

## LOOKING BACKWARDS: ASSESSING THE PROJECTIONS OF A TRANSITION MATRIX MODEL

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**Abstract.** Analyses of population projection models are increasingly being used by conservation biologists and land managers to assess the health of sensitive species and to evaluate the likely effects of management strategies, harvesting, grazing, or other manipulations. Here I describe some of the limitations of this approach and illustrate how these limitations may affect its usefulness. I do this by comparing the results of such an analysis, performed in 1979 on two populations of a perennial plant, *Arisaema triphyllum*, with new information about the size and structure of these same populations gathered in 1994, 15 years later. While one population changed as the model projected it would, the other behaved quite differently from the projection. Instead of increasing in size, this population decreased between 1979 and 1994.

Possible shortcomings in the data and in the model include: too few plants to provide accurate transition probabilities; too few years to capture accurately the complete range of year-to-year environmental variability; and the failure of the most commonly used form of the model to account for density-dependent vital rates. In addition, the asymptotic growth rates ( $\lambda$ ) these models yield may sometimes be irrelevant and even misleading if one's primary interest is in a population's short-term prospects for survival, as is often the case in studies of sensitive species. These shortcomings may apply to many studies involving the use of projection models, and they have important implications for the value of this approach in conservation biology and species management decisions.

**Key words:** *Arisaema*; *bootstrapping*; *conservation*; *demography*; *management*; *transition matrix*.

### INTRODUCTION

Population projection matrix models, also known as transition matrix models, were introduced to biologists by Leslie (1945) and Lefkovitch (1965). They were first applied to data from natural populations of animals in the 1960s (e.g., Pennycuik et al. 1968) and to plant populations in the 1970s (Hartshorn 1975, Werner and Caswell 1977, Caswell and Werner 1978, Enright and Ogden 1979). These studies and others (e.g., Bierzychudek 1982, Meagher 1982, Fiedler 1987, Huenneke and Marks 1987, Lasker 1990, McFadden 1991, Byers and Meagher 1997) used matrix models to assess the fitness consequences of alternative life history strategies. Others have used projection models to document spatial and temporal variation in a species' vital rates (e.g., Gregg 1991, Horvitz and Schemske 1995, Oostermeijer et al. 1996, Kephart and Paladino 1997, Vavrek et al. 1997).

In the last 10 yr, as interest in applied ecology and conservation biology has grown, matrix models have begun to be used in additional ways. Since repeated iterations of a matrix can result in a projection of a population's equilibrium growth rate (under certain assumptions), projection matrices can provide a measure of the health of populations of rare species (Menges

1986, 1990, Waite 1989, Charron and Gagnon 1991, Aplet et al. 1994, Doak et al. 1994, Price and Kelly 1994, Oostermeijer et al. 1996, Kephart and Paladino 1997). Matrix models have been used to assess the likely effects on population growth rates of various management strategies (Crouse et al. 1987, Waite and Hutchings 1991, Aplet et al. 1994, Doak et al. 1994, Smith and Trout 1994, Maschinski et al. 1997, Shea and Kelly 1998) or of natural or anthropogenic disturbances like fire, grazing, or harvesting (de Kroon et al. 1987, Silva et al. 1991, Nault and Gagnon 1993, O'Connor 1993, Pinard 1993, Bullock et al. 1994, Kaye et al. 1994, Moloney et al. 1994, Bastrenta et al. 1995, Olmstead and Alvarez-Buylla 1995, West 1995, Ratsirarson et al. 1996, Batista et al. 1998). Sensitivity or elasticity analyses of these models can identify the life history stages most critical to a rare species' persistence or most in need of additional study (Menges 1986, Crouse et al. 1987, Aplet et al. 1994, Doak et al. 1994, Ginsberg and Milner-Gulland 1994, Schemske et al. 1994, Hitchcock and Gratto-Trevor 1997, Crooks et al. 1998). For this reason, several papers have appeared urging resource managers to employ these models when making management decisions about the conservation of rare species (e.g., Menges 1986, Waite and Hutchings 1991, Schemske et al. 1994).

The enthusiasm with which these models are currently being embraced, however, is sometimes insufficiently tempered by a recognition of their limitations.

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The population growth rate ( $\lambda$ ) that can be calculated from demographic data using a projection matrix is an asymptotic growth rate, i.e., the growth rate that would result, eventually, if the population's observed vital rates were to be maintained indefinitely. For that reason projection matrix analyses are subject to several important limitations. First, deterministic and stochastic changes in a population's environment make it very unlikely that the vital rates measured for a population will in fact remain constant over time. Caswell (1989) emphasizes that for this reason, matrix analyses should be regarded as projections (what *would* happen to a population if vital rates remain unchanged) rather than as forecasts (what *will* happen to a population).

Secondly, applied ecologists and conservation biologists in particular are often forced to be most intensely interested not in a small population's asymptotic, long-term behavior, but rather in whether it can survive into the immediate future—its transient behavior (Menges 1986). A population's short-term, transient behavior may be quite different from its asymptotic behavior. This is because, unlike asymptotic rates, short-term growth rates can be very strongly influenced by a population's current age or size distribution (Caswell and Werner 1978, Caswell 1989, Burgman et al. 1993). A population that is far from its stable size distribution may behave over the short term very differently from the asymptotic projection.

Thirdly, the form of projection matrix model most commonly used assumes that a population's vital rates are independent of population density. In many cases this assumption is appropriate for the size of the population at the time of the study. But any population with a growth rate  $>1.0$  is expected to increase in density and may eventually reach a population size at which density does begin to exert an influence on its birth and death rates.

I present here a vivid example of the ways some of these limitations can exert their influence. The data come from a re-census of two populations of *Arisaema triphyllum*, jack-in-the-pulpit, that I studied between 1977 and 1979. That study (Bierzychudek 1982) used a transition matrix approach to project asymptotic growth rates for this herbaceous perennial of the forest understory. Here I compare the projections and conclusions of Bierzychudek (1982), as well as the results of a new transient analysis of those same data, with the states of these two populations 15 yr later.

#### METHODS

##### *Transition matrix analysis*

A projection matrix model specifies a matrix of transition probabilities between different size classes, age classes, or stages in a population from time  $t$  to time  $t + 1$ . These transition probabilities represent observed values of survival, growth, and reproduction (see Bierzychudek 1982, Menges 1986, Groenendaal et al. 1988,

Caswell 1989, and Horvitz and Schemske 1995 for more detailed explanations). When multiplied by a column vector whose values represent the numbers of individuals in each class at time  $t$ , the matrix projects the expected number of individuals in each class at time  $t + 1$ . When the matrix is multiplied by the original population vector a sufficient number of times, the population eventually converges to a "stable distribution," at which time each size or age class is changing by the factor  $\lambda$  each time period.  $\lambda$  is the population's asymptotic rate of growth. When  $\lambda$  exceeds 1.0 the population is projected to increase over time; when  $\lambda$  is  $<1.0$  the population is projected to decline. A population's  $\lambda$  and its stable distribution are independent of the original column vector and depend only on the values in the matrix. In the terminology of linear algebra,  $\lambda$  is the dominant eigenvalue of the matrix, and the stable distribution is its right eigenvector.

The analysis in Bierzychudek (1982) was based on 3 yr of demographic data (and thus two different "transition periods") from two populations of *A. triphyllum* growing near Ithaca, New York: Fall Creek and Brooktondale. In that paper I projected the long-term (asymptotic) population growth rates,  $\lambda$ , of these two populations, creating separate matrices for each of the 1977–1978 and the 1978–1979 transition periods. I incorporated environmental stochasticity into these projections by assuming that the transition matrices from these two intervals represented a "good" and a "bad" year, and that in the future such years would occur randomly and independently, each with an expected frequency of 0.5. A stochastic simulation of this process converges to the same result as that obtained from using the average of the two individual matrices (Cohen 1977 and *personal communication*). For that reason, I also determined the value of  $\lambda$  associated with the average of the two matrices. Finally, I calculated the stable size distribution that each of these populations would be expected to eventually attain, if their vital rates remained unchanged from those I measured (see Bierzychudek 1982).

Since 1982, two improvements on the method of projection matrix analysis have been introduced, and I chose to incorporate these improvements into my analysis before comparing its results with the 1994 status of these two populations. First, Caswell (1989) pointed out that, except in cases where seeds spend a dormant year before germinating, there should not be a separate "seed" category in the analysis. (Plants that flower in year  $n$  have produced seedlings, not seeds, in year  $n + 1$ .) Since there is no evidence that *A. triphyllum* seeds spend a year in enforced dormancy, I have redone my original analysis with the seed category removed. Unlike Caswell's (1989) case, where correcting this error made a substantive difference in the value of  $\lambda$  generated by the analysis, in my case it made virtually no difference.

*Bootstrapping to calculate confidence limits*

In addition, in 1982 no one had yet attempted to place confidence limits on the value of  $\lambda$  generated by a projection matrix analysis. Lande's (1988) analysis of spotted owl demography was the first to place confidence limits on  $\lambda$ ; he did this by using an analytical approach that made rather restrictive assumptions about the sampling distributions of the parameters in the matrix. Caswell (1989) described methods for both analytical and resampling approaches to setting confidence limits on  $\lambda$ ; resampling approaches are less constrained by assumptions about parameter distributions.

All these procedures were reviewed by Alvarez-Buylla and Slatkin (1991), who emphasized, however, that resampling methods like jackknife and bootstrap approaches could not be applied to most long-lived organisms, because they required that all the demographic data be obtained from a single cohort of individuals. It is typical, when studying long-lived organisms, to use several different subsets of the population to estimate the different parameters (e.g., seedling survival, adult survival, seed dormancy) in a matrix. By 1993, McPeck and Kalisz had introduced a bootstrapping approach to setting confidence limits on  $\lambda$  that could be used even when different demographic parameters were estimated using different subsets of the population.

I have adopted McPeck and Kalisz's (1993) methodology to place confidence limits on my original estimates of  $\lambda$ . In this procedure, I used one resampling protocol to obtain bootstrapped seed germination rates, a second resampling protocol to obtain bootstrapped transition probabilities for the subsampled plants (see Sampling methods), and a third resampling protocol to obtain the seed production values and transition probabilities for the rest of the population. I originally estimated seed germination rates from seeds planted in only one year at only one of the two sites, and used this information as the base population for the resampling protocol in both years and at both sites. Similarly, the small, nonflowering plants were only subsampled (at both sites) from 1978 to 1979, not in the previous year; these subsamples were used as the base population for the resampling protocol for both of the transition periods. Finally, because I no longer have records of the individual data values that yielded observed rates of clonal reproduction at the two sites, I was unable to bootstrap these values, and instead inserted the mean clonal reproduction rate for each population into the appropriate positions in the matrices.

The bootstrapping procedure for each population involved generating a resampled 1977–1978 matrix, then a resampled 1978–1979 matrix, computing the element-by-element average of these two matrices, and calculating its  $\lambda$ . I repeated this process 1000 times. This data set was then used to compute a bias-corrected

estimate of  $\lambda$  and to determine 95% and 99% confidence limits using the percentile method (Caswell 1989, McPeck and Kalisz 1993). For a very clear explanation of these procedures, see McPeck and Kalisz (1993). (However, note that there is an error on page 248 of their article; the upper bound of the confidence interval should be  $1 - (\alpha/2)$ , not  $(1 - \alpha)/2$ .) These and all the other analyses presented here were performed using MATLAB (MathWorks, Incorporated).

*Sampling methods*

In late May of 1994, 15 yr after completing my original study, I returned to these two populations to measure their 1994 sizes and size distributions. Descriptions of these sites and of their vegetation can be found in Bierzychudek (1982). The areas around these sites have been undisturbed by development, and neither site has experienced any visually obvious environmental changes.

In the original census, I recorded plants as members of one of six size classes, based on the area of their leaf surface (which remains static during the growing season). These were classes 2 through 7 in the projection matrices. Size class 1 comprised seeds. In the original study, I individually tagged and numbered all plants large enough to flower and subsampled the more abundant nonreproductive plants (mostly members of size class 2) using 10 randomly located 1-m<sup>2</sup> quadrats.

For consistency, I used the same census technique in the current study. I recorded the leaf area (size) of all flowering plants, and subsampled nonflowering plants using 10 randomly placed 1-m<sup>2</sup> quadrats. Consistent with the reanalysis that removed the seed class, I have ignored seeds, and all references to "totals" mean total *plants* (not including seeds). To facilitate comparison with Bierzychudek (1982), I continue to refer to size classes 2–7 (rather than 1–6); however, class 1 (the former seed category) no longer exists.

The short-term nature of the 1994 census necessitated some adjustments in the data for the following reason: this census was accomplished in the course of a few days' visit, rather than over the entire flowering period. At each site there is a window of about 4 wk within which plants emerge from the ground, expand their leaves, and come into bloom. The Brooktondale population typically emerges earlier than the Fall Creek population (P. Bierzychudek, *unpublished data*). My census took place at the optimal time for Brooktondale, when leaves were fully expanded. However, this was a week or two before the optimal time for Fall Creek. While most of the population had appeared above ground, many plants had not completely expanded their leaves, making my size measures underestimates of these plants' true sizes. Since in the original study I measured some plants at this stage, as well as after complete leaf expansion, I used these data to correct this underestimate. In the repeated-measure data set the fully expanded leaf areas averaged 1.28 times the par-

tially expanded leaf areas ( $N = 20$ ,  $r^2 = 0.901$ ,  $F_{1,19} = 173$ ,  $P = 0.0001$  using the General Linear Models (GLM) procedure in SAS and suppressing the  $y$  intercept to assure that  $y = 0$  when  $x = 0$ ). Therefore, I multiplied all the Fall Creek plant areas by 1.28 before proceeding with further analysis. This estimation process may have led me to classify some individuals into the wrong size class; however, it will become clear that the conclusions of my analysis are not materially affected by such potential misclassifications.

In 1979, at the end of the study reported in Bierzychudek (1982), I destructively sampled between 2% and 3% of each population, in order to determine the relationship between corm mass and leaf area. This means that the populations that have subsequently been developing over the last 15 yr started from a size vector different from the one at the endpoint of the analysis in Bierzychudek (1982). The analysis presented here is based on the states of the populations after destructive sampling in 1979.

#### *The asymptotic analysis*

To determine whether the 1994 populations had achieved the population sizes projected by Bierzychudek (1982), I used census data from 1979 and 1994 to calculate the average annual rate of increase of each of the two populations over the period 1979 to 1994. I compared this value with the estimate of  $\lambda$  from the bootstrap analysis, and determined whether the observed rate of increase lay within the 95% confidence limits generated by that analysis. As in Bierzychudek (1982), I quantified differences between observed size distributions and projected stable distributions as Keyfitz's index of dissimilarity, the sum of the positive differences between the percentages of individuals in the observed and stable distributions (Keyfitz 1977). The projected stable distributions were calculated as the right eigenvectors of the average matrices for the base populations.

#### *Short-term (transient) population behavior*

Lambda ( $\lambda$ ) is the rate at which a population is expected to grow once it has achieved a stable size or age distribution. But if a population has not achieved a stable size or age distribution, it will not grow at the rate  $\lambda$ . Instead, the actual population growth rate from one year to the next will be influenced both by the vital rates in the transition matrix and, quite importantly, by the current distribution of individuals among size or age categories. Depending on that distribution, it is even possible for a population to have a  $\lambda$  that exceeds 1.0 but that nevertheless decreases in total population size for one or more years. For this reason, I investigated whether a transient analysis might provide a more accurate prediction of these populations' 1994 states.

There are several ways to perform a transient analysis (see Caswell 1989). I use a simple projection method here, using each site's 1977–1978 and 1978–1979

TABLE 1. Population growth rates for both populations of *Arisaema triphyllum* calculated from observed population totals in 1979 and 1994, as well as values of  $\lambda$  generated by the projection matrix analysis, bootstrapped estimates of  $\lambda$ , and their 95% and 99% confidence limits.

Parameter	Fall Creek	Brooktondale
Actual growth rate, 1979–1994	0.8892	0.9375
$\lambda$ (by standard analysis)	1.2904	0.8973
Bootstrapped $\lambda$	1.2900	0.8934
95% confidence limits	1.2287–1.3570	0.8331–0.9635
99% confidence limits	1.2111–1.3748	0.8029–0.9782

bootstrapped matrices. This analysis does not make any assumptions about whether the population's structure has reached stability, and does not assume that the population is growing at the rate  $\lambda$ , although it uses the same matrices of transition probabilities that generated  $\lambda$  in the asymptotic analysis. It takes as its starting point the population structure present after destructive sampling in 1979.

I simulated 15 yr of population change in the following way. The bootstrap analysis generated 1000 matrices using the 1977–1978 transition data, and another 1000 matrices using the 1978–1979 data. For each of 15 yr, I chose one matrix at random (with replacement) from either the 1977–1978 set or the 1978–1979 set, choosing from each set with a probability of 0.5. I postmultiplied this matrix by the previous year's population vector to project the population into the next year. I repeated this 15-yr simulation 1000 times, and present means and 95% confidence intervals, determined by the percentile method for the projected total population size, and for the number of individuals in each size class in 1994.

## RESULTS

### *Asymptotic analysis*

My reworked analysis (as well as the original one) projected that, once the Fall Creek population of 4166 plants reached a stable size distribution, it would increase by a factor ( $\lambda$ ) of 1.29/yr (Table 1 and Bierzychudek 1982: Table 5). A population of 4166 individuals growing at this rate for 15 yr would be expected to reach nearly 190 000 individuals by 1994 (Table 2A). This is not what occurred over this time period. Not only did the Fall Creek population not increase at this rate, it actually decreased. Its observed growth rate was only 0.89 over this 15-yr period, which resulted in a 1994 population of only  $\sim 700$  individuals (Tables 1, 2A). The 95% confidence limits on the bootstrapped estimate of  $\lambda$  range from 1.23 to 1.36; the 99% confidence limits range from 1.21 to 1.37. The observed growth rate of 0.89 is well outside the range of even the 99% confidence limits, and thus is clearly different from the projected outcome (Table 1).

At Brooktondale, my reworked analysis (and the

TABLE 2. Observed size distributions of *Arisaema triphyllum* at Fall Creek and Brooktondale (New York) in 1979 and in 1994, and results of the asymptotic and transient projections.

Population and size class	Observed 1979 vector	Observed 1994 vector	Asymptotic projection for 1994	Transient projection for 1994	95% confidence intervals for transient projection
A) Fall Creek					
Class 2	3480	492	161 809	123 470	95 675–158 210
Class 3	554	175	19 372	14 770	7967–23 391
Class 4	90	20	5508	4400	1235–9225
Class 5	11	14	760	450	173–1025
Class 6	11	7	760	120	53–254
Class 7	20	10	1519	490	283–791
Total	4166	716	189 917	143 700	105 386–192 896
B) Brooktondale					
Class 2	2980	1267	349	141	76–244
Class 3	630	115	199	80	31–155
Class 4	44	9	38	7	4–12
Class 5	16	5	22	3	1–5
Class 6	22	4	23	4	2–6
Class 7	12	6	14	6	4–9
Total	3704	1406	645	241	118–431

Note: The asymptotic projection gives the expected stable size distribution; the transient projection gives the result of a 15-year stochastic simulation that does not assume that a stable size distribution has been attained. The 95% confidence intervals for the transient projection are based on 1000 runs, using the percentile method.

original) projected that the population of ~4000 plants would decline at an annual rate of 0.89 (Table 1 and Bierzychudek 1982: Table 5), reaching ~650 individuals by 1994 (Table 2B). This population has indeed declined, though at a somewhat slower rate than the one projected, 0.94 rather than 0.89. The 95% confidence limits on the bootstrapped estimate of  $\lambda$  range from 0.83 to 0.96; the 99% confidence limits range from 0.80 to 0.98. The observed growth rate of 0.89 is well within even the 95% confidence limits, and thus is not clearly different from the projected outcome (Table 1).

By 1994, neither population displayed the stable size

distribution associated with the average transition matrix for its site. In fact, by 1994, both populations were further away from their projected stable size distributions than they had been 15 yr earlier (Table 3). In 1979, the Fall Creek population had a size distribution that was quite similar to its projected stable size distribution (only 2.9% of the plants were in the “wrong” category, see Table 3), but it had diverged from that projected stable size distribution by 1994. The Brooktondale population was already quite different from its projected stable size distribution in 1979 (with 26.4% of the population in the wrong category), and was even further away from this projection by 1994.

#### Short-term (transient) population behavior

Since neither of these two populations displays a stable size distribution, we might expect that the transient analysis would provide a better fit to the observed 1994 data. However, this did not turn out to be the case.

Between 1979 and 1994, the Fall Creek population changed in a way that was radically different from what had been projected from the asymptotic analysis. The transient analysis was no better at forecasting how this population actually behaved over this 15-yr interval (Table 2A). Like the asymptotic analysis, the transient analysis projected a much higher rate of growth than what was actually observed. In fact, as was the case with the asymptotic projection, the actual population in 1994 lay well outside the 95% confidence limits for the transient analysis (Table 2A).

There are relatively minor differences (see Table 2A) between the size distribution projected for 1994 by the transient analysis and the one projected by the asymptotic

TABLE 3. Observed size distributions in 1979 and 1994, and projected stable size distributions, expressed as percentages, for Fall Creek and Brooktondale populations of *A. triphyllum*.

Size	Fall Creek			Brooktondale		
	1979	Stable distribution	1994	1979	Stable distribution	1994
Class 2	83.5	85.2	68.7	80.5	54.1	90.1
Class 3	13.3	10.2	24.4	17.0	30.8	8.2
Class 4	2.2	2.9	2.8	1.2	5.9	0.6
Class 5	0.3	0.4	2.0	0.4	3.4	0.4
Class 6	0.3	0.4	1.0	0.6	3.6	0.3
Class 7	0.5	0.8	1.4	0.3	2.2	0.4
$\Delta$	2.9		17.0	26.8		35.9

Notes: Size classes are as described in *Methods: sampling methods*. Stable size distributions are the right eigenvalues of the actual (not bootstrapped) average matrix for each site.  $\Delta$  is Keyfitz's index of dissimilarity between observed and stable distributions for each population (the sum of the positive differences between the stable and observed distributions).

otic analysis. Since the main difference between these two approaches is in the influence of the population's initial size distribution, and since the 1979 size distribution at Fall Creek was very close to a stable size distribution (Table 3), this is not unexpected.

The growth rate of the Brooktondale population between 1979 and 1994, while not as low as the bootstrapped asymptotic estimate of  $\lambda$ , was within the 95% confidence limits for that estimate. The projection from the transient analysis, on the other hand, did not provide even this good a match (Table 2B). What actually occurred between 1979 and 1994 was well outside the 95% confidence limits of the transient projection; the Brooktondale population did not grow as slowly as that projection forecast it would.

Since the Brooktondale population was quite far from its stable size distribution, it is not surprising that there should be a relatively large difference between the asymptotic and transient projections (Table 2B).

#### DISCUSSION

The asymptotic analysis, which is the standard tool used for many demographic analyses, provided a reasonable forecast only for the Brooktondale population. For Fall Creek, this asymptotic projection was not borne out, either in magnitude or in the direction of the forecast change. Instead of increasing, this population has decreased. The transient analysis, a less frequently used tool, did not provide an accurate forecast for either of these two populations; in each case the observed population behavior lay outside the 95% confidence limits of the projection. The kinds of departures from the projections that were observed in this study provide some clues about why they did not adequately represent these populations' behavior.

It is telling that the transient projections were not more successful at forecasting the behavior of these populations. The major difference between this analysis and the asymptotic analysis is the heavy dependence of the transient analysis on the population's initial size distribution. If our analysis failed to provide an accurate forecast principally because the populations had not reached stable size distributions, we would expect the transient analysis to provide an improved forecast. Since it did not, we should look to other sources to explain the observed lack of fit.

The use of  $\lambda$  to project a population's rate of growth, as is typically done in transition matrix analyses, relies on the assumption that the population's vital rates have been accurately measured during the period of the study and will not change in the future. There are several (nonmutually exclusive) reasons why this assumption may be incorrect. These flaws probably apply not only to the present study, but to many of the other matrix projection studies that have been performed over the last 20 yr.

First, the numbers of individuals involved in a study may not be large enough to provide accurate estimates

of the probabilities of transition for the various life stages involved. In this study, each of the two populations studied comprised between 1000 and 4000 individuals, distributed among six size classes. In the absence of other knowledge (such as the results of the present study), one might expect sample sizes like these to provide reasonably accurate estimates of transition probabilities, at least for the 1977–1979 period. However, it is likely that they did not, particularly for the larger size classes, which are represented by tens rather than thousands of individuals. And it is not uncommon to read of studies where the entire sampled population consisted of fewer than 100 individuals, divided among four or more size classes. As the number of individuals per size class decreases, the accuracy of the transition probability's estimate decreases as well. This problem is likely to be most pronounced in studies of rare species, where sample sizes are unavoidably small.

It is for this reason that it is important to report confidence limits on parameter estimates like  $\lambda$ . Unfortunately, commercially available software like RAMAS/stage (Ferson 1990), which is being widely adopted by both academic biologists and land managers interested in demographic analysis, does not generate confidence limits. To do so requires computer algorithms that are tailored to an individual data set. Such algorithms can be relatively easily written using MATLAB or several other programs.

A second consideration is that one, two, or even three transitions may not be enough time to accurately sample the range of environmental variability experienced by a population. The current study amply demonstrates this problem. *A. triphyllum* is a plant of mature forest, which is not the kind of habitat typically thought of as highly temporally variable. In addition, these two sites were chosen precisely because of their protection from habitat destruction and other external threats. Finally, Bierzychudek (1982) attempted to capture some of the inevitable environmental variability by observing the populations over two transition periods rather than one. Nevertheless, the behavior of one of these two populations has been very different from that projected by the model.

The implication is that a population's vital rates can be expected to vary significantly between years, even if it lives in a relatively stable environment, and that three years is not enough time to assess this variation. Though few studies have gathered data over more than three years (for exceptions see Meagher 1982, Pinerio et al. 1984, Enright and Watson 1991, 1992, Waite and Hutchings 1991, Bengtsson 1993, Svensson et al. 1993, Horvitz and Schemske 1995, Lesica and Shelly 1995, Oostermeijer et al. 1996), those that did have typically revealed more temporal variation in vital rates than have studies of shorter duration (Enright and Watson 1991). Huenneke and Marks (1987) point out that a population's distance from its stable distribution can provide an important clue about how well the values

in a transition matrix have captured past environmental variability. In this study, the fact that over the last 15 yr these populations have moved farther away from their supposed stable distributions implies that their vital rates have probably been changing.

Finally, another reason that projections might be inaccurate is because most of them fail to account for density-dependent effects. Most matrix model analyses are density independent (for some exceptions see de Kroon et al. 1987, Solbrig et al. 1988, Gillman et al. 1993, Alvarez-Buylla 1994, and Escos et al. 1994). Ignoring density effects makes sense for many populations, especially those of rare organisms. But for matrices with  $\lambda > 1.0$ , populations are projected to grow, and they may eventually reach a size where density effects are important. At this point the values in the transition matrix are likely to change.

For example, the size of the *Arisaema* population at Fall Creek in 1979 was 4166 individuals distributed over 350 m<sup>2</sup>, an average density of 12 individuals/m<sup>2</sup>, with over half of these in the smallest size class (see Table 2A). But an annual growth rate ( $\lambda$ ) of 1.29 would produce, in 15 yr, a population of about 190 000 individuals, or >5000/m<sup>2</sup>. Long before this density was attained, we would expect *Arisaema*'s fecundity and mortality to be affected by intraspecific competition. The model, however, did not take such effects into account.

For these three reasons, many studies that make use of matrix models include the disclaimer that values of  $\lambda$  are only valid so long as vital rates remain constant as measured, something that all but the most naive users of this methodology admit is unlikely to be the case. Many authors explicitly state that the value of calculating  $\lambda$  is not that it provides an accurate prediction of population size in the future, but rather that it provides a way to compare the potential of different populations, or of different management strategies. (A particularly cogent discussion of this issue can be found in Enright and Watson 1991 and in Burgman et al. 1993.) Some emphasize that the value of a matrix analysis lies not in the value of  $\lambda$  it can generate, but rather in the results of sensitivity or elasticity analyses, which pinpoint the life stages or transitions most critical to population persistence. But even these uses of matrix models are susceptible to being invalidated by environmental variability. Sensitivity and elasticity values are a function of the specific entries in the transition matrix.

For example, using matrix models to compare the likely fate of different populations, as is often done, requires that the environment (including the effects of density) be changing in similar ways for the different populations being compared. However, in this study, the Fall Creek population was projected to have a higher asymptotic growth rate than the Brooktondale population, when in fact the reverse turned out to be the case. And no one has yet explored how robust elasticity

analyses might be to environmental variability. Moloney's (1988) study of two transitions for a perennial grass yielded very different vital rates in the two years, and consequently rather different elasticity values.

Finally, even if we can be certain that the data used in a transition matrix model do accurately estimate probabilities of transition, and have captured the full range of environmental variation, and even the effects of density, there is an additional concern about the use of matrix models, especially in studies of rare species. When we deal with threatened species, we are often very concerned about their behavior in the near future—over the next decade or two. The behavior of populations over the short term can be strongly influenced by the distribution of individuals in size classes at the start of the study (i.e., the so-called initial distribution). This is illustrated by the differences between the outcomes of the asymptotic and transient analyses (Table 2), especially at Brooktondale, where the population was farthest from its stable size distribution. One of the earliest uses of matrix models was a transient analysis (Caswell and Werner 1978), and Menges pointed out in 1986 that transient analyses may be particularly appropriate for rare species, but such analyses are still quite rare (for exceptions see Ang 1987, Law and Edley 1990, Carlsson and Callaghan 1991, Slooten and Lad 1991, Gillman et al. 1993, Kephart and Paladino 1997).

Because of the influence on short-term growth rates of a population's initial size structure, it is possible for a population having an equilibrium growth rate ( $\lambda$ ) > 1.0 to actually decline over the short term rather than to increase. In a small population of a threatened species, a  $\lambda$  of 1.0 or higher may be no protection against imminent extinction, and an analysis that includes only an asymptotic projection may produce misleading results.

As an example, consider the matrix in Fig. 1, which represents a perennial plant with four life stages: seedlings (1), juveniles (2), small reproductive individuals (3), and large reproductive individuals (4). From one year to the next, seedlings either die ( $P = 0.8$ ) or grow into juvenile plants ( $P = 0.2$ ). Juvenile plants either remain in that stage ( $P = 0.6$ ), mature into small reproductive individuals ( $P = 0.3$ ), or die ( $P = 0.1$ ). Small reproductive plants produce an average of 1.2 seedlings per year, and can either revert to the non-flowering juvenile stage ( $P = 0.2$ ), remain small reproductive individuals ( $P = 0.6$ ), grow larger ( $P = 0.1$ ), or die ( $P = 0.1$ ). Finally, the larger reproductive individuals produce an average of 2.5 seedlings per year, and either remain in their current stage ( $P = 0.7$ ), become smaller ( $P = 0.2$ ), revert to juveniles ( $P = 0.05$ ), or die ( $P = 0.05$ ). This matrix has a  $\lambda$  of 1.05.

To the right of the matrix in Fig. 1 are three hypothetical population vectors, all of 100 individuals. The first represents a size distribution very similar to the stable size distribution. The second is a population with

Size class (year $t + 1$ )	Size class in year $t$				Vector 1	Vector 2	Vector 3
	1	2	3	4			
1	0	0	1.2	2.5	40	60	20
2	0.2	0.6	0.2	0.5	30	20	70
3	0	0.3	0.6	0.2	25	15	5
4	0	0	0.1	0.7	5	5	5

FIG. 1. Matrix for a hypothetical plant population. Vectors represent three initial size distributions, each yielding different results when multiplied by the matrix. All vectors contain 100 individuals. See *Discussion* for results.

a large proportion of seedlings, and the third has a large proportion of juvenile plants. These departures from the stable size distribution could result from demographic stochasticity in such a small population. Multiplying each of these vectors by the matrix yields the following population sizes in the subsequent year: 105 individuals for vector 1 (as expected, given the value of  $\lambda$ ), 79 individuals for vector 2, and 95 individuals for vector 3.

Why do these three hypothetical populations behave so differently over the short term? This is a consequence of the specific values in the three vectors. In this example, seedlings have a much higher mortality rate than juveniles do, so the vector in which most of the population is in the seedling stage represents a population that is declining over the short term. This example illustrates that transient behavior coupled with demographic stochasticity may cause a population to decline, perhaps even to go extinct, even though it has a favorable asymptotic growth rate. Thus paying attention only to the value of  $\lambda$  may fail to provide all the information needed to assess the health of a sensitive population.

Transient behavior will be most different from projected asymptotic behavior when a population's structure is far from its stable distribution. How often is this the case in natural populations? In a survey of recent studies, I found 17 that compared a population's actual age or size distribution with its stable distribution; of these 17, only 7 found that the study population(s) had in fact neared that stable distribution. More commonly (in 59% of the studies), there were large, significant differences between the population's actual distribution and its projected stable distribution. This suggests that transient behavior will be important to consider for many species.

This study has demonstrated that a 3-yr demographic study of two populations of a long-lived perennial herb in a climax community did not provide an accurate prediction of one of those populations' growth rates or of their size distributions 15 yr later. Whether this is because density effects were not incorporated into the model, because three years was not enough time to capture a sufficient range of environmental stochastic-

ity, or because vital rates were not accurately estimated, is impossible to say. But the problem is likely to be endemic in studies of rare species, where sample sizes will be smaller and demographic stochasticity may be more pronounced.

Among some applied ecologists and conservation biologists, matrix models are coming to be regarded as a "magic bullet"—the ideal way to predict the health of endangered populations and to assess the effects of manipulation or management. This enthusiasm has been fueled by the widespread availability of computer software, such as RAMAS/stage (Ferson 1990) for performing matrix analyses. Greater consciousness of the limitations of these models will help assure that they are used in appropriate ways, and that their conclusions are biologically reasonable. In particular, this study should serve as a cautionary tale about the importance of accurately measuring vital rates, especially across a large sample size and a wide range of environmental variation. Though long-term studies of many individuals are expensive and laborious, they are the only way to acquire data of the quality that transition matrix models require.

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