecological Applications 5:484-500.

Oostermeijer, G. 1996. Population viability of the rare *Gentiana pneumonanthe*. The relative importance of demography, genetics, and reproductive biology. Ph.D. dissertation. Institute for Systematics and Population Biology, University of Amsterdam, The Netherlands.

Oostermeijer, G. 2000. Population viability analysis of the rare *Gentiana pneumonanthe*: importance of demography, genetics, and reproductive biology. Pages 313-334 in A. Young and G. Clarks (eds.), Genetics, Demography, and Viability of Fragmented Populations. Cambridge University Press, London.

Oostermeijer, G., M.L. Brugman, E.R. de Boer, and H.C.M. den Nijs. 1996. Temporal and spatial variation in the demography of Gentiana pneumonanthe, a rare perennial herb. Journal of Ecology 84:153-166.

Oregon Natural Heritage Program. 2001. Rare, threatened and endangered plants and animals of Oregon. Oregon Natural Heritage Program, Portland, Oregon.

Orzack, S.H. 1993. Life history evolution and population dynamics in variable environments: Some insights from stochastic demography. Pages 63-104 in J. Yoshimura and C.W. Clark, editors. Adaptation in Stochastic Environments. Springer-Verlag, New York.

Orzack, S.H. 1997. Life history evolution and extinction. Pages 273-302 in S. Tuljapurkar and H. Caswell, editors. Structured Population Models in Marine, Terrestrial, and Freshwater Systems. Chapman and Hall, New York.

Osho, J.S.A. 1996. Modelling the tree population dynamics of the most abundant species in a Nigerian tropical rain forest. Ecological Modelling 89:175-181.

Owen, W.R. and R. Rosentreter. 1992. Monitoring rare perennial plants: techniques for demographic studies. Natural Areas Journal 12:32-39.

Parenti, R.L., A.F. Robinson, and J.S. Kagan. 1993. Bradshaw's lomatium recovery plan. U.S. Fish and Wildlife Service, Portland, OR.

Parker, I.M. 2000. Invasion dynamics of Cytisus scoparius: a matrix model approach. Ecological Applications 10:726-743.

Pascual, M.A., P. Kareiva, and R. Hilborn. 1997. The influence of model structure on conclusions about the viability of harvesting of Serengeti wildebeest. Conservation Biology 11:966-976.

Pendergrass, K.L. 1995. Vegetation composition and response to fire of native Willamette Valley wetland prairies. MS Thesis, Oregon State University, Corvallis, OR. 241 pp.

Pendergrass, K.L., P.M. Miller, and J.B. Kauffman. 1998. Prescribed fire and the response of woody species in Willamette Valley wetland prairies. Restoration Ecology 6:303-311.

Pendergrass, K.L., P.M. Miller, J.B. Kauffman, and T.N. Kaye. 1999. The role of prescribed burning in maintenance of an endangered plant species, *Lomatium bradshawii*. Ecological Applications 9:1420--1429.

Pfab, M.F. and E.T.F. Witkowski. 2000. A simple population viability analysis of the critically endangered Euphorbia clivicola R.A. Dyer under four management scenarios. Biological Conservation 96:263-270.

Phillips, B.G., H. Green, S. Dudley, and R. Galeano-Popp. 1992. Prescribed fire research on Flagstaff pennyroyal (*Hedeoma diffusum* Greene). Pages 162-169 in R. Sivinski and K. Lightfoot, editors. Proceedings of the Southwestern rare and endangered plant conference. New Mexico Forestry Resources and Conservation Division, Santa Fe, New Mexico.

Pinero, D., M. Martinez-Ramos, and J. Sarukhan. 1984. A population model of *Astrocaryum mexicanum* and a sensitivity analysis of its finite rate of increase. Journal of Ecology 72:977-991.

Ratner, S., R. Lande and B.B. Roper. 1997. Population viability analysis of spring Chinook salmon in the South Umpqua River, Oregon. Conservation Biology 11:879-889.

Sarukhan, J. and M. Gadgil. 1974. Studies on plant demography: *Ranunculus repens* L., *R. bulbosus* L., and *R. acris* L. III. A mathematical model incorporating multiple modes of reproduction. Journal of Ecology 62:921-936.

SAS Institute, Inc. 1990. SAS/STAT User's Guide, version 6. Fourth edition, volume 2. SAS Institute, Inc., Cary, North Carolina.

Schemske, D.W., B.C. Husband, M.H. Ruckleshaus, C. Goodwillie, I.M. Parker, and J.H. Bishop. 1994. Evaluating approaches to the conservation of rare and endangered plants. Ecology 75:584-606.

Schlessman, M.A. 1978. Systematics and reproductive biology of *Lomatium farinosum* (Geyer ex Hooker) Coulter & Rose (Umbelliferae). Madrono 25:1-9.

Schmidt, K.P. and L.R. Lawlor. 1983. Growth rate projection and life history sensitivity for annual plants with a seed bank. American Naturalist 121:525-539.

Seno, H. and H. Nakajima. 1999. Transition matrix model for persistence of monocarpic perennial plant population under periodically ecological disturbance. Ecological Modelling 117:65-80.

Shaw, R.G. 1987. Density-dependence in *Salvia lyrata*: Experimental alteration of densities of established plants. Journal of Ecology 75:1049-1063.

Shea, K. and D. Kelly. 1998. Estimating biocontrol agent impact with matrix models: Carduus nutans in New Zealand. Ecological Applications 8:924-832.

Silva, J.F., J. Raventos, and H. Caswell. 1990. Fire and fire exclusion effects on the growth and survival of two savanna grasses. Acta Œcologica 11:783-800.

Silva, J.F., J. Raventos, H. Caswell, and M.C. Trevisan. 1991. Population responses to fire in a tropical savanna grass, *Andropogon semiberbis*: a matrix model approach. Journal of Ecology 79:345-356.

Silvertown, J., M. Franco, and E.S. Menges. 1996. Interpretation of elasticity matrices as an aid to the management of plant populations for conservation. Conservation Biology 10:591-597.

Silvertown, J., M. Franco, I. Pisanty, and A. Mendoza. 1993. Comparative plant demography: relative importance of demographic components to the finite rate of increase in perennial plants. Journal of Ecology 81:465-476.

Slade, N.A. and H. Levinson. 1984. The effects of skewed distributions of vital statistics on growth of age-structured populations. Theoretical Population Biology 26:361-366.

Sorribas, A., J. March, and E.O. Voit. 2000. Estimating age-related trends in cross-sectional studies using S-distributions. Statistics in Medicine 19:697-713.

Soulé, M.E. 1987. Viable populations for conservation. Cambridge University Press, Cambridge, England.

Steel, R.G.D., J.H. Torrie, and D.A. Dickey. 1997. Principles and procedures of statistics, a biometrical approach. Third edition. The McGraw-Hill Companies, Inc. New York.

Stone, C.P. and J.M. Scott. 1985. Hawaii's terrestrial ecosystems: preservation and management. Cooperative National Park Resources and Studies Unit, University of Hawaii, Manoa, Hawaii.

Streatfield, R. and R.E. Frenkel. 1997. Ecological survey and interpretation of the Willamette Valley Floodplain Research Natural Area, W.L. Finley National Wildlife Refuge, Oregon, USA. Natural Areas Journal 17:346-354.

Tallie, C., G.P. Patil, and R.C. Hennemuth. 1995. Modelling and analysis of recruitment distributions. Environmental and Ecological Statistics 2:315-329.

Tamura, R.N. and S.S. Young. 1987. A stabilized moment estimator for the beta-binomial distribution. Biometrics 43:813-824.

Thompson, J.N. 1985. Postdispersal seed predation in *Lomatium* spp. (Umbelliferae): variation among individuals and species. Ecology 66:1608-1616.

Tuljapurkar, S.D. 1982. Population dynamics in variable environments. II. Correlated environments, sensitivity analysis and dynamics. Theoretical Population Biology 21:114-140.

Tuljapurkar, S.D. 1990. Population dynamics in variable environments. Springer-Verlag, New York.

Tuljapurkar, S.D. and S.H. Orzack. 1980. Population dynamics in variable environments. I. Long-run growth rates and extinction. Theoretical Population Biology 18:314-342.

Usher, M.B. 1976. Extensions to models, used in renewable resource management, which incorporate an arbitrary structure. Journal of Environmental Management 4:123-140.

Vacanti, P.L. and K.N. Geluso. 1985. Recolonization of a burned prairie by meadow voles (Microtus pennsylvanicus). Prairie Naturalist 17:15-22.

van Groenendael, J.M. and P. Slim. 1988. The contrasting dynamics of two populations of *Plantago lanceolata* classified by age and size. Journal of Ecology 77:162-181.

Vandermeer, J. 1978. Choosing category size in a stage projection matrix. Oecologia 32:79-84.

Voit, E.O. and L.H. Schwake. 2000. Random number generation from right-skewed, symmetric, and left skewed distributions. Risk analysis 20:59-71.

Warren, P.L., R.J. Frye, D. Gori, and A. Laurenzi. 1992. Population biology of *Pediocactus paradinei*, a rare cactus from northern Arizona. Pages 132-143 in

R. Sivinski and K. Lightfoot, editors. Proceedings of the Southwestern rare and endangered plant conference. New Mexico Forestry Resources and Conservation Division, Santa Fe, New Mexico.

Wilson, M.V., E.R. Alverson, D.L. Clark, R.H. Hayes, C.A. Ingersoll, and M.B. Naughton. 1995. The Willamette Valley Natural Areas Network: Promoting restoration through science and stewardship. Restoration and Management Notes 13:26-28.

Wisdom, M.J., L.S. Mills, and D.F. Doak. 2000. Life stage simulation analysis: estimating vital-rate effects on population growth for conservation. Ecology 81:628-641.

Yang, Y., J.C. Allen, J.L. Knapp, and P.A. Stansly. 1997. An age-structured population model of citrus rust mite: a fruit-mite-fungal pathogen system. Ecological Modelling 104:71-85.

APPENDIX

Appendix

Field Sampling Techniques and Matrix Construction Notes for Each Species

ASTRAGALUS TYGHENSIS

A total of 15 permanent monitoring plots at five sites were sampled to obtain demographic data from five populations of *Astragalus tyghensis*. Monitored populations were at sites 4, 10, 13, 25, and 41 (Kaye and Brady 1991). Plot locations were selected by visually partitioning each population into homogeneous areas, then randomly placing plot locations. All permanent plots were 5 x 5 m square, marked in each corner with a 1 m piece of iron rebar protruding at least 30 cm from the soil. The upper left corner-rebar of each plot (facing up-slope) was labeled with an aluminum tag noting plot number. To sample, each side of the plot was marked temporarily at 1 m intervals with nails, and string was tossed back and forth over the plot (looped each time around a nail) to create a grid of 1 x 1 m subplots within the 5 x 5 m macroplot. The location of each *Astragalus tyghensis* individual in every subplot was mapped and numbered on map sheets. A dot and a corresponding plant number were placed on the map sheets to mark the position of each plant. In some cases, it was difficult to determine whether tufts of plants were clusters of individuals or merely a single plant that had branched below the soil surface, or a combination of these. In these cases, the loose soil was gently excavated and probed with fingers to check for root connections. On a separate data sheet, we noted diameter (cm), length of longest stem (cm), number of inflorescences, and evidence of grazing (yes or no) of each mapped and numbered plant.

To assess seed production, we sampled between 25 and 80 plants at each monitoring site. Plants were sampled at random for number of inflorescences and fruits adjacent to and outside of the permanent macroplots. In addition, whole infructescences were collected at random and inspected for seed set per fruit and insect seed predation. At sites 4 and 41, the number of fruits per plant was measured for all plants in the plots, instead of subsampling outside the plots, because of the relatively low number of flowering plants at those sites. The samples were collected each season when fruits were mature. For each site, we performed linear regressions to determine the number of fruits expected from a plant given the number of inflorescences (for these tests, $P < 0.05$) (except at sites 4 and 41 in 1992-98, and 4, 10, 25, and 41 in 1999 where fruit production was measured directly). These data were multiplied by the average number of seeds per fruit at each site to give an estimate of the number of seeds produced by each monitored plant. The following formulae were used to calculate the number of seeds produced per plant given the number of inflorescences or fruits [(#inflorescences × regression coefficient for fruits/inflorescences) × average number of seeds per fruit].

For the purposes of the model, the individuals in a population were assigned to categories (stages) based on age (for seedlings only) and size. The number of seedlings produced per plant in each category was determined, and the probability of individual stasis in the same stage or transition to another was be calculated. The transition probabilities were the proportion of individuals in each stage that made the transition to another stage (e.g., become smaller or larger) from one year to the next. We recognized five stages for this species based primarily on stem length: seedling, longest stem <10 cm, 10-20 cm, 20-30 cm, and >30 cm. These stages were defined subjectively after displaying the size data graphically in several different ways. In a few cases, data for a particular stage were lacking for a given year due to absence of that category from the population samples. When this occurred, the column for that stage was replaced by the mean transition elements from all other years (Table A.1).

CIMICIFUGA ELATA

We used data from three *C. elata* populations to derive transition matrices: EUGRASS, EUNORR and WIL032 (Kaye and Kirkland 1994). At each population, we measured all the following characteristics of each plant: number of leaves, number of reproductive stems, and number of racemes. In addition, we mapped and tagged individuals within 40-m on either side of a reference transect. Plants were mapped according to a coordinate system in which the first (x) coordinate is the distance along the reference transect to a plant, and the second (y) is the lateral (perpendicular) distance from the transect to the plant. Because plants usually were found on both sides of the transect center-line, plants to the right of the transect (facing in the direction of the transect) were given positive y-axis ordinates, and those to the left were assigned negative y-axis ordinates. Distances were measured to the nearest decimeter to the base of the plant where it rooted into the soil. Plants were permanently tagged by inserting a stiff wire (12 gauge) into the soil 15-cm away from the plant perpendicular to the transect center-line. The wire was looped at the top and a machine-numbered aluminum tag was fixed in the loop. In this way, each individual was tagged with a permanent and unique number and set of coordinates. Data from tagged plants were used to classify each individual into five stages, including seedling, vegetative with 1 or 2 leaves, vegetative with 3 or more leaves, reproductive (having at least one flower stalk), or dormant (for plants that skipped one or more years then reappeared). As in matrices for *A. tyghensis*, when too little data were available to calculate transitions for a particular stage, the matrix column for that stage was replaced by the mean. This occurred for the EUGRASS population in which the large vegetative stage was replaced by means in year 2, for EUNORR where seedlings, recuitment, and dormany were replaced by means only in year 4, and WIL032 where seedling and large vegetative transitions were replaced by means in year 1 (Table A.1).

HAPLOPAPPUS RADIATUS

Ten plots were established at five sites within the Oregon portion of the range of *Haplopappus radiatus* (Kaye and Meinke 1992). Plots were assigned to a fenced or unfenced treatment by a toss of a coin. All plots, whether inside or outside of an exclosure, were 10 x 10 m square and followed the same basic form. It was necessary to incorporate walk-ways into the plot set-up in order to reach the individual subplots for close inspection. Therefore, each plot was composed of five 1-m wide belt transects alternating with 1-m wide walk-ways. The belt transects were marked permanently with rebar posts anchored at each end. Each transect was broken into 10 contiguous 1 x 1 m subplots in which plants were mapped and measured. Thus, there were five transects of ten subplots each, for a total of fifty subplots per plot (plot 1-out was an exception, with only 25 subplots). To locate the plots for sampling, a meter tape was run from the left post to the right post (left and right as if facing up-hill), and each 1-m segment of meter tape formed the lower edge of each subplot. A 1 x 1 m frame was then placed on the ground (with one edge along the meter tape) to delineate the subplot.

In 1991 the plots were sampled twice, on April 15-18 and July 19-23; 1992 sampling occurred on May 7-10 and July 20-24; 1993 sampling occurred on May 11-12 and July 13-14; 1994 sampling occurred on May 17-19 and August 2-4; 1995 sampling was conducted on May 22-26 and August 7-11; 1996 sampling occurred August 12-16; 1997 sampling was on May 28-29 and August 5-7; 1998 sampling was done on May 19-20 and July 28-30, and sampling in 1999 was conducted on May 18-19 and July 26-29. The early spring samples were conducted primarily to maintain the plots and locate seedlings. All plants were measured and remapped during the summer sample. In every subplot, all *Haplopappus radiatus* individuals were mapped onto special map forms and numbered consecutively on the map. Data on plant height (cm), length of longest leaf (cm), number of leaves, number of healthy and aborted flower heads (capitula), number of grazed stems, and percentage herbivory by grasshoppers, were recorded onto a second data sheet. In 1991, the density of *Haplopappus radiatus* was so high at the Lime sites (1 & 2) that we reduced the area of the subplots where non-reproductive plants are mapped and measured to the lower left-hand quarter of the subplots. All reproductive individuals in the entire subplot were mapped and measured in the Lime plots (1 & 2). In addition, only even numbered subplots were sampled at Upper Lime plot 1-out. All portions of all subplots were sampled at the Lookout Mountain Road sites (plots 3, 4 & 5). In 1996, protocol was changed at the Lime sites so that mapping and measuring included all plants in all plots. Each individual was assinged to ne of four stages based primarily on number of leaves and reproductive status: seedling, juvenile(≤four leaves), vegetative (>4 leaves and non-reproductive), and reproductive (producing at least one flowering capitulum). These stages were defined subjectively after displaying the size data graphically. Occasionally, no seedlings survived at all in a given population and year, and in others, all seedlings survived. Also, in some plots, no reproductive plants were observed in some years, so no data were available to estimate transition probabilities of this stage class. As above, where data were lacking, we used the average of transition probabilities from the years when these data were available (Table A.1).

LOMATIUM BRADSHAWII

We used information from three populations that were part of a prairie burning experiment (Kaye et al. 2001) to collect demographic data on *Lomatium bradshawii.*

All three, Fisher Butte, Rose Prairie, and Long Tom, were within the southwest part of the species' range, in an area west and north of Eugene, Oregon. Three burning treatments were conducted at two of the locations, making a total of seven independent demographic data sets for this species. Permanent monitoring plots were sampled annually. To establish these plots, mature *Lomatium bradshawii* plants (reproductive or large vegetative) were randomly chosen from throughout the population areas and tagged in 1988. These individuals were numbered, and a subset, ten at Fisher Butte, six at Rose Prairie, and ten at Long Tom, were randomly selected from each treatment area to serve as center points for permanent circular plots (2-m radius). All *L. bradshawii* individuals were mapped in each circular plot in May or June of each year (prior to burning) from 1988 through 1993. Leaf number, seed production, and umbel number were recorded annually for all tagged plants, including those at the center of each circular plot and outside the plots, and seed production per reproductive plant category was used to estimate per capita seedling recruitment for each reproductive stage. We used a biological classification that combined plant size and reproductive state to classify each *Lomatium bradshawii* individual into one of five stages: seedling, vegetative plant with one or two leaves, vegetative plant with three or more leaves, and reproductive plant with one, or two or more umbels. Reproductive plants were segregated by umbel number because one-umbel plants rarely produce seed, while two-umbel plants produce seeds on the second umbel, and plants with three or more umbels may produce many seeds (T.N. Kaye, unpublished data). We combined vegetative plants with one or two leaves into a single stage because field observations indicated that plants with one leaf often produced a second leaf later in the year, and therefore leaf number of small plants may be a function of sampling date and/or variation in seasonal phenology, not plant vigor. Seedlings were defined as first year plants, often with cotyledons. All vegetative plants with one leaf were considered seedlings in 1988 (Table A.1).

LOMATIUM COOKII

Long-term monitoring plots were established at two populations in near Cave Junction, Oregon (Kaye 2000). At each population (Middle and South), 20 plots were randomly placed. These plots were 0.5 x 0.5-m, and all individual *Lomatium cookii* plants were mapped to their approximate location, given unique numbers, and assigned to the categories defined below. To sample, a 0.5 x 0.5-m frame was placed over the plot and all plant positions were mapped to scale on a map form. Plant categories were seedling, vegetative with 1 or 2 leaves, vegetative with 3 or more leaves, reproductive with 1 umbel, reproductive with 2 umbels, and reproductive with 3 or more umbels. As above, where data were lacking, we used the average of transition probabilities from the years when these data were available (Table A.1).

Table A.1. Annual transition matrices. The transition matrices reported below are in a condensed format. Each column represents a transition matrix for a single year of observation. The entries in a column of the table are the entries in each column of the matrix, stacked one above the other, beginning with seedling transitions at the top. To reconstruct a square matrix, each column must be reshaped so that the first five entries (or four for *Haplopappus radiatus* and six for *Lomatium cookii*) form the first (left hand) column of the matrix, the next five (or four or six, as above) the next column, and so on. See the details for each species above for stage definitions.

Astragalus tyghensis, site 4

0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.407	0.220	0.479	0.120	0.632	0.556	0.681	0.345	0.514
0.019	0.017	0.010	0.160	0.035	0.037	0.000	0.034	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.515	0.254	0.444	0.151	0.261	0.423	0.350	0.455	0.216
0.182	0.222	0.083	0.093	0.130	0.231	0.300	0.127	0.255
0.015	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.020
0.000	0.000	0.000	0.012	0.000	0.000	0.000	0.000	0.000
0.176	0.228	0.062	0.247	0.046	0.529	0.316	0.054	0.207
0.163	0.121	0.195	0.133	0.280	0.033	0.184	0.241	0.125
0.372	0.576	0.463	0.367	0.560	0.733	0.368	0.552	0.344
0.256	0.152	0.000	0.300	0.000	0.133	0.237	0.000	0.188
0.047	0.000	0.000	0.000	0.000	0.000	0.026	0.000	0.000
2.176	2.815	0.619	3.081	0.790	2.710	1.543	1.737	1.934
0.000	0.037	0.160	0.000	0.154	0.000	0.000	0.083	0.000
0.188	0.185	0.240	0.071	0.615	0.333	0.375	0.500	0.000
0.812	0.630	0.520	0.214	0.231	0.444	0.250	0.083	1.000
0.000	0.111	0.000	0.643	0.000	0.222	0.250	0.000	0.000
3.332	3.116	2.321	6.468	1.556	0.736	2.314	3.648	2.936
0.000	0.000	0.333	0.000	0.000	1.000	0.000	0.250	0.198
0.200	0.250	0.000	0.000	0.100	0.000	0.000	0.500	0.131
0.400	0.750	0.333	1.000	0.600	0.000	0.500	0.000	0.448
0.400	0.000	0.333	0.000	0.100	0.000	0.500	0.000	0.167

Table A.1, Continued.

Astragalus tyghensis, site 10

0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.278	0.062	0.319	0.217	0.530	0.512	0.363	0.202	0.113
0.111	0.021	0.017	0.029	0.034	0.047	0.022	0.024	0.005
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.021	0.000	0.000	0.005	0.000	0.010	0.000	0.008	0.005
0.286	0.217	0.478	0.161	0.300	0.459	0.455	0.326	0.233
0.171	0.130	0.217	0.274	0.300	0.235	0.247	0.157	0.407
0.171	0.043	0.000	0.048	0.000	0.000	0.026	0.000	0.058
0.000	0.000	0.000	0.016	0.000	0.000	0.000	0.000	0.012
0.557	0.191	0.208	0.564	0.054	0.441	0.311	1.018	0.418
0.020	0.033	0.170	0.029	0.235	0.156	0.055	0.247	0.014
0.320	0.533	0.638	0.186	0.500	0.531	0.616	0.438	0.507
0.560	0.200	0.128	0.414	0.176	0.188	0.192	0.067	0.333
0.060	0.033	0.000	0.257	0.029	0.016	0.014	0.014	0.029
2.677	1.018	0.992	2.691	0.325	2.154	1.780	3.593	1.904
0.000	0.065	0.023	0.000	0.051	0.051	0.000	0.207	0.000
0.125	0.339	0.568	0.040	0.615	0.308	0.621	0.448	0.083
0.550	0.387	0.364	0.240	0.308	0.410	0.379	0.138	0.500
0.275	0.097	0.023	0.640	0.000	0.103	0.000	0.000	0.417
4.857	2.358	1.216	3.179	0.749	4.376	1.384	3.75	2.588
0.083	0.000	0.000	0.000	0.026	0.000	0.000	0.000	0.014
0.000	0.150	0.583	0.000	0.211	0.600	0.429	0.500	0.309
0.330	0.500	0.250	0.000	0.553	0.000	0.286	0.500	0.302
0.500	0.250	0.167	1.000	0.105	0.400	0.143	0.000	0.321

Table A.1, Continued.

Astragalus tyghensis, site 13

0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.373	0.147	0.288	0.358	0.281	0.297	0.384	0.377	0.192
0.026	0.058	0.006	0.039	0.045	0.059	0.088	0.038	0.026
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.094	0.004	0.000	0.105	0.005	0.004	0.005	0.002	0.002
0.417	0.188	0.438	0.271	0.362	0.215	0.335	0.437	0.256
0.188	0.188	0.062	0.161	0.179	0.192	0.335	0.121	0.171
0.076	0.031	0.000	0.060	0.015	0.024	0.023	0.004	0.014
0.014	0.000	0.000	0.021	0.000	0.006	0.000	0.000	0.000
1.435	0.424	0.066	6.667	0.235	0.296	0.090	0.065	0.109
0.074	0.061	0.538	0.116	0.175	0.105	0.058	0.249	0.124
0.278	0.318	0.290	0.231	0.320	0.363	0.562	0.472	0.355
0.417	0.364	0.000	0.273	0.117	0.121	0.190	0.036	0.204
0.157	0.121	0.000	0.240	0.039	0.048	0.036	0.000	0.000
5.550	4.182	0.729	2.836	1.247	3.512	1.929	0.879	1.232
0.062	0.014	0.379	0.096	0.067	0.040	0.016	0.157	0.028
0.062	0.162	0.515	0.205	0.167	0.100	0.222	0.486	0.139
0.438	0.378	0.000	0.361	0.350	0.540	0.460	0.229	0.361
0.375	0.432	0.000	0.242	0.233	0.140	0.270	0.029	0.278
14.566	11.301	1.835	6.819	2.998	5.478	5.093	2.691	2.541
0.000	0.000	0.221	0.041	0.000	0.026	0.000	0.068	0.000
0.143	0.050	0.691	0.174	0.075	0.026	0.057	0.386	0.111
0.143	0.250	0.000	0.216	0.350	0.237	0.314	0.250	0.333
0.643	0.700	0.000	0.495	0.500	0.500	0.629	0.159	0.556

Table A.1, Continued.

Astragalus tyghensis, site 25

0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.381	0.176	0.338	0.238	0.402	0.240	0.375	0.423	0.136
0.044	0.072	0.032	0.270	0.073	0.020	0.087	0.064	0.034
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.023	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.003
0.133	0.115	0.549	0.126	0.748	0.310	0.391	0.370	0.274
0.382	0.230	0.127	0.347	0.087	0.267	0.141	0.050	0.178
0.325	0.000	0.000	0.085	0.065	0.017	0.016	0.000	0.041
0.049	0.000	0.000	0.045	0.000	0.009	0.000	0.000	0.000
0.932	0.261	0.045	0.162	0.002	0.029	0.019	0.074	0.191
0.000	0.016	0.204	0.017	0.111	0.085	0.199	0.318	0.054
0.086	0.590	0.611	0.046	0.606	0.529	0.581	0.307	0.380
0.617	0.279	0.080	0.197	0.071	0.196	0.059	0.006	0.293
0.259	0.016	0.018	0.665	0.020	0.078	0.000	0.000	0.065
6.864	1.691	0.290	2.207	0.052	0.342	0.297	0.704	1.556
0.000	0.019	0.069	0.000	0.121	0.022	0.161	0.235	0.000
0.061	0.292	0.678	0.026	0.517	0.169	0.495	0.333	0.000
0.303	0.453	0.195	0.053	0.207	0.483	0.237	0.059	0.400
0.636	0.179	0.000	0.868	0.069	0.270	0.011	0.000	0.600
6.040	3.403	0.727	5.577	0.264	0.716	0.655	1.394	2.483
0.000	0.000	0.022	0.000	0.012	0.000	0.027	0.143	0.026
0.000	0.111	0.467	0.000	0.231	0.095	0.493	0.571	0.246
0.200	0.407	0.267	0.000	0.376	0.254	0.260	0.000	0.221
0.800	0.463	0.222	1.000	0.318	0.540	0.082	0.000	0.428

Table A.1, Continued.

Astragalus tyghensis, site 41

0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.588	0.406	0.461	0.167	0.370	0.292	0.333	0.312	0.000
0.059	0.203	0.026	0.083	0.167	0.250	0.083	0.031	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.049	0.003	0.000	0.005	0.000	0.000	0.000	0.007
0.686	0.082	0.625	0.114	0.368	0.281	0.389	0.321	0.050
0.229	0.344	0.031	0.190	0.053	0.375	0.278	0.036	0.300
0.014	0.344	0.000	0.219	0.105	0.062	0.056	0.000	0.125
0.000	0.131	0.000	0.171	0.000	0.000	0.000	0.000	0.000
0.000	2.386	0.083	0.000	0.037	0.028	0.008	0.005	0.023
0.231	0.037	0.561	0.000	0.000	0.031	0.171	0.147	0.048
0.769	0.222	0.195	0.111	0.556	0.375	0.341	0.500	0.262
0.000	0.407	0.000	0.111	0.222	0.250	0.220	0.000	0.405
0.000	0.333	0.000	0.556	0.148	0.031	0.000	0.000	0.048
1.885	1.885	0.326	1.885	0.151	0.219	0.176	0.035	0.151
0.097	0.097	0.424	0.097	0.000	0.000	0.059	0.176	0.000
0.199	0.199	0.303	0.199	0.250	0.207	0.235	0.412	0.000
0.293	0.293	0.000	0.293	0.536	0.517	0.412	0.029	0.500
0.320	0.320	0.000	0.320	0.214	0.241	0.147	0.000	0.500
0.683	0.683	0.542	0.683	0.566	0.821	0.917	0.181	0.712
0.125	0.125	0.500	0.125	0.000	0.000	0.000	0.300	0.160
0.138	0.138	0.330	0.138	0.000	0.114	0.107	0.400	0.190
0.192	0.192	0.000	0.192	0.182	0.229	0.357	0.050	0.164
0.466	0.466	0.000	0.466	0.758	0.571	0.536	0.000	0.373

Table A.1, Continued.

Cimicifuga elata, EUNORR

0.000	0.000	0.000	0.000
0.279	0.250	0.600	0.400
0.000	0.000	0.000	0.000
0.000	0.000	0.200	0.000
0.302	0.250	0.200	0.200
0.000	0.000	0.000	0.000
0.520	0.539	0.480	0.424
0.000	0.000	0.000	0.000
0.000	0.039	0.000	0.030
0.280	0.231	0.280	0.182
0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000
0.250	0.000	0.000	0.063
0.000	0.000	1.000	0.500
0.750	1.000	0.000	0.438
4.000	5.000	5.000	2.500
0.000	0.000	0.000	0.000
0.000	1.000	0.000	0.500
1.000	0.000	0.000	0.000
0.000	0.000	1.000	0.000
0.000	0.000	0.000	0.000
1.000	0.435	0.810	0.769
0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000
0.000	0.565	0.191	0.231

Table A.1, Continued.

Cimicifuga elata, EUGRASS

0.000	0.000	0.000	0.000
0.615	1.000	0.875	0.667
0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000
0.154	0.000	0.000	0.000
0.000	0.000	0.000	0.000
0.529	0.621	0.677	0.738
0.000	0.000	0.029	0.000
0.000	0.138	0.029	0.048
0.382	0.138	0.088	0.071
0.000	0.000	0.000	0.000
0.500	0.833	1.000	1.000
0.000	0.000	0.000	0.000
0.500	0.167	0.000	0.000
0.000	0.000	0.000	0.000
5.000	8.000	0.600	4.000
0.000	0.000	0.600	0.000
0.000	0.000	0.000	0.000
0.000	1.000	0.200	1.000
1.000	0.000	0.200	0.000
0.000	0.000	0.000	0.000
1.000	0.688	0.750	1.000
0.000	0.063	0.000	0.000
0.000	0.000	0.125	0.000
0.000	0.250	0.125	0.000

Table A.1, Continued.

Cimicifuga elata, WIL032

0.000	0.000	0.000	0.000	0.000
0.588	0.600	0.833	0.250	0.667
0.050	0.200	0.000	0.000	0.000
0.063	0.000	0.000	0.250	0.000
0.042	0.000	0.167	0.000	0.000
0.000	0.000	0.000	0.000	0.000
0.561	0.579	0.588	0.476	0.611
0.078	0.000	0.118	0.238	0.000
0.145	0.368	0.118	0.048	0.056
0.043	0.053	0.059	0.000	0.000
0.000	0.000	0.000	0.000	0.000
0.256	0.333	0.667	0.000	0.111
0.111	0.333	0.000	0.000	0.222
0.289	0.000	0.333	0.500	0.111
0.150	0.333	0.000	0.250	0.000
0.251	0.273	0.129	0.231	0.423
0.075	0.000	0.065	0.154	0.077
0.075	0.000	0.065	0.154	0.077
0.721	0.909	0.710	0.615	0.769
0.067	0.046	0.129	0.039	0.000
0.000	0.000	0.000	0.000	0.000
0.393	0.286	0.500	0.286	0.500
0.098	0.143	0.000	0.000	0.250
0.339	0.429	0.250	0.429	0.250
0.170	0.143	0.250	0.286	0.000

Table A.1, Continued.

Haplopappus radiatus, 1-in

0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.222	0.125	0.075	0.020	0.138	0.229	0.370	0.172	0.047
0.000	0.000	0.075	0.002	0.034	0.000	0.000	0.035	0.007
0.000	0.104	0.050	0.011	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.609	0.340	0.381	0.244	0.500	0.545	0.689	0.532	0.686
0.185	0.107	0.127	0.232	0.152	0.287	0.126	0.177	0.144
0.000	0.369	0.079	0.244	0.130	0.069	0.126	0.044	0.052
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.247	0.095	0.233	0.040	0.210	0.109	0.103	0.150	0.151
0.584	0.121	0.233	0.475	0.400	0.709	0.451	0.591	0.454
0.045	0.724	0.100	0.337	0.250	0.136	0.422	0.181	0.319
2.342	7.765	11.270	2.074	0.719	1.174	0.387	3.570	0.000
0.195	0.000	0.170	0.000	0.172	0.148	0.040	0.064	0.070
0.537	0.000	0.390	0.315	0.266	0.426	0.133	0.419	0.298
0.159	0.882	0.189	0.630	0.484	0.391	0.813	0.454	0.570

Haplopappus radiatus, 1-out

0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.353	0.667	0.013	0.105	0.577	0.167	0.105	0.041
0.000	0.059	0.000	0.095	0.000	0.000	0.008	0.035	0.016
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.585	0.405	0.316	0.158	0.500	0.512	0.612	0.483	0.390
0.098	0.054	0.184	0.246	0.286	0.279	0.149	0.172	0.169
0.024	0.378	0.079	0.316	0.143	0.116	0.134	0.081	0.104
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.063	0.087	0.111	0.019	0.164	0.214	0.240	0.154	0.215
0.688	0.065	0.333	0.321	0.345	0.543	0.347	0.673	0.456
0.063	0.783	0.222	0.566	0.164	0.157	0.360	0.096	0.229
1.514	0.800	9.723	2.345	0.506	2.400	1.357	4.033	0.000
0.243	0.100	0.215	0.000	0.152	0.182	0.071	0.167	0.088
0.514	0.000	0.477	0.207	0.342	0.364	0.333	0.400	0.441
0.189	0.900	0.215	0.621	0.367	0.436	0.548	0.350	0.294

Table A.1, Continued.

Haplopappus radiatus, 2-in

0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.256	0.039	0.000	0.133	0.125	0.273	0.055	0.039
0.000	0.000	0.000	0.000	0.200	0.000	0.000	0.039	0.000
0.000	0.047	0.007	0.016	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.330	0.270	0.283	0.018	0.167	0.307	0.267	0.333	0.130
0.049	0.067	0.067	0.158	0.333	0.154	0.200	0.000	0.087
0.035	0.281	0.100	0.298	0.000	0.077	0.133	0.222	0.130
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.263	0.093	0.231	0.091	0.077	0.114	0.026	0.156	0.033
0.158	0.047	0.154	0.136	0.154	0.364	0.385	0.375	0.167
0.211	0.628	0.077	0.409	0.115	0.341	0.461	0.281	0.633
1.745	5.920	2.250	0.536	0.295	0.183	4.379	0.785	0.000
0.106	0.060	0.143	0.000	0.053	0.067	0.017	0.015	0.070
0.298	0.040	0.107	0.134	0.295	0.217	0.207	0.246	0.123
0.394	0.860	0.643	0.619	0.537	0.617	0.724	0.692	0.719

Haplopappus radiatus, 2-out

0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.250	0.368	0.385	0.000	0.750	0.000	0.286	0.053	0.226
0.000	0.132	0.000	0.000	0.125	0.000	0.286	0.007	0.007
0.000	0.000	0.000	0.000	0.000	0.333	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.443	0.167	0.195	0.158	0.154	0.316	0.154	0.200	0.200
0.043	0.139	0.024	0.193	0.154	0.105	0.308	0.000	0.000
0.000	0.292	0.073	0.140	0.154	0.053	0.231	0.200	0.200
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.333	0.091	0.200	0.067	0.138	0.095	0.000	0.077	0.077
0.083	0.227	0.200	0.467	0.241	0.286	0.615	0.539	0.539
0.000	0.409	0.160	0.267	0.172	0.381	0.231	0.039	0.039
1.707	36.000	0.735	0.552	0.097	0.368	13.591	1.667	1.667
0.387	0.000	0.449	0.035	0.097	0.158	0.045	0.133	0.133
0.200	0.000	0.143	0.207	0.258	0.263	0.454	0.800	0.800
0.013	1.000	0.265	0.414	0.323	0.421	0.409	0.067	0.067

Table A.1, Continued.

Haplopappus radiatus, 3-in

0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.111	0.000	0.444	0.000	0.305	0.187	0.154	0.130	0.163
0.022	0.000	0.111	0.000	0.017	0.031	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.430	0.188	0.581	0.344	0.450	0.482	0.471	0.500	0.486
0.056	0.200	0.065	0.203	0.275	0.071	0.157	0.075	0.114
0.028	0.400	0.129	0.219	0.025	0.054	0.098	0.000	0.029
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.230	0.068	0.353	0.029	0.143	0.175	0.105	0.207	0.059
0.333	0.182	0.294	0.529	0.738	0.550	0.263	0.379	0.265
0.035	0.591	0.353	0.265	0.071	0.162	0.526	0.069	0.500
0.235	1.800	0.963	1.035	0.517	2.294	0.958	0.745	0.000
0.177	0.000	0.256	0.193	0.133	0.059	0.042	0.098	0.000
0.353	0.100	0.232	0.175	0.617	0.412	0.208	0.392	0.000
0.177	0.800	0.488	0.632	0.200	0.412	0.625	0.255	0.933

Haplopappus radiatus, 3-out

0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.364	0.000	0.095	1.000	0.026	0.040	0.093	0.033
0.091	0.000	0.000	0.000	0.000	0.000	0.000	0.013	0.008
0.000	0.182	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.385	0.148	0.652	0.267	0.478	0.542	0.333	0.600	0.250
0.096	0.284	0.217	0.333	0.348	0.292	0.292	0.267	0.375
0.010	0.444	0.000	0.222	0.087	0.083	0.250	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.271	0.015	0.263	0.039	0.050	0.094	0.048	0.064	0.034
0.448	0.194	0.447	0.416	0.767	0.469	0.524	0.830	0.534
0.063	0.746	0.237	0.429	0.133	0.417	0.397	0.043	0.375
0.478	0.250	0.198	0.022	0.520	0.833	1.271	1.627	0.000
0.130	0.000	0.132	0.067	0.107	0.033	0.051	0.053	0.000
0.478	0.000	0.491	0.178	0.600	0.333	0.119	0.573	0.280
0.304	0.938	0.293	0.689	0.293	0.567	0.746	0.307	0.680

Table A.1, Continued.

Haplopappus radiatus, 4-in

0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.333	0.000	0.000	0.083	0.038	0.200	0.333	0.071
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.071
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.506	0.414	0.600	0.436	0.682	0.458	0.591	0.500	0.650
0.006	0.115	0.089	0.103	0.045	0.208	0.091	0.273	0.050
0.000	0.069	0.156	0.205	0.045	0.042	0.091	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.400	0.000	0.308	0.444	0.083	0.241	0.107	0.300	0.500
0.400	0.143	0.231	0.222	0.667	0.586	0.250	0.300	0.065
0.100	0.429	0.385	0.222	0.250	0.069	0.536	0.300	0.375
2.400	0.333	1.917	0.667	1.130	1.250	2.250	0.722	0.000
0.200	0.000	0.417	0.000	0.217	0.125	0.500	0.167	0.222
0.400	0.333	0.083	0.278	0.609	0.750	0.250	0.389	0.556
0.400	0.333	0.417	0.556	0.130	0.125	0.250	0.333	0.111

Haplopappus radiatus, 4-out

0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.455	0.600	0.000	0.125	0.200	0.217	0.235	0.048
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.575	0.391	0.796	0.455	0.707	0.500	0.513	0.588	0.548
0.035	0.065	0.020	0.152	0.098	0.148	0.282	0.177	0.065
0.009	0.217	0.082	0.091	0.049	0.074	0.000	0.000	0.032
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.385	0.077	0.500	0.300	0.364	0.444	0.600	0.250	0.263
0.385	0.154	0.100	0.400	0.364	0.278	0.133	0.550	0.263
0.000	0.462	0.400	0.200	0.091	0.167	0.200	0.000	0.053
1.571	2.500	0.393	1.067	0.833	5.750	2.125	4.000	0.000
0.429	0.000	0.429	0.200	0.500	0.250	0.000	0.200	0.000
0.286	0.500	0.250	0.400	0.417	0.250	0.750	0.400	0.500
0.000	0.500	0.250	0.200	0.000	0.250	0.250	0.400	0.500

Table A.1, Continued.

Haplopappus radiatus, 5-in

0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.306	0.000	0.306	0.000	1.000	0.000	0.188	0.286	0.667
0.009	0.000	0.009	0.000	0.000	0.000	0.062	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.440	0.556	0.857	0.619	0.500	0.182	0.250	0.800	0.846
0.020	0.000	0.000	0.143	0.357	0.182	0.250	0.200	0.000
0.000	0.111	0.095	0.095	0.143	0.000	0.000	0.000	0.077
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.222	0.000	0.076	0.000	0.200	0.000	0.000	0.333	0.000
0.000	0.000	0.342	0.000	0.400	0.571	0.375	0.333	0.714
0.000	0.333	0.392	1.000	0.400	0.000	0.500	0.222	0.286
0.250	0.000	0.500	0.250	0.200	2.286	7.000	0.750	0.000
0.000	0.000	0.500	0.000	0.400	0.143	0.000	0.000	0.000
0.500	0.000	0.250	0.500	0.000	0.286	1.000	0.750	0.250
0.250	0.000	0.250	0.500	0.600	0.143	0.000	0.250	0.500

Haplopappus radiatus, 5-out

0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.400	1.000	0.395	0.000	0.395	0.538	0.333	0.097
0.000	0.000	0.000	0.008	0.000	0.008	0.000	0.048	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.500	0.474	0.786	0.400	0.500	0.333	0.250	0.417	0.727
0.000	0.105	0.000	0.267	0.200	0.000	0.500	0.042	0.045
0.000	0.158	0.071	0.133	0.100	0.167	0.250	0.042	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.333	0.000	0.500	0.156	0.000	0.200	0.000	0.000	0.250
0.333	0.000	0.000	0.239	0.167	0.000	0.500	1.000	0.375
0.000	0.000	0.500	0.288	0.667	0.600	0.250	0.000	0.188
5.000	1.903	0.000	1.000	0.000	5.571	3.000	3.750	0.000
0.000	0.048	0.333	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.393	0.000	0.500	0.500	0.571	0.429	0.750	0.000
0.000	0.512	0.667	0.500	0.500	0.429	0.571	0.250	0.667

Table A.1, Continued.

Lomatium bradshawii, Rose Prairie 0

0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.203	0.133	0.000	0.000	0.091	0.500	0.155
0.017	0.200	0.000	0.250	0.000	0.000	0.078
0.017	0.000	0.000	0.000	0.091	0.000	0.018
0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.250	0.867	0.133	0.000	0.000	0.000	0.000
0.250	0.000	0.000	0.000	0.600	0.000	0.222
0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.100	0.111	0.000	0.429	0.000	0.182	0.000
0.600	0.444	0.700	0.143	0.222	0.818	0.304
0.200	0.333	0.100	0.286	0.556	0.000	0.304
0.000	0.000	0.000	0.000	0.222	0.000	0.000
0.091	1.572	0.032	0.416	0.128	0.162	0.000
0.000	0.000	0.000	0.000	0.000	0.071	0.000
0.400	0.125	0.250	0.250	0.125	0.500	0.000
0.600	0.563	0.250	0.375	0.625	0.286	0.750
0.000	0.250	0.167	0.250	0.250	0.071	0.000
1.780	4.123	1.118	0.957	3.941	1.639	0.000
0.000	0.000	0.000	0.000	0.000	0.167	0.000
0.200	0.000	0.000	0.000	0.000	0.333	0.000
0.600	0.500	0.667	0.750	0.333	0.333	0.000
0.200	0.500	0.333	0.250	0.667	0.000	0.000

Table A.1, Continued.

Lomatium bradshawii, Rose Prairie 1

0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.333	0.500	0.301	0.286	0.379	0.632	0.444
0.000	0.125	0.012	0.036	0.116	0.055	0.000
0.000	0.000	0.012	0.018	0.021	0.000	0.000
0.000	0.000	0.000	0.000	0.011	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.500	0.500	0.250	0.472	0.429	0.567	0.279
0.333	0.400	0.000	0.167	0.214	0.105	0.114
0.000	0.000	0.000	0.056	0.054	0.000	0.000
0.000	0.000	0.000	0.028	0.054	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.118	0.000	0.188	0.154	0.182	0.136	0.074
0.529	0.281	0.188	0.000	0.182	0.636	0.324
0.294	0.250	0.125	0.385	0.409	0.023	0.029
0.059	0.406	0.000	0.231	0.227	0.000	0.044
0.010	0.100	0.014	0.066	0.094	0.006	0.000
0.000	0.063	0.188	0.143	0.071	0.148	0.000
0.200	0.063	0.250	0.071	0.143	0.482	0.077
0.600	0.313	0.250	0.214	0.357	0.222	0.154
0.200	0.563	0.063	0.500	0.357	0.000	0.077
1.995	2.653	0.363	0.785	0.957	0.496	0.000
0.000	0.000	0.067	0.091	0.000	0.031	0.000
0.364	0.133	0.167	0.000	0.083	0.500	0.000
0.091	0.067	0.267	0.091	0.250	0.313	0.333
0.546	0.800	0.333	0.818	0.583	0.063	0.000

Table A.1, Continued.

Lomatium bradshawii, Rose Prairie 2

0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.313	0.542	0.141	0.447	0.244	0.469	0.000
0.125	0.125	0.000	0.000	0.089	0.021	0.000
0.000	0.083	0.000	0.000	0.022	0.000	0.000
0.063	0.000	0.000	0.000	0.022	0.010	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.833	0.154	0.154	0.448	0.320	0.217
0.500	0.000	0.000	0.231	0.172	0.120	0.022
0.500	0.000	0.077	0.154	0.035	0.040	0.000
0.000	0.167	0.000	0.000	0.035	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.091	0.000	0.000	0.000	0.136	0.200	0.175
0.636	0.421	0.273	0.286	0.273	0.600	0.175
0.182	0.105	0.182	0.286	0.364	0.000	0.048
0.091	0.211	0.000	0.143	0.182	0.050	0.032
0.061	0.060	0.000	0.175	0.032	0.014	0.000
0.000	0.000	0.000	0.000	0.100	0.044	0.000
0.333	0.333	0.500	0.231	0.000	0.391	0.286
0.333	0.000	0.250	0.308	0.500	0.391	0.000
0.333	0.667	0.000	0.308	0.400	0.000	0.143
2.529	1.293	0.283	0.914	0.767	0.576	0.000
0.000	0.000	0.071	0.000	0.000	0.125	0.250
0.200	0.071	0.071	0.000	0.071	0.438	0.000
0.000	0.143	0.571	0.000	0.571	0.188	0.250
0.800	0.714	0.214	0.667	0.357	0.125	0.000

Table A.1, Continued.

Lomatium bradshawii, Fisher Butte 0

0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.214	0.531	0.219	0.071	0.214	0.500	0.250
0.071	0.219	0.000	0.179	0.071	0.289	0.000
0.000	0.031	0.016	0.000	0.036	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.111	0.375	0.264	0.350	0.120	0.417	0.297
0.222	0.250	0.113	0.225	0.480	0.583	0.243
0.037	0.125	0.057	0.050	0.000	0.000	0.000
0.000	0.125	0.000	0.000	0.080	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.029	0.083	0.137	0.036	0.012	0.023	0.158
0.400	0.556	0.480	0.679	0.494	0.864	0.586
0.229	0.250	0.137	0.089	0.193	0.023	0.040
0.029	0.111	0.027	0.071	0.084	0.011	0.000
0.168	0.536	0.096	0.226	0.145	1.576	0.154
0.000	0.000	0.081	0.107	0.000	0.000	0.095
0.158	0.143	0.324	0.393	0.136	0.804	0.524
0.526	0.429	0.297	0.321	0.546	0.196	0.191
0.105	0.429	0.189	0.071	0.182	0.000	0.095
1.332	4.212	0.492	3.104	10.946	8.013	0.383
0.000	0.000	0.080	0.000	0.000	0.000	0.056
0.235	0.000	0.160	0.250	0.077	0.526	0.278
0.471	0.250	0.320	0.188	0.231	0.263	0.222
0.235	0.750	0.320	0.438	0.539	0.158	0.389

Table A.1, Continued.

Lomatium bradshawii, Fisher Butte 1

0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.737	0.296	0.471	0.357	0.100	0.539	0.000
0.105	0.370	0.059	0.143	0.600	0.192	0.000
0.000	0.037	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.029	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.410	0.647	0.571	0.539	0.200	0.467	0.341
0.333	0.147	0.179	0.256	0.525	0.533	0.159
0.051	0.118	0.000	0.077	0.050	0.000	0.023
0.000	0.029	0.000	0.000	0.025	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.179	0.106	0.225	0.129	0.023	0.054	0.100
0.643	0.277	0.275	0.323	0.442	0.794	0.536
0.071	0.255	0.125	0.323	0.256	0.054	0.064
0.107	0.277	0.100	0.097	0.116	0.033	0.073
0.057	0.697	0.183	0.982	1.088	0.178	0.183
0.125	0.091	0.042	0.136	0.000	0.000	0.042
0.375	0.000	0.417	0.273	0.103	0.677	0.167
0.250	0.364	0.333	0.273	0.172	0.226	0.333
0.125	0.546	0.083	0.182	0.724	0.000	0.375
0.873	5.770	1.435	7.190	9.199	3.589	1.542
0.000	0.000	0.111	0.000	0.000	0.000	0.000
0.158	0.000	0.083	0.111	0.111	0.522	0.194
0.211	0.000	0.333	0.111	0.222	0.217	0.161
0.632	0.941	0.361	0.500	0.611	0.217	0.290

Table A.1, Continued.

Lomatium bradshawii, Fisher Butte 2

0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.444	0.360	0.520	0.500	0.111	0.136	0.000
0.074	0.220	0.040	0.100	0.333	0.455	0.000
0.037	0.000	0.040	0.000	0.000	0.000	0.000
0.000	0.020	0.000	0.000	0.037	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.360	0.148	0.217	0.212	0.133	0.091	0.115
0.360	0.444	0.087	0.546	0.267	0.636	0.481
0.040	0.037	0.174	0.091	0.000	0.000	0.019
0.000	0.074	0.044	0.030	0.200	0.000	0.019
0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.091	0.074	0.234	0.000	0.060	0.015	0.044
0.546	0.426	0.297	0.852	0.434	0.687	0.483
0.182	0.185	0.188	0.074	0.253	0.060	0.044
0.091	0.204	0.047	0.037	0.060	0.000	0.105
0.037	0.178	0.112	1.115	0.654	0.029	0.000
0.143	0.000	0.083	0.030	0.000	0.028	0.000
0.000	0.063	0.167	0.394	0.000	0.694	0.063
0.429	0.500	0.417	0.333	0.333	0.167	0.250
0.429	0.375	0.083	0.242	0.583	0.000	0.313
4.755	5.210	1.825	10.132	6.819	3.486	0.000
0.050	0.000	0.000	0.000	0.000	0.023	0.000
0.100	0.000	0.051	0.120	0.000	0.318	0.250
0.100	0.000	0.359	0.200	0.179	0.364	0.083
0.750	0.909	0.462	0.600	0.714	0.136	0.250

Table A.1, Continued.

Lomatium bradshawii, Long Tom

0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.750	0.000	0.231	0.474	0.232	0.486	0.082
0.250	0.143	0.128	0.158	0.048	0.029	0.197
0.000	0.000	0.103	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.214	0.294	0.100	0.375	0.395	0.314	0.286
0.071	0.294	0.500	0.375	0.116	0.198	0.071
0.071	0.235	0.300	0.000	0.023	0.012	0.000
0.000	0.118	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.163	0.039	0.056	0.054	0.257	0.130	0.051
0.286	0.269	0.278	0.378	0.270	0.348	0.254
0.163	0.269	0.306	0.135	0.122	0.116	0.119
0.122	0.231	0.222	0.000	0.054	0.000	0.085
0.009	0.194	0.254	0.088	0.257	0.144	0.452
0.033	0.000	0.000	0.073	0.091	0.167	0.065
0.200	0.071	0.026	0.342	0.091	0.000	0.097
0.433	0.464	0.342	0.293	0.273	0.417	0.097
0.233	0.464	0.553	0.146	0.205	0.042	0.161
0.256	2.019	1.633	1.677	1.146	2.557	2.442
0.063	0.000	0.000	0.046	0.177	0.000	0.111
0.250	0.056	0.051	0.292	0.118	0.143	0.111
0.375	0.167	0.180	0.369	0.118	0.333	0.111
0.313	0.722	0.744	0.169	0.471	0.333	0.111

Table A.1, Continued.

Lomatium cookii, Middle

0.000	0.000	0.000	0.000	0.000
0.312	0.540	0.644	0.650	0.866
0.250	0.238	0.092	0.200	0.036
0.031	0.000	0.000	0.000	0.000
0.000	0.016	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000
0.200	0.217	0.581	0.453	0.581
0.280	0.478	0.326	0.442	0.156
0.040	0.000	0.023	0.000	0.000
0.040	0.000	0.000	0.000	0.000
0.000	0.043	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000
0.066	0.064	0.033	0.066	0.228
0.311	0.532	0.633	0.566	0.551
0.164	0.106	0.167	0.250	0.125
0.098	0.043	0.117	0.092	0.015
0.066	0.021	0.017	0.013	0.000
0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.03125	0.026
0.062	0.080	0.235	0.063	0.211
0.219	0.280	0.765	0.313	0.553
0.375	0.320	0.000	0.438	0.158
0.125	0.200	0.000	0.063	0.026
1.000	2.900	0.244	0.301	0.196
0.000	0.000	0.000	0.000	0.095
0.000	0.000	0.067	0.029	0.143
0.294	0.083	0.200	0.171	0.310
0.235	0.250	0.500	0.514	0.357
0.235	0.375	0.167	0.229	0.024
2.900	8.400	0.722	0.888	0.577
0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.043
0.000	0.000	0.071	0.059	0.174
0.000	0.154	0.464	0.176	0.435
0.990	0.769	0.393	0.706	0.304

Table A.1, Continued.

Lomatium cookii, South

0.000	0.000	0.000	0.000	0.000
0.382	0.750	0.426	0.294	0.603
0.182	0.125	0.115	0.157	0.032
0.000	0.000	0.000	0.000	0.016
0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000
0.160	0.185	0.405	0.464	0.321
0.400	0.481	0.230	0.232	0.262
0.000	0.000	0.014	0.043	0.024
0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000
0.038	0.025	0.200	0.288	0.057
0.212	0.550	0.540	0.356	0.434
0.192	0.175	0.040	0.034	0.132
0.135	0.100	0.040	0.034	0.000
0.000	0.000	0.020	0.034	0.000
0.000	0.00	0.000	0.000	0.000
0.000	0.000	0.000	0.167	0.111
0.000	0.154	0.154	0.167	0.333
0.222	0.231	0.000	0.000	0.111
0.333	0.308	0.385	0.500	0.000
0.000	0.154	0.000	0.000	0.000
1.40	1.90	0.252	0.344	0.445
0.000	0.000	0.000	0.000	0.333
0.000	0.000	0.231	0.167	0.000
0.000	0.231	0.077	0.167	0.111
0.250	0.231	0.231	0.250	0.111
0.125	0.462	0.154	0.167	0.111
8.80	12.00	1.567	2.139	2.765
0.000	0.000	0.000	0.143	0.000
0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.083	0.143	0.400
0.000	0.000	0.167	0.000	0.000
0.990	0.990	0.333	0.143	0.200