

## DEMOGRAPHY OF CENTRAL AND MARGINAL POPULATIONS OF MONKEYFLOWERS (*MIMULUS CARDINALIS* AND *M. LEWISII*)

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**Abstract.** Every species occupies a limited geographic area, but how spatiotemporal environmental variation affects individual and population fitness to create range limits is not well understood. Because range boundaries arise where, on average, populations are more likely to go extinct than to persist, range limits are an inherently population-level problem for which a demographic framework is useful. In this study, I compare demographic parameters and population dynamics between central and marginal populations of monkeyflowers, *Mimulus cardinalis* and *M. lewisii*, along an elevation gradient spanning both species' ranges. Central and marginal populations of both species differed in survival and fecundity. For *M. lewisii*, these components of fitness were higher in central than in marginal populations, but for *M. cardinalis* the converse was true. To assess spatiotemporal variation in population dynamics, I used transition matrix models to estimate asymptotic population growth rates ( $\lambda$ ) and found that population growth rates of *M. lewisii* were highest at the range center and reduced at the range margin. Population growth rates of *M. cardinalis* were highest at the range margin and greatly reduced at the range center. Life table response analysis decomposed spatiotemporal variation in  $\lambda$  into contributions from each transition between life stages, finding that transitions from large nonreproductive and reproductive plants to the seed class and stasis in the reproductive class made the largest contributions to spatial differences in  $\lambda$ . These transitions had only low to moderate sensitivities, indicating that differences in projected population growth rates resulted mainly from observed differences in transition matrix parameters and their underlying vital rates.

**Key words:** life table response experiment; LTRE; matrix population models; *Mimulus cardinalis*; *Mimulus lewisii*; monkeyflower; population dynamics; range limit.

### INTRODUCTION

Every species occupies a limited geographic area. Sometimes ranges stop at obvious environmental discontinuities, but more often ranges end at seemingly arbitrary points along gradual environmental gradients (Kirkpatrick and Barton 1997). Linking spatial and temporal variation in the environment to variation in individual and population fitness is critical to understanding species' distribution limits (Holt and Keitt 2005). Because range boundaries arise where, on average, the probability of population extinction exceeds the probability of persistence, range limits are an inherently population-level problem for which a demographic framework is informative.

Range margins are often assumed to be coincident with ecological margins, such that species reach the limit of their environmental tolerance at a range boundary and are maladapted to conditions beyond the range (Antonovics 1976, Lesica and Allendorf 1995). Consistent with this characterization, species abundance (i.e.,

local population density) often decreases with distance from the range center, presumably in response to an increasingly unfavorable environment (McClure and Price 1976, Brown et al. 1996, but see Sagarin and Gaines 2002). Observations of individual performance across the range frequently find lower survival or reduced fecundity at the range margin relative to the range center (Marshall 1968, Pigott and Huntley 1981, Jump and Woodward 2003). However, whether reductions in some fitness components impact population growth and persistence is not always evident. In some instances, reductions in individual performance alone, without consideration of secondary effects on population dynamics, may not explain the position of a range boundary (Prince and Carter 1985).

Carter and Prince (1988) suggested that the small reductions in fecundity observed across the range boundary of *Lactuca serriola* cannot explain failure to occur beyond its present distribution. If populations are not seed limited, reductions in fecundity may not translate into reduced recruitment and population growth rates (Turnbull et al. 2000, Maron and Simms 2001). A decrease in one fitness component from the center to the edge of the range also may be mitigated by other differences. For example, a loss of migratory behavior may counterbalance lower juvenile fitness in

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southern marginal populations of the Iberian Robin, *Erithacus rubecula* (Perez-Tris et al. 2000), and vegetative reproduction may offset reduced sexual reproduction in northern peripheral populations of the aquatic plant *Decodon verticillatus* (Dorken and Eckert 2001). To thoroughly understanding geographic range limits, components of performance must be integrated into models of population growth across species' distributions (Pulliam 2000).

Temporal patterns of variation and the interaction between spatial position and temporal dynamics are also important to understanding the dynamics of populations across species' ranges (Ives and Klopfer 1997). Central populations might exhibit greater variability if intrinsic rates of increase are high in optimal habitat or if biotic regulation is stronger when population density is high (Williams et al. 2003). On the other hand, marginal populations may be near the limit of environmental tolerance, and consequently more vulnerable to environmental fluctuations that exceed tolerance levels in some years (Gaston 1990, Olmsted et al. 1993, Mehlman 1997). If marginal populations are small and highly variable, they may be prone to extinction (Curnutt et al. 1996, Maurer and Taper 2002).

Several studies hypothesize that spatial gradients in extinction risk, colonization rates, and/or habitat availability can create stable range boundaries (Carter and Prince 1981, Lennon et al. 1997, Holt and Keitt 2000, Maurer and Taper 2002). Other models suggest that marginal populations may be demographic sinks, sustained only by immigration from central populations (Kawecki 1995, Curnutt et al. 1996, Kirkpatrick and Barton 1997, Guo et al. 2005). However, there are very few detailed comparisons of the demography of central vs. marginal populations (Nantel and Gagnon 1999, Stokes et al. 2004, Volis et al. 2004).

This paper compares demographic parameters and population dynamics between central and marginal populations of sister species of monkeyflowers, *Mimulus cardinalis* and *M. lewisii*, along an elevation gradient spanning both species' ranges. To assess spatiotemporal variation in population dynamics, I used several analyses based on transition matrix models. I estimated the asymptotic population growth rate ( $\lambda$ ) in central and marginal populations over three yearly transition intervals and used life table response experiments (Caswell 2001) to decompose spatiotemporal variation in  $\lambda$  into contributions from each transition between life cycle stages. I hypothesized that marginal populations would exhibit reductions in at least some components of individual fitness (e.g., survival, fecundity) and reduced asymptotic population growth rates (population mean fitness). Specifically, this study investigated the following questions. (1) How do vital rates and population growth rates vary between central and marginal populations? (2) Which life cycle transitions are responsible for observed differences in population growth rate between populations?

## METHODS

*Study system.*—*Mimulus cardinalis* and *M. lewisii* (Phrymaceae) are rhizomatous perennial herbs that grow along seeps and stream banks in western North America. *Mimulus cardinalis* occurs from southern Oregon, USA, to northern Baja California, Mexico, and from coastal California to Arizona and Nevada, USA (Hickman 1993). *Mimulus lewisii* is composed of two races, a northern form occurring in the Pacific Northwest and the Rocky Mountains and a southern form occurring primarily in the Sierra Nevada Mountains of California (Hiesey et al. 1971, Hickman 1993, Beardsley et al. 2003). Here I study only the Sierran race of *M. lewisii*. In California, *M. cardinalis* occurs from sea level to 2400 m, and *M. lewisii* occurs from 1200 to 3100 m (Hickman 1993). However, in the Yosemite National Park region where this research was conducted, the species co-occur between 1200 and 1600 m altitude; repeated attempts to locate extant natural populations of *M. cardinalis* above 1600 m were unsuccessful (Angert 2005). Therefore, I consider 1200–1600 m to be the shared mid-altitude distribution limit of both species in the Yosemite region.

Four populations of each species were monitored along an altitude transect from 830 to 2750 m within 37°32' and 37°57' N latitude in Yosemite National Park and the surrounding Stanislaus and Inyo National Forests. Although this transect contains only a small fraction of each species' geographic range, it provides a gradient from altitude range center to altitude range margin for both species at a tractable spatial scale. Two sites were located at the mid-altitude range margin where both species occur sympatrically ("Wawona," South Fork Merced River, 37°32' N, 119°39' W, 1208 m; and "Carlton," South Fork Tuolumne River, 37°49' N, 119°52' W, 1320 m). Additionally, two sites were at the *M. cardinalis* low-altitude range center ("Buck Meadows," Moore Creek, 37°46' N, 120°2' W, 830 m; and "Rainbow Pool," South Fork Tuolumne River, 37°49' N, 120°0' W, 833 m), and two sites were at the *M. lewisii* high-altitude range center ("May Lake," Snow Creek, 37°50' N, 119°29' W, 2690 m; and "Warren Fork," Lee Vining River, 37°57' N, 119°13' W, 2750 m). All locations selected for demographic study fell within the range of plant densities observed at similar altitudes (Angert 2005).

*Census plots.*—During July–August 2000, multiple plots were established at each site. Plots varied in size and number across sites due to differences in habitat and plant density (average plot size 103.4 m<sup>2</sup>; plot range 8–459 m<sup>2</sup>; average total area per site 800.7 m<sup>2</sup>; site range 437.8–1160.5 m<sup>2</sup>). The plots spanned natural environmental variation at each site and encompassed areas suitable for all life history transitions, so that together they represent performance at the site as a whole. I marked the corners of each plot with rebar to facilitate relocation and to establish an ( $x$ ,  $y$ )-coordinate system

for mapping plant locations. Within each plot, every *M. cardinalis* and/or *M. lewisii* individual was mapped to within 5 cm on the ( $x$ ,  $y$ )-coordinate grid and marked with a uniquely numbered aluminum tag, except when rocks prevented tag placement. When tag placement was impossible, ( $x$ ,  $y$ )-coordinates were used to identify individuals. Individuals were defined as discrete clusters of stems separated from other stems by at least 10 cm, except when stems had evidence of physical connection or were known to have arisen from multiple seedlings. Because both species can grow clonally via rhizomes, a small number of individuals, particularly at the beginning of the study, may have been ramets of the same genet.

Annual censuses were conducted from 2001 to 2003 each autumn, when development was complete, to capture yearly survival, growth, and reproduction and to tag all new recruits. Stem number, stem length, flowering status, and flower and fruit number of all plants present at the autumn census were recorded. For each plant, up to 20 nonflowering and 20 flowering stems were measured from the ground to the base of the last pair of expanded leaves; all remaining stems were tallied and used to estimate total stem length based on the average stem length of the 40 measured stems. From 2000 to 2003, the fates of 16 849 plants were recorded (Buck Meadows, 569; Rainbow Pool, 2157; Wawona, 128 *M. lewisii*, 4557 *M. cardinalis*; Carlon, 1537 *M. lewisii*, 3721 *M. cardinalis*; May Lake, 1513; and Warren Fork, 2667).

I estimated plant fecundity as the number of fruits per plant multiplied by the population mean seed number per fruit. Each fruit contains ~500–2500 tiny seeds, and flowering individuals may have hundreds of fruits. Each fall, two fruits were harvested from each of 10 individuals growing several hundred meters downstream of the census plots. At Michigan State University, samples of ~200 seeds per fruit were counted under a dissecting microscope and weighed to determine the relationship between seed mass and seed number. Seed number per fruit was then estimated from total seed mass. Seed samples could not be obtained for *M. lewisii* at Carlon in 2002 or for *M. cardinalis* at Rainbow Pool in 2002 and Buck Meadows in 2003, so average seed number per fruit across all other years at the particular location was used instead.

*Seed dormancy.*—Seeds of both species may remain dormant and viable for at least one year in the seed bank (Angert 2005). In September 2002, studies of seed dormancy were initiated to obtain parameter estimates for seed survival in the seed bank (Appendix A).

*Stage classification.*—Each population was classified into four stages present at the autumn census (seeds, both newly produced and those in the seed bank, plus three vegetative classes) using biological criteria based on relationships between size, survival, and reproduction and examination of frequency distributions of stem lengths for different-aged cohorts of plants. To facilitate

comparisons among sites and years, classification criteria were developed using pooled data from all sites and years for each species. The boundary between small and large nonreproductive plants was defined as the midpoint between the median total stem length of first-year nonreproductives (i.e., seedlings) and the median total stem length of nonreproductives aged two and older (midpoint: *M. cardinalis*, 3 cm; *M. lewisii*, 5 cm). A seedling class based on age alone was not retained because first-year plants frequently surpassed older plants in size. Only one reproductive stage class was used because of differences in the size distribution of reproductive plants between sites. Survival of reproductive plants at each site was not related to stem length, so subdivision of the reproductive class was not warranted.

*Variation in fates of vegetative plants.*—To examine spatiotemporal variation in annual survival, I modeled survival of each stage class as a function of position within the range, population nested within range position, yearly transition interval, and all interactions, using a binomial distribution and a logit link function (PROC GLIMMIX; SAS 2003). Position within the range and yearly transition interval were considered fixed effects, and I used Type III estimable functions to evaluate their significance. Population within range position was considered a random effect, and I evaluated its significance by testing whether its  $Z$  value was different from zero (Juenger and Bergelson 2000). For this and all other analyses, I considered effects to be statistically significant when  $P < 0.05$ . I also reported statistically significant  $P$  values when the sequential Bonferroni procedure was applied to maintain tablewide Type I error rates at 0.05 for each species (Rice 1989, but see Moran 2003).

To examine spatiotemporal variation in transition probabilities, I performed log-linear analyses (Horvitz and Schemske 1995, Caswell 2001). All vegetative plants were classified into stage classes each year, including an extra class for dead plants. For each species, these analyses considered the following categorical variables: state (stage at time  $t$ ), year (transition interval), population, and fate (stage at time  $t + 1$ ). The first set of analyses examined each state separately to ask whether the fate of a particular state varied among years and populations, using three-way contingency tables and the null hypothesis that fate was independent of year and population, given the predetermined distribution of plants into year and population categories (Horvitz and Schemske 1995). The second set of analyses examined whether the entire state  $\times$  fate transition table varied between populations and years using four-way contingency tables, and the null hypothesis that fate was affected by state but was independent of year and population (Caswell 2001). Log-likelihood statistics were obtained with PROC CATMOD (SAS 2001a), using the LOGLIN option and adding 0.5 to all cell counts to avoid estimation problems caused by zeros (Horvitz and Schemske 1995).

*Variation in reproduction.*—To examine spatiotemporal variation in reproduction, I analyzed the effects of position within the range, population nested within range position, and year on plant fecundity (seeds per plant) and on three components of fecundity: flower number per plant, fruit set (the proportion of flowers maturing seeds), and seed number per fruit, using PROC MIXED (SAS 2001b). Missing seed counts per fruit at some populations in some years prevented the analysis of interactions with year for the dependent variable seed number per fruit. Flower number was log-transformed, and fruit set was arcsine square-root transformed prior to analysis. Range position and year were considered as fixed effects and their significance evaluated with Type III estimable functions, with denominator degrees of freedom obtained by Satterthwaite's (1946) approximation. Population within range position was considered as a random effect, and its significance was evaluated with likelihood-ratio tests.

*Matrix analysis.*—Transition matrix models of population dynamics were assembled for each population and transition interval using estimates of reproduction, seed dormancy, recruitment, and transition probabilities among vegetative stages, generating a set of 12 population-year matrices per species. The calculations were also performed on data pooled across all years within each population to generate a set of four pooled population matrices per species. Due to the small sample size ( $N=5$ ) of *M. lewisii* large nonreproductive plants at Wawona during 2002–2003, estimates of transitions from the large nonreproductive stage class were obtained from average transition frequencies across all years at Wawona (as in Menges and Dolan 1998).

The projection matrix model for these analyses was a linear, time-invariant model of the form  $\mathbf{n}(t+1) = \mathbf{A} \cdot \mathbf{n}(t)$ , where  $\mathbf{n}(t)$  is a vector of stage-classified individuals in the population at time  $t$ ,  $\mathbf{n}(t+1)$  is the stage-classified vector of individuals at one time step in the future, and  $\mathbf{A}$  is a  $4 \times 4$  matrix of transition probabilities and stage-specific fecundities that shows how individuals in stage  $j$  at time  $t$  contribute to stage  $i$  at time  $t+1$ . The top left-hand corner,  $a_{11}$ , is seed dormancy, and other entries along the diagonal represent stasis in a particular vegetative class from  $t$  to  $t+1$ . Other cells in the top row,  $a_{12}$ – $a_{14}$ , are fecundities (mean number of seeds produced by a reproductive plant at time  $t+1$ ) weighted by the probability of an individual in class  $j$  at time  $t$  becoming reproductive at time  $t+1$ . Nonreproductive stages have a nonzero contribution to the seed class if they may become reproductive within one time step. Transitions from seed to vegetative stages are represented by the first column, primarily in the second and third rows. Occasionally, rapid growth of spring germinants enabled them to reach the reproductive class by the autumn census, in which case the top left-hand corner is both seed dormancy and the seed contribution of one-year-old reproductives. The dominant eigenvalue of each projection matrix is the asymptotic population growth

rate, lambda (Caswell 2001). Although other interesting demographic parameters may be obtained from matrix projection analysis, I focus on lambda as a synthetic measure of demographic success in each environment.

I used a fixed-design life table response experiment (LTRE; Caswell 2001) to model lambda ( $\lambda$ ) of each species as a linear function of population,  $p$ , yearly transition interval,  $y$ , and their interaction,  $py$ :

$$\lambda^{(py)} = \lambda^{(\cdot)} + \alpha^{(p)} + \beta^{(y)} + (\alpha\beta)^{(py)}$$

where  $\alpha^{(p)}$  is the effect of the  $p$ th level of the population treatment,  $\beta^{(y)}$  is the effect of the  $y$ th level of the year treatment, and  $(\alpha\beta)^{(py)}$  is the interaction of the  $p$ th population and  $y$ th year, measured relative to the projected growth rate of the reference matrix ( $\lambda^{(\cdot)}$ ). The reference matrix may be obtained from an unmanipulated control or by combining data from all treatments into a mean (calculated by averaging transition frequencies) or pooled (calculated from pooled raw data) matrix (Miriti et al. 2001). I chose to use a pooled reference matrix, which weighted observed transitions by their frequency in the entire data set (Horvitz and Schemske 1995) and better approximated observed lambdas than a mean reference matrix. Treatment effects were estimated as

$$\begin{aligned} \alpha^{(p)} &= \lambda^{(p)} - \lambda^{(\cdot)} \\ &\approx \sum \left[ a_{ij}^{(p)} - a_{ij}^{(\cdot)} \right] \cdot (\partial\lambda/\partial a_{ij}) \Big|_{[\mathbf{A}^{(p)} + \mathbf{A}^{(\cdot)}]/2} \\ \beta^{(y)} &= \lambda^{(y)} - \lambda^{(\cdot)} \\ &\approx \sum \left[ a_{ij}^{(y)} - a_{ij}^{(\cdot)} \right] \cdot (\partial\lambda/\partial a_{ij}) \Big|_{[\mathbf{A}^{(y)} + \mathbf{A}^{(\cdot)}]/2} \\ \alpha\beta^{(py)} &= \lambda^{(py)} - \lambda^{(\cdot)} - \alpha^{(p)} - \beta^{(y)} \\ &\approx \sum \left[ a_{ij}^{(py)} - a_{ij}^{(\cdot)} \right] \cdot (\partial\lambda/\partial a_{ij}) \Big|_{[\mathbf{A}^{(py)} + \mathbf{A}^{(\cdot)}]/2} \\ &\quad - \alpha^{(p)} - \beta^{(y)} \end{aligned}$$

where sensitivities,  $\partial\lambda/\partial a_{ij}$ , were evaluated midway between the treatment and the reference matrices and obtained from the relationship  $\partial\lambda/\partial a_{ij} = v_i w_j / \langle \mathbf{w}, \mathbf{v} \rangle$ , where  $\mathbf{v}$  and  $\mathbf{w}$  are the right and left eigenvectors of the matrix (Caswell 2001). Treatment matrices (e.g.,  $\mathbf{A}^{(p)}$ ,  $\mathbf{A}^{(y)}$ ) were obtained by pooling data across all levels of the other treatments (e.g., for a particular  $\mathbf{A}^{(p)}$ , data were combined across all years within that population, and for a particular  $\mathbf{A}^{(y)}$ , data were combined across all populations within that year). The above equations can be interpreted to mean that the effect of the treatments on population growth depends on both observed variation in matrix elements and the sensitivity of population growth to variation in those elements. The contribution of a particular matrix element  $a_{ij}$  to variation in lambda may be low if  $a_{ij}$  did not vary between treatments and/or if

lambda is insensitive to variation in  $a_{ij}$ . A matrix element with high sensitivity may not contribute to variation in lambda if the transition was unaltered by the treatments. Conversely, a matrix element with slight variation but high sensitivity may make a large contribution to variation in lambda.

To assess uncertainty in population projections, I used bootstrapping to calculate bias-corrected 95% confidence intervals (CI) around estimates of lambda, sensitivities, and LTRE contributions (Caswell 2001). Individuals were stored as columns in a data array, where rows represented fates and fruit numbers, and randomly selected with replacement to generate a bootstrapped data set of size equal to the population sample size. For each bootstrapped data set, vegetative transition probabilities, fruit number at times  $t$  and  $t - 1$  (used to estimate recruitment from the seed class), and fruit number per reproductive at time  $t + 1$  (used to estimate contributions to the seed class) were calculated. For estimates involving seed number, I drew a seed number per fruit from the empirical cumulative probability distribution of seed number derived from the samples of fruits used to estimate population mean seed number per fruit, and then multiplied by fruit number within every bootstrap replicate. An estimate of seed dormancy was drawn at random from the cumulative probability distribution of seed dormancy, which was assumed to be normally distributed with mean and standard deviation derived from estimates across multiple seed stations for each species.

Nonparametric randomization tests based on random permutations of individuals between groups were used to test specific hypotheses about differences in lambda among yearly transition intervals and between populations (Caswell 2001). To assess whether lambda varied among yearly transition intervals within a population, individuals were randomly permuted among pairs of years, keeping sample sizes for each transition interval fixed (Fréville et al. 2004). Transition frequencies and fruit counts for each permuted data set were calculated as described for each bootstrapped data set. Mean seed counts at times  $t - 1$ ,  $t$ , and  $t + 1$  were permuted independently, then combined with transition frequencies and fruit counts to generate matrices and calculate lambda for each transition interval for each of 2000 permuted data sets. The significance of the observed standard deviation of lambda among yearly transition intervals within each population was then compared to the randomized distribution of standard deviations with a one-tailed test (Caswell 2001, Fréville et al. 2004). To assess whether lambda differed between populations, data were first pooled over all years within each population. Individuals, with their complete histories, and mean seed counts were randomly permuted between populations in a similar fashion to permutations among transition intervals as described previously. The observed absolute value of the difference in lambda was compared to the randomized distribution of absolute differences with a

two-tailed test (Brys et al. 2004). Because six pairwise comparisons of populations were made for each species, significance levels were adjusted according to the sequential Bonferroni procedure (Rice 1989, Edgington 1995). All matrix calculations were performed in Matlab (2001).

## RESULTS

*Spatiotemporal variation in fates of vegetative plants.*—Small nonreproductive plants showed the lowest annual survival (*M. cardinalis*, 11–22%; *M. lewisii*, 7–26%), and reproductive plants showed the highest annual survival (*M. cardinalis*, 72–91%; *M. lewisii*, 81–97%; Appendix B). Position within the altitude range affected survival of reproductive plants of both species (*M. cardinalis*,  $F_{1,2} = 20.2$ ,  $P < 0.05$ ; *M. lewisii*,  $F_{1,2} = 19.53$ ,  $P < 0.05$ ) and marginally affected survival of *M. lewisii* large nonreproductive plants ( $F_{1,2} = 13.32$ ,  $P < 0.10$ ). Survival of *M. cardinalis* reproductive plants was higher at the range margin than at the range center, whereas survival of *M. lewisii* reproductive plants was higher at the range center than at the range margin (Appendix B). Year did not affect annual survival, and the interaction of year and range position affected survival of *M. lewisii* small nonreproductive plants only (Appendix B). The random effects of population within range position and the interaction of population and year were not related to annual survival of any stage class (Appendix B).

Log-linear analyses of transition probabilities for each stage class revealed that population significantly affected the fate of all stage classes for both *M. cardinalis* (small nonreproductive,  $G^2 = 154.0$ ,  $P < 0.0001$ ; large nonreproductive,  $G^2 = 49.3$ ,  $P < 0.0001$ ; reproductive,  $G^2 = 96.3$ ,  $P < 0.0001$ ) and *M. lewisii* (small nonreproductive,  $G^2 = 97.9$ ,  $P < 0.0001$ ; large nonreproductive,  $G^2 = 108.0$ ,  $P < 0.0001$ ; reproductive,  $G^2 = 97.5$ ,  $P < 0.0001$ ). Year significantly affected the fate of nonreproductive but not reproductive stages (*M. cardinalis*: small nonreproductive,  $G^2 = 58.5$ ,  $P < 0.0001$ ; large nonreproductive  $G^2 = 60.2$ ,  $P < 0.0001$ ; reproductive  $G^2 = 10.2$ ,  $P > 0.10$ ; *M. lewisii*: small nonreproductive,  $G^2 = 108.5$ ,  $P < 0.0001$ ; large nonreproductive  $G^2 = 12.8$ ,  $P < 0.05$ ; reproductive  $G^2 = 9.0$ ,  $P < 0.10$ ). Conditional tests of the effects of population and year produced results very similar to marginal tests (Appendix C). Log-linear analyses of the four-way contingency table of state  $\times$  fate transitions across populations and years showed that the null model SLY, SF did not fit the data (*M. cardinalis*,  $G^2 = 609.5$ ,  $P < 0.0001$ ; *M. lewisii*,  $G^2 = 526.2$ ,  $P < 0.0001$ ). Lack of fit of the null model indicates that initial state was not sufficient for predicting fate, given the distribution of states over populations and years. Population, year, and the interaction between population and year made significant contributions to explaining variation in state  $\times$  fate transitions for both *M. cardinalis* and *M. lewisii* (Appendix C).

*Spatiotemporal variation in reproduction.*—Position within the range affected overall plant fecundity of both *M. cardinalis* and *M. lewisii* (*M. cardinalis*,  $F_{1,10.7} =$

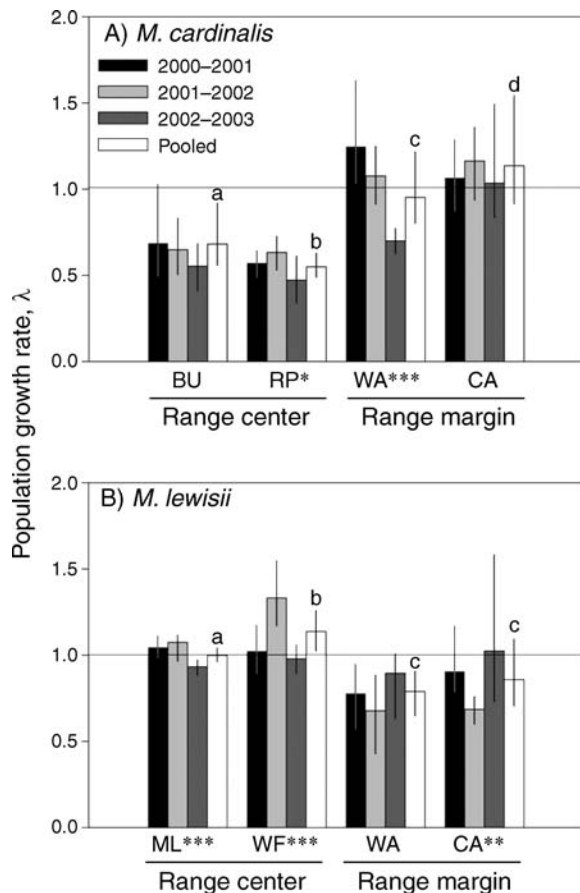


FIG. 1. Asymptotic population growth rates ( $\lambda$ ), with bias-corrected 95% CI (Caswell 2001) for each population and transition interval and for pooled population matrices for (A) *Mimulus cardinalis* and (B) *M. lewisii*. Asterisks indicate significant variation among transition intervals within a population based on randomization tests (\* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ ). Pooled lambda values (open bars) not sharing lowercase letters differ significantly from one another based on randomization tests. Population abbreviations and altitudes above sea level (m a.s.l.) are as follows: BU, Buck Meadows (830 m); RP, Rainbow Pool (833 m); WA, Wawona (1208 m); CA, Carlon (1320 m); ML, May Lake (2690 m); and WF, Warren Fork (2750 m).

20.97,  $P < 0.001$ ; *M. lewisii*,  $F_{1,8.77} = 13.83$ ,  $P < 0.01$ ). For *M. cardinalis*, position within the range affected flower number per plant ( $F_{1,9.5} = 23.3$ ,  $P < 0.001$ ) and marginally affected fruit set ( $F_{1,2.0} = 15.9$ ,  $P < 0.10$ ). For *M. lewisii*, position within the range affected fruit set ( $F_{1,7.1}$ ,  $P < 0.001$ ) and seed number per fruit ( $F_{1,138}$ ,  $P < 0.0001$ ). Year affected *M. cardinalis* seed number per fruit ( $F_{3,107} = 12.4$ ,  $P < 0.0001$ ) but did not affect *M. lewisii* reproductive variables (Appendix D). The effect of position within the range did not depend on year, as indicated by nonsignificant year  $\times$  range position interactions for both species (Appendix D). Population and population  $\times$  year interactions affected some reproductive variables for both species, but in general, between-population variation at a given range position

did not overwhelm differences in reproduction between central and marginal areas of the altitude range. *M. cardinalis* displayed reduced fecundity at the low-altitude range center compared to the mid-altitude range margin, due primarily to reduced flower number per reproductive plant (Appendix D). *M. lewisii* displayed reduced fecundity at the mid-altitude range margin due to lower fruit set and an approximately two-fold reduction in seed number per fruit (Appendix D).

*Projection matrix analyses.*—Lambda values ranged from 0.4724 to 1.1629 for *M. cardinalis* and from 0.6772 to 1.3319 for *M. lewisii* (Fig. 1; Appendix E). For *M. cardinalis*, lambdas at the low-altitude range center were significantly lower than lambdas at the mid-altitude range margin (Fig. 1). The 95% CI for *M. cardinalis* low-altitude lambdas never overlapped 1.0, the value for stable population size, except at Buck Meadows from 2000–2001. In contrast, 95% CI for all *M. cardinalis* mid-altitude lambdas overlapped 1.0 except at Wawona from 2002–2003. For *M. lewisii*, lambdas at the high-altitude range center were significantly higher than lambdas at the mid-altitude range margin (Fig. 1). However, most 95% CI at one marginal population (Carlon) overlapped one, whereas 95% CI at the second marginal population (Wawona) did not. At high altitude, the 95% CI for all lambdas overlapped one except at May Lake from 2002–2003. For *M. cardinalis*, significant temporal variation in lambda was detected at one central (Rainbow Pool) and one marginal (Wawona) population (Fig. 1). For *M. lewisii*, significant temporal variation in lambda was detected at all populations except for Wawona (Fig. 1).

Because separate estimates of dormancy from central and marginal populations were not available, I varied the dormancy component of the seed-to-seed transition by  $\pm 50\%$ . Decreasing seed dormancy by 50% decreased lambdas by 0.9–1.9% for *M. cardinalis* and by 0.03–0.2% for *M. lewisii*, and increasing seed dormancy by 50% increased lambdas by 1.3–3.0% for *M. cardinalis* and by 0.04–0.2% for *M. lewisii*. For both species, lambdas at all populations responded similarly to increases or decreases in seed dormancy, and the magnitude of change in lambda due to variation in the dormancy transition was not sufficient to erase differences in lambdas between central and marginal populations.

Transition matrices and sensitivity matrices are given in Appendix E. For both species at all populations and for all transition intervals, lambda was most sensitive to perturbations in transitions from seeds to vegetative individuals, particularly from seeds to the reproductive stage class (Appendix E). Lambdas of both species were also sensitive to perturbations in transitions to the reproductive stage class from vegetative stages. Bias-corrected 95% CI were broadly overlapping among transition intervals and populations, indicating that all population-year matrices had similar sensitivity structure (data not shown).

*Life table response experiment.*—LTRE analysis confirmed that, for *M. cardinalis*, sites at the range center

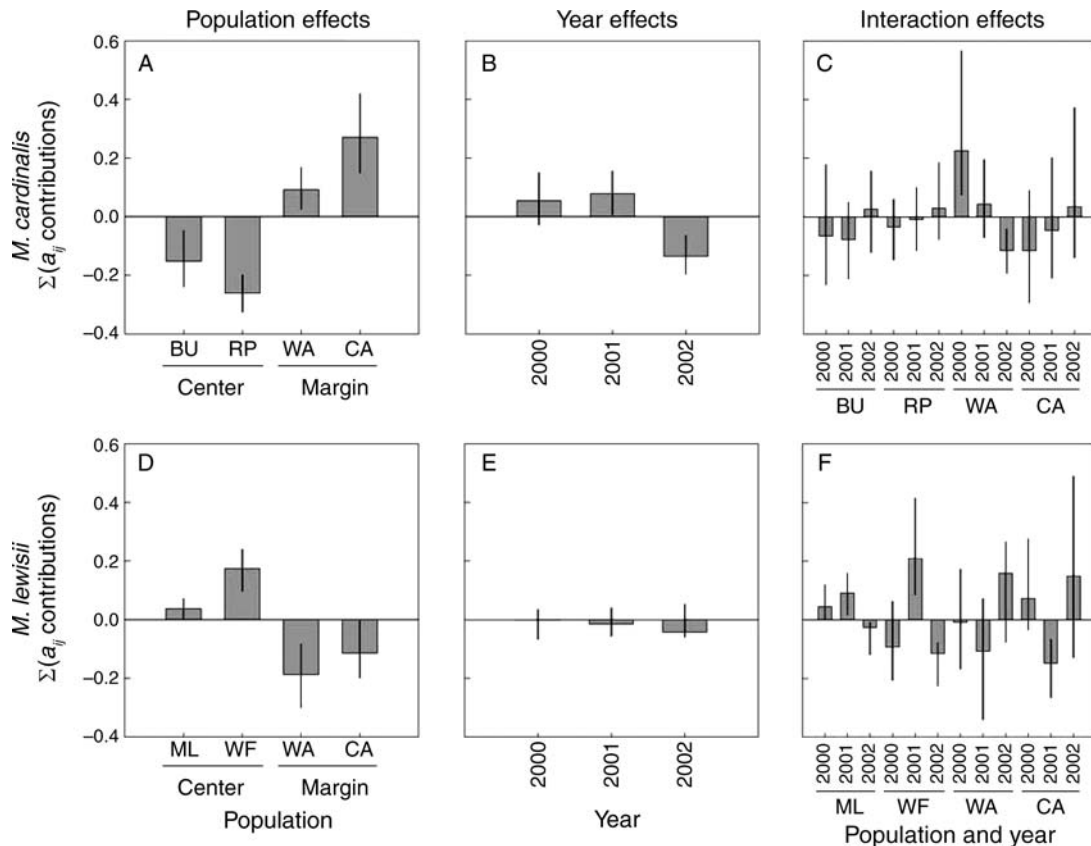


FIG. 2. Life table response experiment (LTRE), with effects of (A) *M. cardinalis* population, (B) *M. cardinalis* yearly transition interval, (C) *M. cardinalis* interaction of population and year, (D) *M. lewisii* population, (E) *M. lewisii* yearly transition interval, and (F) *M. lewisii* interaction of population and year on  $\lambda$ . Effects were obtained by summing the contribution of each transition matrix element ( $a_{ij}$ ) to variation in  $\lambda$ . Vertical bars indicate bias-corrected 95% CI (Caswell 2001). Year labels shown are first year of transition interval. Abbreviations are as in Fig. 1.

had a negative effect on lambda, whereas sites at the range margin had a positive effect on lambda, where the overall effect of a particular treatment level is obtained by summing the contribution of each matrix element to variation in lambda (Fig. 2A). For *M. lewisii*, on the other hand, sites at the range center had a positive effect on lambda, and sites at the range margin had a negative effect on lambda (Fig. 2D). For both species, yearly transition interval had a much smaller effect on lambda than did population. For *M. cardinalis*, 2001–2002 had a positive effect on lambdas, and 2002–2003 had a negative effect on lambdas (Fig. 2B). For *M. lewisii*, year effects did not differ from zero (Fig. 2E). The interaction of population and year affected *M. cardinalis* lambdas at Wawona and *M. lewisii* lambdas at all sites except Wawona. At Wawona, *M. cardinalis* lambdas were significantly higher than expected based on the main effects of population and year in 2000–2001 and significantly lower than expected in 2002–2003 (Fig. 2C). For *M. lewisii*, lambdas in 2001–2002 were higher than expected at the range center and lower than expected at the range margin. The converse was true in 2002–2003 (Fig. 2F).

Several transitions made large contributions to spatial variation in lambda ( $a_{ij}$  contributions to  $\alpha^{(p)}$ ; Fig. 3). For *M. cardinalis*, fecundity transitions from large non-reproductive and reproductive individuals to the seed class and stasis in the reproductive class had large negative effects on range center lambdas and large positive effects on range margin lambdas. In contrast, recruitment from seed to the large nonreproductive class made a positive contribution to lambda at the range center (Fig. 3). In contrast to *M. cardinalis*, fecundity transitions from large nonreproductive and reproductive classes to seeds and stasis in the large nonreproductive and reproductive classes negatively affected *M. lewisii* range margin lambdas and positively affected range center lambdas (Fig. 3). A large positive contribution of recruitment from seed to the large nonreproductive class also partially offset the negative contributions of other *M. lewisii* transitions at Carlon (Fig. 3).

The *M. cardinalis* year and population  $\times$  year interaction effects (Fig. 2B, C) were due to contributions from the same fecundity and stasis transitions that gave rise to the population effect (data not shown). For *M. lewisii*, however, population  $\times$  year interaction effects

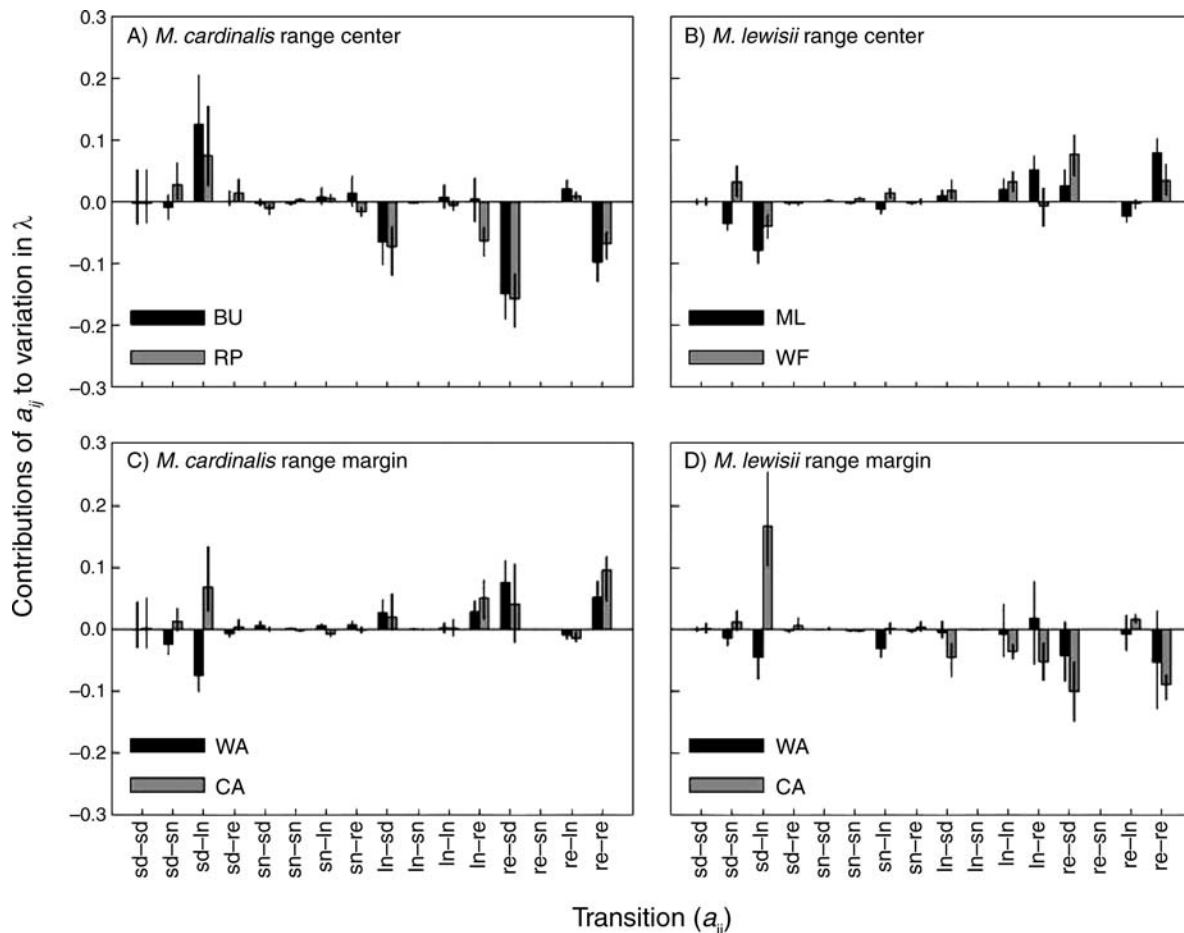


FIG. 3. Transition matrix element ( $a_{ij}$ ) contributions to spatial variation in  $\lambda$  for (A) *Mimulus cardinalis* range center, (B) *M. lewisii* range center, (C) *M. cardinalis* range margin, and (D) *M. lewisii* range margin. Vertical error bars indicate bias-corrected 95% CI (Caswell 2001). Site abbreviations are as in Fig. 1. Stage class abbreviations are as follows: sd, seed; sn, small nonreproductive; ln, large nonreproductive; re, reproductive.

arose primarily from spatiotemporal variation in the contribution of recruitment from seeds to the large nonreproductive stage class, a transition with high sensitivity. From 2000 to 2001 and 2001 to 2002, recruitment at the range center was high, and recruitment at the range margin Carlon site was low; however, this difference was reversed from 2002 to 2003, when recruitment of large nonreproductive plants at Carlon was high, and recruitment at the range center was low (data not shown).

#### DISCUSSION

*Variation in vital rates.*—Observations of central and marginal populations demonstrated significant temporal and spatial variation in the fates of vegetative plants. Components of plant fecundity also displayed significant variation between central and marginal populations. Fecundity of *M. lewisii* was reduced at its mid-altitude range margin due to fewer flowers maturing fruit and an approximately two-fold reduction in seed number per

fruit. It is unclear whether reduced fruit set and seed number per fruit resulted from physiological limitations on seed maturation or from pollen limitation. Fecundity of *M. cardinalis* was reduced at its low-altitude range center. Reproductive plants at the range center produced fewer flowers per stem and were of overall smaller size than reproductive plants at the range margin, resulting in fewer flowers per reproductive plant than at the range margin.

*Variation in population growth rates.*—The projection matrix summarizes how a particular environment affects the demographic parameters of a population. The asymptotic population growth rate, lambda, is the rate at which the population would grow were the present environmental conditions to remain constant. Although the assumption of time invariance is invalid, matrix projections remain extremely useful for summarizing the effects of different environmental conditions on population growth rates and population structure. Because  $\ln \lambda = r$ , the instantaneous growth rate, lambda may also be interpreted as the average fitness of the population in



the given environment (Fisher 1930, Charlesworth 1980, Caswell 2001). In this study, matrix projections revealed large differences in lambda of central and marginal populations for both *M. cardinalis* and *M. lewisii*. Asymptotic projections were similar to observed year-to-year changes in population size. For example, the observed 2002–2003 population growth rate at Rainbow Pool was 0.4769, as compared to the asymptotic population growth rate of 0.4724.

Although statistically significant variation among years was detected at most populations with randomization tests, in general the magnitude of temporal variation was smaller than spatial variation during the short study period, a finding supported by results from LTRE analysis. However, much longer study is necessary to determine the relative roles of spatial and temporal variation in this system. Temporal environmental variation can play an important role in the population dynamics of riparian plant species (Menges 1990, Lytle and Merritt 2004), and it remains possible that temporal variation acting over a longer time scale or at irregular intervals has important consequences for *Mimulus* population dynamics.

Population growth rates of *M. lewisii* fit the expectation that central populations have high fitness and marginal populations have reduced fitness. Population growth rates of *M. cardinalis*, on the other hand, displayed the opposite pattern. The difference between species observed in the present study is somewhat surprising given their similar life history and morphology (both are rhizomatous, perennial, animal-pollinated herbs that make many-seeded fruits). This suggests that the opposing patterns of spatial variation between central and marginal populations may not arise from intrinsic biological differences between the species, but rather may be due to external factors. The strikingly low lambdas observed for *M. cardinalis* at its range center contrast with results from a reciprocal transplant experiment in which *M. cardinalis* and *M. lewisii* were grown at 415, 1400, 2395, and 3010 m, and both species displayed the greatest average fitness at their respective low (415 m) and high (2395 m) altitude range centers (Angert and Schemske 2005). Reciprocal transplants and demographic observations have distinct advantages and disadvantages, and together, the two methods provide complementary information about how performance varies across species' ranges. Reciprocally transplanted seedlings were grown in relatively uniform, favorable conditions (e.g., irrigated plots, minimal competition) to isolate the effects of climate on performance. Observations of natural populations, on the other hand, integrate performance throughout the life cycle over all underlying, but often unknown, environmental variables.

One possible explanation for low lambdas at the *M. cardinalis* range center and the *M. lewisii* range margin is that these populations are at higher density. However, central and marginal populations of each species do not

show systematic variation in density that could explain the observed patterns of spatial variation in lambda (Angert 2005). Another possible explanation is that downstream populations are demographic sinks maintained by immigration from upstream populations. Little is known about mechanisms of dispersal of *M. cardinalis* and *M. lewisii* seeds. It is possible that seed dispersal via downstream currents provides a mechanism for primarily unidirectional long-distance dispersal among populations, as has been demonstrated for *M. guttatus* (Waser et al. 1982). This hypothesis can be tested by examining populations of each species at the opposite range margin.

Alternatively, temporal variation, particularly related to flood cycles, may operate over a longer time scale than the duration of this study and may have different effects on low-altitude vs. mid-altitude populations of *M. cardinalis*, leaving open the possibility that low-altitude populations experience better “good” years than mid-altitude populations. Periodic floods may cause boom–bust cycles of mortality, bursts of recruitment, and subsequent population attrition (Lytle and Merritt 2004). Low-altitude populations may undergo greater variation following floods due to increased magnitude of floods on larger waterways at low altitude and/or to greater potential growth and fecundity of plants at low altitude in wet years. Examination of regional stream flow records (USGS National Water Information System Web data for California; available online)<sup>2</sup> confirms that flood magnitudes, both in absolute terms and in deviation from average peak flows, increase at lower altitudes as catchment area increases. This hypothesis is consistent with the observation that at low altitude, plants were recorded high on riverbanks and relatively distant from water at the beginning of the study, only three years after the largest recorded flood in the region (January 1997), and populations have since retreated to areas closer to water. This hypothesis is also consistent with plant performance in irrigated reciprocal transplant gardens, in which plant performance was measured under optimal conditions, and *M. cardinalis* exhibited the greatest growth and reproduction at the low-altitude range center (Angert and Schemske 2005). A similar interaction between temporal variation and range position may also be possible for *M. lewisii*, although it is likely to be of limited extent due to smaller flood magnitude at mid- and high altitudes and limited growth potential of plants at mid-altitudes (Angert and Schemske 2005). When the effects of floods on the transition matrix are quantified, historical flood frequencies can be used to simulate the effects of stochastic environmental variation on lambdas at different range positions. Further studies of both seed dispersal and spatiotemporal variation in population dynamics are clearly necessary.

<sup>2</sup> (<http://waterdata.usgs.gov/ca/nwis/nwis>)

Only a handful of studies have examined the demography of geographically central and marginal native plant populations, each finding unique patterns of variation between central and marginal populations. Nantel and Gagnon (1999) found that all populations of two clonal plant species, *Helianthus divaricatus* and *Rhus aromatica*, exhibited high growth rates at least some of the time, but that northern peripheral populations exhibited greater temporal variation in population growth rates than central populations. In a study of the annual grass *Hordeum spontaneum* along an aridity gradient from the center to the margin of its range, Volis et al. (2004) reported greater population growth rates in central populations in most years. However, local adaptation of seed dormancy traits in marginal desert populations ensured population persistence through drought periods. Finally, Stokes et al. (2004) examined congeneric shrubs, *Ulex gallii* and *U. minor*, whose parapatric distributions they hypothesized were limited by competition, but found that both species exhibited greatest population growth in marginal, sympatric areas.

The present study also examined the population dynamics of closely related congeners in marginal areas of sympatry, but it was not designed to estimate the effects of competition on vital rates and population growth. Marginal populations at mid-altitude had negative effects on *M. lewisii* lambdas and positive effects on *M. cardinalis* lambdas, but from this study it is not clear to what extent this is due to competitive superiority of *M. cardinalis* vs. adaptation of *M. lewisii* to high-altitude environments. However, even with minimal competition, *M. lewisii* exhibits low fitness in reciprocal transplant gardens at middle and low altitudes (Angert and Schemske 2005) as well as in temperature regimes characteristic of low altitude (Angert, *in press*), suggesting that adaptation, or lack thereof, to the abiotic environment plays an important role in the performance of *M. lewisii* at its range margin. The combined results of these studies also suggest that *M. lewisii* may be particularly vulnerable in the face of a warming climate.

Under many climate change scenarios, species distributions are expected to shift to higher latitudes and altitudes. The high lambdas of both species at higher altitudes within their present ranges suggest that populations may be able to expand upward. However, dispersal upstream may be limited, making it difficult for populations to move upward quickly. Because *M. lewisii* has less expansion range than *M. cardinalis*, it may be exposed to increased competition from *M. cardinalis*. It also remains uncertain how the effects of temperature will interact with changing precipitation (and hence flood) patterns.

*Contribution of life history transitions to variation in population growth rates.*—Analysis of transition matrix data as a life table response experiment revealed several important life history transitions that contributed to lambda differences between central and marginal

populations. Transitions from large nonreproductive and reproductive plants to the seed class and stasis in the reproductive class made the largest contributions to spatial differences in lambda. These transitions had only low to moderate sensitivities, indicating that differences in projected population growth rates resulted mainly from observed differences in transition matrix parameters. At the mid-altitude range margin, *M. cardinalis* was more likely to become or remain reproductive and made more seeds per individual than at low altitudes, and these differences in vital rates contributed to the observed differences in key transition matrix elements. However, some vital rates varied in opposition to these (e.g., recruitment from seeds to large nonreproductives), and looking at them in isolation would have yielded misleading results. Similar patterns of difference were observed for *M. lewisii* at the high-altitude range center vs. the mid-altitude range margin. In sum, this study demonstrates that central and marginal populations of *M. cardinalis* and *M. lewisii* differ in vegetative stage class transitions and fecundity, and that these differences in vital rates contribute to marked spatial variation in population growth rates.

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#### APPENDIX A

Methods for estimation of seed dormancy and recruitment parameters (*Ecological Archives* E087-126-A1).

#### APPENDIX B

A figure and table showing spatiotemporal variation in survival (*Ecological Archives* E087-126-A2).

#### APPENDIX C

A table showing statistical analyses of spatiotemporal variation in stage class transitions (*Ecological Archives* E087-126-A3).

#### APPENDIX D

A figure and table showing spatiotemporal variation in reproduction (*Ecological Archives* E087-126-A4).

#### APPENDIX E

A table of transition matrices, sensitivity matrices, and lambdas for each species, population, and yearly transition interval (*Ecological Archives* E087-126-A5).