

THE EVOLUTION OF SPECIES' DISTRIBUTIONS: RECIPROCAL TRANSPLANTS ACROSS THE ELEVATION RANGES OF *MIMULUS CARDINALIS* AND *M. LEWISII*

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Abstract.—Every species occupies a limited geographic area, but it remains unclear why traits that limit distribution do not evolve to allow range expansion. Hypotheses for the evolutionary stability of geographic ranges assume that species are maladapted at the range boundary and unfit beyond the current range, but this assumption has rarely been tested. To examine how fitness varies across species' ranges, we reciprocally transplanted two species of monkey-flowers, *Mimulus cardinalis* and *M. lewisii*, within and beyond their present elevation ranges. We used individuals of known parentage from populations collected across the elevation ranges of both species to examine whether populations are adapted to position within the range. For both species we found the greatest average fitness at elevations central within the range, reduced fitness at the range margin, and zero or near-zero fitness when transplanted beyond their present elevation range limits. However, the underlying causes of fitness variation differed between the species. At high elevations beyond its range, *M. cardinalis* displayed reduced growth and fecundity, whereas at low elevations *M. lewisii* experienced high mortality. Weak differences in performance were observed among populations within each species and these were not related to elevation of origin. Low fitness of both species at their range margin and weak differentiation among populations within each species suggest that adaptation to the environment at and beyond the range margin is hindered, illustrating that range margins provide an interesting system in which to study limits to adaptation.

Key words.—Distribution, elevation gradient, range limit, reciprocal transplant, survivorship analysis.

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Every species occupies a restricted geographic area. In some cases, geographic ranges stop at an obvious barrier, such as a land-water interface. However, more frequently, ranges end at seemingly arbitrary points in space (Kirkpatrick and Barton 1997). Historically, ecologists and biogeographers have correlated range boundaries with climate to identify environmental determinants of range boundaries (Griggs 1914; Good 1931; Dahl 1951). Subsequent analyses have shown that range limits are associated with abiotic variables such as temperature or precipitation (Root 1988; Cumming 2002), biotic factors such as competitors (Terborgh and Weske 1975; Bullock et al. 2000), or complex interactions between biotic and abiotic variables (Randall 1982; Taniguchi and Nakano 2000).

Even a mechanistic understanding of the relationship between environmental variables and distribution limits presents an evolutionary conundrum. Natural selection should continually improve adaptation at a range boundary and thus overcome current geographic limits, causing species' ranges to "grow by a process of annual accretion like the rings of a tree" (Mayr 1963, p. 524). Several hypotheses for the evolutionary stability of range limits propose that populations at range boundaries do not have sufficient genetic variation to respond to natural selection (Bradshaw and McNeilly 1991; Hoffman and Blows 1994; Gaston 2003). Other hypotheses focus on other factors that may prevent populations from adapting to the environment at the range margin, such as genetic trade-offs among fitness-related traits in the marginal environment (Antonovics 1976), genetic trade-offs between fitness in central and border environments (Holt 2003), or gene flow from populations adapted to the range center (Haldane 1956; Garcia-Ramos and Kirkpatrick 1997; Kirkpatrick and Barton 1997). These hypotheses are not necessarily mutually exclusive, and may act synergistically to constrain range expansion.

All of the above hypotheses are united by the assumption that populations are maladapted at a range boundary and unfit beyond the current range. A corollary of this generalization is that concomitant environmental changes impose selection for local adaptation to the range edge. Surprisingly, these assumptions have rarely been directly tested.

Indirect evidence for a decline in fitness with distance from the range center is provided by the observation that, in some species, numerical abundance decreases with distance from the range center, presumably in response to an increasingly unfavorable environment (Brown 1984; Brown et al. 1996; Sagarin and Gaines 2002). Other indirect evidence for changes in fitness across species ranges comes from studies of fluctuating asymmetry. Developmental instability may increase when organisms are under genetic or environmental stress, as is predicted for individuals at range boundaries, and several studies of fluctuating asymmetry have found that populations at range boundaries do have higher levels of fluctuating asymmetry than central populations (Møller 1995; Carbonell and Telleria 1998; Gonzalez-Guzman and Mehlman 2001).

A more critical test for reduced fitness in marginal populations involves direct observation of fitness components across species ranges. Such studies have often found lower survival of certain life-history stages or reduced fecundity at the range margin relative to the range center (Marshall 1968; Pigott and Huntley 1981; McKee and Richards 1996; Garcia et al. 2000; Hennenberg and Bruelheide 2003). Unfortunately, the demographic consequences for such reductions in fitness are generally unclear. Perhaps the biggest stumbling block to observations of fitness variation, however, is that by definition, observations of extant populations cannot determine fitness levels beyond present range boundaries (Woodward 1990).

Reciprocal transplant experiments are a powerful way to test for fitness variation both within and beyond present range limits as well as for the presence of genetically based local adaptation (e.g., Schemske 1984; Stanton and Galen 1997; Verhoeven et al. 2004). Although many classic studies used reciprocal transplants between areas within species ranges (Turesson 1922; Clausen et al. 1940), few have transplanted individuals beyond the range (Gaston 2003). We used reciprocal transplants to evaluate population and geographic variation in fitness for sister species of monkeyflower, *Mimulus cardinalis* and *M. lewisii* (Phrymaceae) across their elevation ranges in California.

The study of closely related species with distinct distributions offers a conceptual advantage for the investigation of range limits. In a comparison of central versus border populations of a single species, one could never reject the possibility that border populations have not yet acquired the right mutation(s) to extend the border. In a comparison of parapatric sister species partitioning an environmental gradient, evolution from the common ancestor toward each species' native environment has already occurred, and the question of interest is what causes and constrains adaptation to different ends of the gradient. *Mimulus cardinalis* and *M. lewisii* have been the subject of ecological and genetic studies for several decades and have many properties that make them ideal research subjects, including high seed number, high germination rates, and low transplant mortality (Vickery 1967, 1978; Hiesey et al. 1971; Bradshaw et al. 1998; Bradshaw and Schemske 2003; Ramsey et al. 2003). Pioneering studies of *M. cardinalis* and *M. lewisii* by Hiesey et al. (1971) revealed variation in performance across elevation, with *M. cardinalis* displaying low survival and reproduction at high elevation and *M. lewisii* displaying low survival and growth in a coastal climate. Unfortunately, several features of this study limit its usefulness for drawing definitive conclusions about variation in fitness versus elevation. First, populations were collected throughout the geographic ranges of both species from Washington to Baja California, but transplanted at only three sites (Stanford, elev. 30 m; Mather, elev. 1400 m; and Timberline, elev. 3050 m) along a narrow elevation transect in northern California. The wide latitudinal and longitudinal distances that separated most populations from the transplant sites are not easily separated from the effects of adaptation to elevation. Although the authors found significant population differentiation within each species (e.g., between coastal Californian and montane Arizonan *M. cardinalis*), regional and subspecies differences are not easily separated from differences related to elevation alone. Second, the use of vegetatively propagated clones eliminated information about the performance of early life-history stages that may experience strong selection and be critical for population establishment (Travis 1994; Caswell et al. 2003; Davis et al. 2003; Lee et al. 2003; Zacherl et al. 2003). Finally, the low elevation transplant station at Stanford (30 m) potentially conflated the effects of low elevation with a maritime climate.

We used reciprocal transplants within and beyond the elevation ranges of *M. cardinalis* and *M. lewisii* to examine how survival, growth, and reproduction of each species change with elevation. We used individuals of known parentage from populations collected across the elevation ranges

of both species along a narrow latitudinal transect to examine whether populations are adapted to their position within the elevation range. Specifically, we asked how fitness components change from the center to the edge of ranges and beyond, and whether populations are locally adapted within their range.

MATERIALS AND METHODS

Study System

Mimulus cardinalis and *M. lewisii* (Phrymaceae) are rhizomatous perennial herbs that grow along seeps and stream banks in western North America. The species are self-compatible and animal pollinated (Hiesey et al. 1971; Schemske and Bradshaw 1999). *Mimulus cardinalis* grows from southern Oregon to northern Baja California and from the coast of California inland to Arizona and Nevada. *Mimulus lewisii* is composed of two races, a northern form growing from southern coastal Alaska to southern Oregon and eastward to 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). The two races are partially incompatible, and recent phylogenetic analysis suggests that the two races are sister to one another and together are sister to *M. cardinalis* (Beardsley et al. 2003). Here we study only the Sierran form of *M. lewisii*.

Mimulus cardinalis and *M. lewisii* segregate by elevation, with *M. cardinalis* found from sea level to 2400 m and *M. lewisii* found from 1200 m to 3100 m in California (Hickman 1993). In the Yosemite National Park region where this research was conducted, the species coexist on larger watercourses between 1200 and 1600 m elevation (A. Angert, unpubl. data). Although the published Californian distributions of *M. cardinalis* and *M. lewisii* extend to 2400 and 3100 m, respectively, repeated attempts to locate extant *M. cardinalis* populations above 1600 m and *M. lewisii* populations above 2900 m in the Yosemite region were unsuccessful. We consider 1200–1600 m to be the shared mid-elevation distribution limit for both species in the Yosemite region.

Genetic Material: Population Collection and Crossing Design

Seeds from eight plants from each of six populations per species were collected in September 1999 along an elevation gradient from 590 m to 2750 m between 37.49 and 37.96°N latitude (Appendix 1). One plant from each field-collected family was grown to flowering in the University of Washington greenhouse under standard greenhouse conditions. The eight plants from each population were crossed with one another in a partial diallel mating design (one per population, for a total of 12 partial diallels), where each plant served as sire and dam twice with no self- or reciprocal pollinations. Pollinations were performed by collecting all of the pollen from one flower with a flat toothpick and fully saturating the stigma of one flower. Seeds from four pollinations per full-sib family were pooled. Our crossing design was intended to provide a genetically variable, outcrossed seed pool for reciprocal transplants rather than to accurately estimate genetic variance components. Sire and dam effects were included in

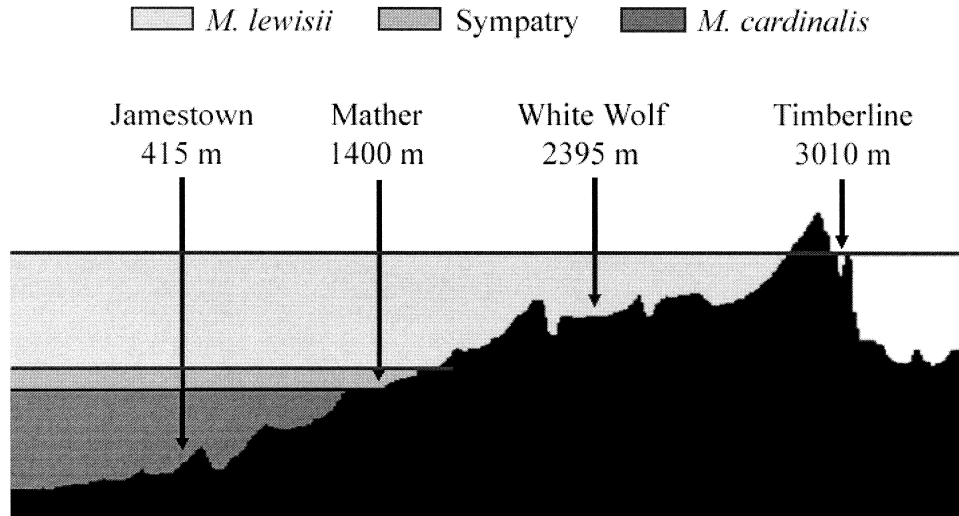


FIG. 1. Transect of the central Sierra Nevada Mountains, California, showing *Mimulus lewisii* and *M. cardinalis* elevation ranges and placement of reciprocal transplant gardens, after Clausen et al. (1948).

statistical models to account for the possible correlation of error and nonindependence of individual measurements due to their family structure.

Reciprocal Transplant Methods

Garden locations.—To examine how species' performance varies across elevation ranges, we established experimental gardens along an elevation transect on the western slope of the Sierra Nevada Mountains. In June–July 2001, gardens were planted near Jamestown, California (415 m), at Carnegie Institution of Washington field stations at Mather (1400 m) and Timberline (3010 m), and at the White Wolf Ranger Station in Yosemite National Park (2395 m; Appendix 1). These gardens were chosen to represent elevations for each species that are central within the range, at the range boundary, and beyond the range boundary in the Yosemite region (Fig. 1). Specifically, for *M. cardinalis*, 415 m is at the range center, 1400 m is at the upper elevation range boundary, and 2395 and 3010 m are beyond the upper range boundary. For *M. lewisii*, 2395 m is at the range center, 1400 and 3010 m are at the lower and upper range boundaries, respectively, and 415 m is beyond the lower range boundary.

Garden conditions.—Due to the tiny seed size and particular microhabitat requirements for germination of *M. cardinalis* and *M. lewisii*, experimental gardens were established with seedlings. Seeds from partial diallel crosses were sown in flats in the University of Washington greenhouse five weeks prior to transport to garden sites. The average age of transplanted seedlings was approximately three weeks after germination, corresponding closely to the size of plants observed in natural populations at the time of planting. Two seedlings from each full-sib family were planted at 10-cm intervals in a randomized block design for a total of 384 seedlings per block (2 seedlings/family \times 16 full-sib families/population \times 6 populations/species \times 2 species). During June–July 2001, seedlings were planted in three blocks at 415 m ($n = 1152$), four blocks at 1400 m ($n = 1536$), four blocks at 2395 m ($n = 1536$), and three blocks at 3010 m ($n = 1152$), for a total of 5376 seedlings across all four trans-

plant sites. Space and water limitations prevented planting a larger number of blocks. Garden plots were covered in landscape fabric and irrigated daily to approximate conditions in the species' native riparian habitat and to standardize water treatments across environments.

Soils assay.—We collected soil samples from each garden site and grew plants under uniformly favorable greenhouse conditions to determine whether site differences in performance were due to the effects of soils as opposed to other environmental factors. We measured the performance of four populations per species, using a subset of four independent full-sib families per population from the partial diallel crosses. Plants were able to flower on all soil types in the greenhouse environment and there was no evidence of local adaptation to soil type (indicated by no significant species \times soil type or population \times soil type interactions). We conclude that differences in soil properties are not primarily responsible for differences in fitness across elevation and we do not consider soil type further.

Measurements.—To assess fitness within each garden, we measured survival, growth, and reproduction. Plants grew at vastly different rates among gardens. At 1400, 2395, and 3010 m, plants grew slowly and rarely attained a size at which larger plants spread via rhizomes into neighboring plants' space. However, at 415 m, *M. cardinalis* plants began to spread via rhizomes into neighbors' space after one growing season, making it difficult to separate individuals and track identity. For this reason, we truncated observations at 415 m after one year, when all *M. lewisii* individuals were dead and surviving *M. cardinalis* were very large. Individuals transplanted in a large preliminary study at 415 m displayed very low mortality and continued rapid growth during the second growing season, indicating that truncation after one year does not bias our results (A. Angert, unpubl. data).

Survival was monitored from 2001 to 2002 at 415 m and from 2001 to 2003 at 1400, 2395, and 3010 m. Survival was recorded at approximately two-week intervals throughout each

growing season. Growth and reproduction were measured for one growing season at 415 m and for two growing seasons at 1400, 2395, and 3010 m. To measure plant growth, we recorded the total stem number and length of all stems. Stem number and total stem length were strongly correlated (*M. cardinalis*: $R^2 = 0.73$, $N = 2065$, $P < 0.0001$; *M. lewisii*: $R^2 = 0.72$, $N = 1790$, $P < 0.0001$). We present stem length data because they better describe overall plant size at high elevations, where plants often have only one stem but differ in stem length. Because permit restrictions prevented seed set at two transplant sites, we use flower number rather than seed number as a proxy for reproductive fitness. Flower number and fruit number measured from 2000 to 2004 in demographic census plots within natural central and border populations are highly correlated (*M. cardinalis*: $R^2 = 0.97$, $N = 1132$, $P < 0.0001$; *M. lewisii*: $R^2 = 0.98$, $N = 1064$, $P < 0.0001$), suggesting that cumulative flower number is a good approximation of total fitness.

We estimated overall plant fitness, retaining zeros for plants that failed to flower or failed to survive, as the cumulative flower number over two growing seasons. We also summed year 1 and year 2 total stem length to estimate cumulative growth. For *M. cardinalis* grown at 415 m, only first-year measurements of stem length and flower number were available. To keep measures comparable across all sites, we annualized measures of growth and fitness and compared average annual stem length and average annual fitness. Comparisons of first-year growth and fitness at all sites as well as cumulative growth and fitness with the 415 m site excluded produced similar results; we present comparisons of annual averages for brevity.

Statistical Analysis

To examine fitness variation across species' elevation ranges, we analyzed the relationships between transplant site and the fitness components of survival and growth and between transplant site and average annual fitness. Too few individuals remained alive and flowering beyond their ranges to allow analysis of flower number for surviving plants. To determine whether populations are adapted to range position, we analyzed the relationship between population origin and performance within each transplant site. All analyses were performed in SAS, version 8.2 (SAS Institute, Inc., Cary, NC).

Survivorship.—We used accelerated failure time models to test for differences between species and populations within species in patterns of survivorship across transplant sites. Accelerated failure time models assume that factors affect failure time (e.g., time to mortality) multiplicatively, shifting the time periods when failures occur (for a general discussion of failure time analyses, see Fox 2001). For our study, accelerated failure time models were biologically appropriate because environmental differences among transplant treatments were expected to shift the distribution of time to failure (Jones and Sharitz 1998; Keith 2002; Denham and Auld 2004). We performed two kinds of analyses. In the first analysis, we tested for interspecific differences across sites using a model with fixed effects of site, species, and the interaction of site and species. In the second analysis, we fit separate

models for each species and tested for intraspecific differences across sites using models with fixed effects of population, site, and the interaction of population and site. These two kinds of analyses were necessary because the coding of categorical variables sets one species' regression coefficients to zero in analyses with two species, making it impossible to assess between-site differences for one species. Because populations were chosen deliberately to span the elevation range of each species and were not drawn at random from within each species' distribution, we consider population as a fixed effect. Standard statistical packages do not incorporate random effects in survival time analyses, so for these analyses we were not able to include sire, dam, or block effects.

To apply the accelerated failure time model, we used PROC LIFEREG with an underlying Weibull distribution of failure time (measured in days after transplantation). Survivorship was described using the function:

$$S(t) = e^{-(\lambda t)^p}, \quad (1)$$

where the scale parameter λ scales the model to a baseline rate of mortality, t is the time since transplantation, and p is a dimensionless shape parameter that describes change in failure hazard over time, such that when $p < 1$ hazard monotonically decreases with time and when $p > 1$ hazard monotonically increases with time (Dudycha and Tessier 1999; Fox 2001; Keith 2002). We also ran models using an alternative plausible distribution, the exponential, which is a special case of the Weibull with the shape parameter $p = 1$, indicating a constant risk of mortality (Fox 2001). The exponential distribution gave a significantly poorer fit to the data than the Weibull according to likelihood ratio tests (species combined: $\chi^2 = 288.9$, $P < 0.0001$; *M. cardinalis*: $\chi^2 = 288.9$, $P < 0.0001$; *M. lewisii*, $\chi^2 = 31.8$, $P < 0.0001$) but yielded qualitatively similar results, indicating that our results are robust to the underlying distribution. Observations were right censored if the individual remained alive at the end of the observation period. For each categorical variable, one level was arbitrarily chosen as the reference level and its regression coefficient was set to zero. Regression coefficients and significance of all other levels were determined relative to the reference, but this did not reveal whether differences among nonreference levels existed. For analyses of intraspecific differences across transplant sites, multiple comparisons were necessary to examine differences among sites other than the reference. We constructed Z-tests for multiple comparisons from estimated regression coefficients and the asymptotic covariance matrix according to the methods of Fox (2001). Because effects act multiplicatively on failure time, regression coefficients less than zero can be interpreted as shrinking the time to failure relative to the reference level, whereas positive regression coefficients expand the expected time to failure relative to the reference (Dudycha and Tessier 1999).

Growth.—To examine the relationship between growth and transplant site, we performed mixed model analysis of variance on log-transformed data with PROC MIXED, which uses the restricted maximum-likelihood method (REML) to estimate variance components. Only two *M. lewisii* individuals remained alive for stem length measurements at 415 m, causing the full model containing all sites to contain many

nonestimable parameters. To remedy this, we ran separate analyses for each species and excluded the 415 m site from the *M. lewisii* stem length analysis. We tested for variation in average annual stem length of each species with respect to transplant site, population of origin, sire within population of origin, dam within each population of origin, block within site, and the interaction of site and population. For this and all subsequent models, we consider transplant site and population of origin as fixed effects and sire, dam, and block as random effects. To evaluate the significance of fixed effects, we used Type III estimable functions with denominator degrees of freedom obtained by Satterthwaite's approximation. When fixed effects were statistically significant, differences among levels were evaluated with Tukey-Kramer adjusted comparisons of least square means. We used the PDMIX800 macro to convert pairwise differences between least square means to letter groupings, where means sharing the same letter code are not significantly different (Saxton 1998). We used likelihood-ratio tests (comparing each reduced model to the full model including all effects) to evaluate the significance of all random effects.

Fitness.—We used mixed linear models to test for variation in average annual fitness with respect to transplant site, species, population within species, sire within population, dam within population, and all interactions among fixed effects. A model containing the random effect of block within site failed to converge, so we also analyzed residuals after accounting for the block effect. The block effect was highly significant ($P < 0.0001$). However, analyses of raw data and of residuals after removing the effect of block gave qualitatively similar results. We present analysis of raw data, rather than residuals, so that differences in least square means are easily interpretable. The distribution of fitness was highly non-normal due to an excess of zeros and a long right tail. Examination of residuals in preliminary analyses revealed significant departures from parametric assumptions, and transformations only slightly improved the distribution of residuals. Therefore, we used two approaches to model annual fitness. First, we performed mixed model analysis of variance on log-transformed data (after adding 1/6 to each observation; Kuehl 2000) with PROC MIXED. Second, we used the GLMM800 macro of PROC MIXED to fit generalized linear models, which are appropriate for a wider range of error structures than traditional linear models (Kuehl 2000). Generalized linear models extend traditional linear models in two key ways. First, they allow the distribution of the response variable to be any member of the exponential family of distributions (e.g., gamma, Poisson, binomial). Second, they relate the response variable to a set of linear predictor variables through a nonlinear link function (SAS Institute 1999). The GLMM800 macro uses restricted/residual pseudolikelihood (REPL) estimation to fit a generalized linear model with random effects. We modeled variation in average annual fitness using a gamma distribution with a log link function, which is appropriate for positive, continuous data (SAS Institute 1999; Juenger and Bergelson 2000). Observations were first transformed by adding one to each observation. Significance of fixed effects was assessed as described above for stem length. To evaluate the significance of random effects, we used the covtest option to obtain Z-tests, which tested whether

the Z-value of each effect (its variance parameter divided by its approximate standard error) was different from zero (Juenger and Bergelson 2000). Because results obtained from PROC MIXED and GLMM800 did not differ qualitatively and because the data violated the assumptions of traditional linear analysis, we present only results from GLMM800.

Population variation.—To evaluate whether populations are adapted to their elevation of origin, we used two approaches. First, we examined population-by-site interactions in the analyses described above. A significant population-by-site effect indicates that populations differ in their response to elevation. If a significant population-by-site effect was found for failure time, we compared the confidence intervals of regression coefficient estimates to determine which population and site combinations were significantly different from one another. If a significant population-by-site effect was found for growth or fitness, we used Tukey-Kramer adjusted comparisons of least square means to determine which population and site combinations were significantly different from one another. Second, if populations are locally adapted to their elevation of origin, then fitness should decrease as the difference between elevation of origin and transplant site elevation increases. For each transplant site, we examined the rank correlations of population average annual fitness with the absolute value of the difference between origin and transplant elevations using PROC CORR.

RESULTS

Survivorship.—Significant interspecific differences in survivorship across the elevation gradient were detected for *M. cardinalis* and *M. lewisii* (species, $\chi^2 = 187.09$, $P < 0.0001$; site, $\chi^2 = 3399.33$, $P < 0.001$; species \times site, $\chi^2 = 2022.04$, $P < 0.0001$). Each species showed greater survivorship than the other at its range center (Jamestown, 415 m: *M. cardinalis* $>$ *M. lewisii*, $\chi^2 = 1364.96$, $P < 0.0001$; White Wolf, 2395 m: *M. lewisii* $>$ *M. cardinalis*, $\chi^2 = 32.79$, $P < 0.0001$). At the shared middle elevation range boundary, *M. cardinalis* displayed greater survivorship than *M. lewisii* ($\chi^2 = 469.02$, $P < 0.0001$).

For both species, transplant site had a highly significant effect on survival time in analyses of intraspecific differences in survivorship (Table 1). All sites (Jamestown, 415 m; Mather, 1400 m; and Timberline, 3010 m) were significantly different from the reference site, White Wolf (2395 m), as indicated by regression coefficients different from zero (Table 1). To examine differences among nonreference sites, we constructed Z-tests for comparisons of regression coefficients and found that all pairwise differences among nonreference sites were also significant, although for *M. cardinalis* the difference between Mather (1400 m) and Timberline (3010 m) was only marginally significant after correcting for multiple comparisons (Table 2). Population did not affect survival time for either species (Table 1). For *M. cardinalis*, the population-by-site effect was significant, indicating that populations differ in their response to elevation (Table 1). There was no population-by-site interaction for *M. lewisii* survivorship (Table 1). For both species, the Weibull shape parameter was significantly greater than one (*M. cardinalis*, 1.57

TABLE 1. Analysis of accelerated failure-time models for survival time, using 1339 uncensored values and 1273 right-censored values for *Mimulus cardinalis*, 1339 uncensored values and 1073 right-censored values for *M. lewisii*, and a Weibull distribution.

Species	Variable	df	Estimate	SE	χ^2	P
<i>M. cardinalis</i>	Site	3			350.2	<0.0001
	(Jamestown, 415 m)	1	-0.69	0.13	28.2	<0.0001
	(Mather, 1400 m)	1	0.47	0.11	16.6	<0.0001
	(White Wolf, 2395 m)	0	0	0		
	(Timberline, 3010 m)	1	0.22	0.10	4.6	0.0330
	Population (Levels not shown)	5			6.2	0.2913
	Site \times population (Levels not shown)	15			30.4	0.0105
<i>M. lewisii</i>	Site	3			4964.5	<0.0001
	(Jamestown, 415 m)	1	-5.06	0.22	530.7	<0.0001
	(Mather, 1400 m)	1	-2.08	0.22	91.1	<0.0001
	(White Wolf, 2395 m)	0	0	0		
	(Timberline, 3010 m)	1	-0.67	0.25	7.0	0.0084
	Population (Levels not shown)	5			3.1	0.6902
	Site \times population (Levels not shown)	15			16.1	0.3784

± 0.04 , *M. lewisii*, 1.13 ± 0.02), indicating that the risk of mortality increased monotonically with time.

Mimulus cardinalis survival during the first year was highest at the 1400 m range border, intermediate at high elevations beyond the upper range limit (2395 and 3010 m), and lowest at the 415 m range center, although first-year survival was relatively high across all sites (Fig. 2A). There was an early decrease in survival during the first growing season at 415 m, whereas survival at 2395 and 3010 m was high during the first growing season and declined over the first winter. During subsequent years, survivorship remained highest at the 1400 m upper range boundary and was reduced at high elevations beyond the range (2395 and 3010 m). Examination of regression coefficient confidence limits for each site and population indicated that the *M. cardinalis* population-by-site interaction arose because of differences in elevation response between the low elevation Mariposa Creek population (590 m) and the midelevation Tenaya Creek population (1210 m; data not shown). At 1400 m, the Mariposa Creek population survived longer than the Tenaya Creek population, and the converse was true at 3010 m.

Mimulus lewisii survivorship was highest at high elevations (2395 and 3010 m) and intermediate at the lower elevation range boundary (1400 m; Fig. 2B). At 415 m, beyond the lower range limit, *M. lewisii* suffered high mortality during the first growing season. The few individuals surviving after one growing season at 415 m died over the winter, resulting in 100% mortality within one year. At 1400 m, *M. lewisii* experienced pulses of mortality at the end of the second and third growing seasons. At the high elevation range center

(2395 m) and upper range boundary (3010 m), mortality rates were roughly constant and low.

Growth.—Transplant site had a highly significant effect on growth of both species (Table 3). There were no significant population or population-by-site effects for *M. cardinalis* growth, but both population and population-by-site effects were significant for *M. lewisii* growth (Tables 3, 4). *Mimulus cardinalis* growth was greatest at the range center (415 m), intermediate at the upper elevation range boundary (1400 m), and greatly reduced at high elevations beyond the range (2395 and 3010 m; Fig. 3A). The difference in growth between the 415 m range center and the 1400 m range margin was not statistically significant in Tukey-Kramer adjusted post-hoc contrasts. Growth of *M. lewisii* peaked at the 2395 m range center and was reduced at both the lower (1400 m) and upper (3010 m) range margins (Fig. 3B). High mortality resulted in small sample size for *M. lewisii* at 415 m ($n = 2$). The *M. lewisii* population main effect is due to the difference between the Warren Fork population (2750 m) and all other populations except for the Tuolumne River population (1320 m; Table 4). The *M. lewisii* population-by-site interaction indicates that populations differ in their growth response to elevation. This difference is driven in part by the greater increase in growth at the range center (2395 m) versus the upper range margin (3010 m) for two middle elevation populations (Tuolumne River, 1320 m, and Tamarack Creek, 1900 m) relative to two high elevation populations (Snow Creek, 2690 m, and Warren Fork, 2750 m; Table 4).

Fitness.—Significant inter- and intraspecific differences in fitness across the elevation gradient were detected (Table 5).

TABLE 2. Pairwise differences of transplant site regression coefficients from accelerated failure-time analyses.

	<i>M. cardinalis</i>		<i>M. lewisii</i>	
	Z	P	Z	P
Jamestown (415 m) vs. Mather (1400 m)	7.9	<0.0001	22.4	<0.0001
Jamestown (415 m) vs. Timberline (3010 m)	6.6	<0.0001	23.2	<0.0001
Mather (1400 m) vs. Timberline (3010 m)	1.9*	0.0265	7.5	<0.0001

* After correcting for multiple comparisons, only Z-scores >2.1 remain significant at the 0.05 level.

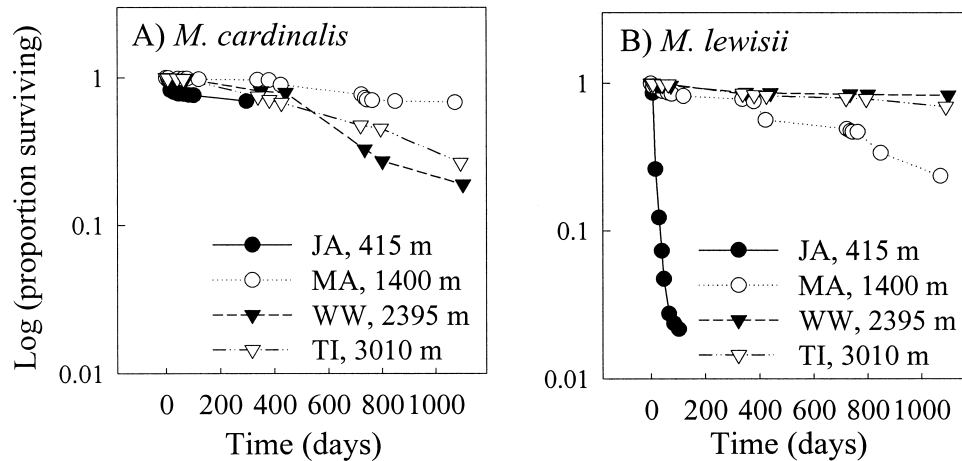


FIG. 2. Survivorship at each transplant site. (A) *Mimulus cardinalis*. (B) *M. lewisii*. Transplant site abbreviations as follows: JA, Jamestown; MA, Mather; WW, White Wolf; TI, Timberline.

Each species was more fit than the other at its range center (Fig. 4). At the shared midelevation range boundary (1400 m), *M. cardinalis* outperformed *M. lewisii*. The species did not differ in fitness at 3010 m, the upper range limit for *M. lewisii* and beyond the upper range limit for *M. cardinalis*.

Mimulus cardinalis fitness was highest at the 415 m range center, reduced at the 1400 m upper range border, and zero or near zero at high elevations beyond the upper range limit (Fig. 4). The significant main effect of population arose from the difference between a population from midelevation (Tenaya Creek, 1210 m) and all other populations except for the Tuolumne River population (1320 m; Tables 5, 6). The population-by-site interaction was driven in part by populations differing in the degree of decrease in fitness from 1400 m to 2395 m. The Moore Creek (830 m), Bear Creek (860 m), and Snow Creek (950 m) populations displayed a greater decrease in fitness from 1400 to 2395 m than did the Tenaya Creek (1210 m) and Tuolumne River (1320 m) populations (Table 6). Similarly, the Mariposa Creek population (590 m) displayed a greater decrease in fitness from 415 m to 1400 m than the Tenaya Creek population (1210 m; Table 6).

Mimulus lewisii fitness was highest at the 2395 m range center and zero or near zero at the lower (1400 m) and upper (3010 m) range borders and beyond its lower range limit (415 m; Fig. 4). Population did not significantly affect *M. lewisii* fitness (Table 6), but the significant population-by-site effect indicated that *M. lewisii* populations differ in reaction norms

of fitness versus elevation (Table 6). This interaction was the result of populations differing in the degree of increase in fitness at 2395 m, relative to the uniformly low fitness at other sites. The Tuolumne River (1320 m), Tamarack Creek (1920 m), and Tioga Road (2580 m) populations showed a large increase in fitness at 2395 m, whereas the Porcupine Creek (2400 m), Snow Creek (2690 m), and Warren Fork (2750 m) populations did not show a statistically significant increase in fitness at 2395 m (Table 6).

To determine whether populations are adapted to their position within the elevation range, we also examined the rank correlation between average fitness and the difference in elevation between transplant site and population origin. If populations are adapted to position within the elevation range, then the correlation between fitness and the difference between origin and transplant elevations should be negative, indicating that fitness declines as the transplant environment becomes more different from the native environment. No correlations were statistically significant, suggesting that fitness variation among populations is not caused by differences in elevation of origin (Table 7).

DISCUSSION

Geographic Variation in Fitness

The results of this reciprocal transplant experiment support the hypothesis that species are most fit at their range center

TABLE 3. Linear mixed model analysis of variance summary for log-transformed average annual stem length. *F*-tests for fixed effects constructed by SAS MIXED procedure, with denominator degrees of freedom (df_D) obtained from the Satterthwaite approximation. Significance of random effects (indicated by [R]) determined by likelihood ratio tests.

Source	<i>M. cardinalis</i>			<i>M. lewisii</i>		
	df	df_D	<i>F</i>	df	df_D	<i>F</i>
Site	3	14.6	25.2****	2	69.1	18.8****
Population	5	71.6	1.4	5	69.2	4.5**
Site \times population	15	1257.0	0.5	10	1258.0	3.2***
Block (site) [R]	—	—	**	—	—	****
Sire (population) [R]	—	—	ns	—	—	ns
Dam (population) [R]	—	—	ns	—	—	ns

ns, $P > 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$.

TABLE 4. Population differences in average annual stem length. For *Mimulus lewisii*, population means sharing the same letter are not significantly different. Number superscripts indicate significant differences among levels of the population main effect, where populations sharing the same number are not significantly different. Differences determined by Tukey-Kramer adjusted comparisons of least square means in analysis of log-transformed data. High mortality resulted in small sample size ($N = 2$) for *M. lewisii* at Jamestown.

Species	Population	Mean (SE)			
		Jamestown, 415 m	Mather, 1400 m	White Wolf, 2395 m	Timberline, 3010 m
<i>M. cardinalis</i>	Mariposa Ck., 590 m	68.4 (2.7)	29.7 (2.4)	11.3 (0.8)	5.3 (0.3)
	Moore Ck., 830 m	63.0 (4.3)	29.3 (2.8)	10.8 (0.6)	5.6 (0.5)
	Bear Ck., 860 m	63.6 (3.8)	27.3 (1.8)	12.1 (0.9)	5.1 (0.3)
	Snow Ck., 950 m	60.8 (4.0)	26.5 (2.0)	10.6 (0.7)	5.6 (0.3)
	Tenaya Ck., 1210 m	65.8 (4.9)	23.0 (1.6)	9.7 (0.7)	5.2 (0.3)
	S. Fork, 1320 m	59.4 (4.2)	24.3 (1.9)	10.5 (0.7)	5.5 (0.3)
<i>M. lewisii</i>	S. Fork, 1320 m ^{1,2}	—	15.8 ^a (1.4)	28.2 ^{de} (1.5)	9.0 ^a (0.5)
	Tamarack Ck., 1920 m ¹	—	18.6 ^{ab} (1.3)	30.2 ^e (1.7)	9.0 ^a (0.5)
	Porcupine Ck., 2400 m ¹	—	17.0 ^{ab} (1.3)	26.3 ^{cde} (1.3)	9.2 ^a (0.5)
	Tioga seep, 2580 m ¹	—	16.6 ^{abc} (1.3)	28.5 ^{cde} (1.7)	9.8 ^a (0.7)
	Snow Ck., 2690 m ¹	—	18.3 ^{abc} (1.6)	25.2 ^{bcd} (1.5)	8.7 ^a (0.5)
	Warren Fork, 2750 m ²	—	—	21.1 ^{bc} (1.0)	7.5 ^a (0.4)
	JA	—	12.0 ^a (1.1)	—	—

and become increasingly maladapted as the distance from the range center increases. Both species exhibited the greatest average fitness at elevations central within their range (415 m for *M. cardinalis*, 2395 m for *M. lewisii*) and reduced fitness at elevations at the range margin (1400 m for both species, 3010 m for *M. lewisii*). Furthermore, both species exhibited zero or near-zero fitness when transplanted beyond their present elevation range limits (2395 and 3010 m for *M. cardinalis*, 415 m for *M. lewisii*).

However, the underlying causes of this fitness variation differed between the species. *Mimulus cardinalis* survival in the first year was relatively high across all elevations. High fitness at the low elevation range center arose due to high growth and fecundity. At higher elevations beyond the upper range boundary, although many *M. cardinalis* were able to survive, growth was greatly reduced and few individuals were able to reach reproductive maturity. The few *M. cardinalis* able to flower at 2395 m did so in September, after most *M.*

lewisii stopped flowering, and did not bear mature seeds before senescence. By contrast, *M. lewisii* encountered a strong survival barrier beyond its lower elevation range limit. Mortality during the first growing season at 415 m was rapid; most individuals died within one month of planting and all were dead within one year. Because experimental planting was timed to match the phenology of natural populations, transplanted seedlings were exposed to the climate they would have encountered if naturally dispersed to low elevation. A large preliminary study conducted at 415 m in June 2000 produced nearly identical results (*M. cardinalis* survival: 85.8% after four months, 76.3% after 10 months, $N = 962$; *M. lewisii* survival: 6.2% after four months, 0% after 10 months, $N = 953$), supporting the inference that observed patterns of mortality are not exaggerated by unusually harsh conditions in 2001.

Our findings are largely congruent with the patterns of variation in performance across elevation described by Hie-

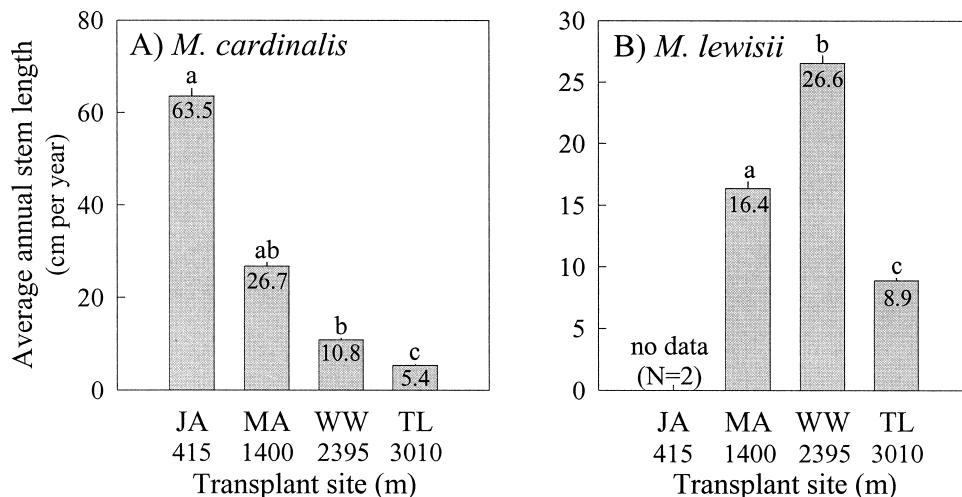


FIG. 3. Species' average annual stem length + SE at each transplant site (mean values given within each bar). (A) *Mimulus cardinalis*. (B) *M. lewisii*. For each species, site means sharing the same letter are not significantly different based on Tukey-Kramer adjusted comparisons of least square means in analysis of log-transformed data. Note that species are graphed on different scales. Transplant site abbreviations as in Figure 2.

TABLE 5. Generalized linear mixed model analysis of average annual fitness, using a gamma distribution and a log link function. *F*-tests for fixed effects constructed by SAS MIXED procedure, with denominator degrees of freedom (*df_D*) obtained from the Satterthwaite approximation. Significance of random effects (indicated by [R]) determined by *Z*-tests.

Source	df	df _D	<i>F</i>
Site	3	4052.0	1342.2***
Species	1	86.3	2495.8****
Site × species	3	4052.0	1795.0****
Population (species)	10	85.4	4.1***
Site × population (species)	30	4049.0	4.5****
Sire (population, species) [R]	—	—	ns
Dam (population, species) [R]	—	—	ns

ns, *P* > 0.05; ** *P* < 0.01; *** *P* < 0.001; **** *P* < 0.0001.

sey et al. (1971) in their landmark reciprocal transplant study of *M. cardinalis* and *M. lewisii*. They demonstrated low survival and reproductive capacity of *M. cardinalis* at high elevation and low survival and growth of *M. lewisii* in a coastal climate. However, in their study, *M. cardinalis* displayed the highest survivorship in the low elevation Stanford transplant garden (30 m), whereas we observed greatest survivorship in the middle elevation Mather garden, which highlights the important difference between the low elevation maritime environment and the low elevation foothills environment. A second difference between the present findings and the previous study is the relatively poor performance of *M. lewisii* that we observed at Timberline, where Hiesey et al. (1971) found that *M. lewisii* achieved its highest performance. This difference is likely due to several factors, including our addition of White Wolf as an intermediate transplant site between Mather and Timberline, exclusion of populations from the northern race of *M. lewisii*, and use of seedlings rather than vegetatively propagated clones. Our use of seedlings provided missing information about the performance of early life-history stages, which may be critical for population establishment (Lee et al. 2003; Zacherl et al. 2003). It is also important to note that none of the transplant sites used by Hiesey et al. (1971) were central within the elevation range of *M. lewisii*.

TABLE 6. Population differences in average annual fitness (in units of flowers per year). For each species, population means sharing the same letter are not significantly different. Number superscripts indicate significant differences among levels of the population main effect, where populations sharing the same number are not significantly different. Differences determined by Tukey-Kramer adjusted comparisons of least square means in generalized linear mixed model analysis.

Species	Population	Mean (SE)			
		Jamestown, 415 m	Mather, 1400 m	White Wolf, 2395 m	Timberline, 3010 m
<i>M. cardinalis</i>	Mariposa Ck., 590 m ¹	16.54 ^a (2.89)	4.10 ^{cd} (0.44)	0.01 ^e (0.01)	0 ^e
	Moore Ck., 830 m ¹	12.93 ^{ab} (2.37)	6.04 ^c (0.68)	0.03 ^e (0.01)	0 ^e
	Bear Ck., 860 m ¹	11.33 ^{ab} (2.10)	5.62 ^c (0.64)	0.13 ^e (0.03)	0 ^e
	Snow Ck., 950 m ¹	11.50 ^{ab} (2.14)	5.28 ^c (0.49)	0.04 ^e (0.02)	0 ^e
	Tenaya Ck., 1210 m ²	9.47 ^b (2.14)	2.98 ^d (0.55)	0.04 ^e (0.01)	0 ^e
	S. Fork, 1320 m ^{1,2}	12.74 ^{ab} (2.93)	3.49 ^d (0.37)	0.08 ^e (0.02)	0 ^e
<i>M. lewisii</i>	S. Fork, 1320 m	0 ^a	0.08 ^a (0.03)	0.48 ^{bcd} (0.07)	0.07 ^a (0.02)
	Tamarack Ck., 1920 m	0 ^a	0.14 ^{ab} (0.04)	0.56 ^{cd} (0.09)	0.01 ^a (0.01)
	Porcupine Ck., 2400 m	0 ^a	0.11 ^{ab} (0.03)	0.26 ^{abc} (0.04)	0.04 ^a (0.02)
	Tioga seep, 2580 m	0 ^a	0.13 ^{abc} (0.04)	0.78 ^d (0.11)	0.05 ^a (0.02)
	Snow Ck., 2690 m	0 ^a	0.12 ^{ab} (0.04)	0.28 ^{abc} (0.06)	0.02 ^a (0.01)
	Warren Fork, 2750 m	0 ^a	0.03 ^a (0.02)	0.12 ^a (0.03)	0.01 ^a (0.01)

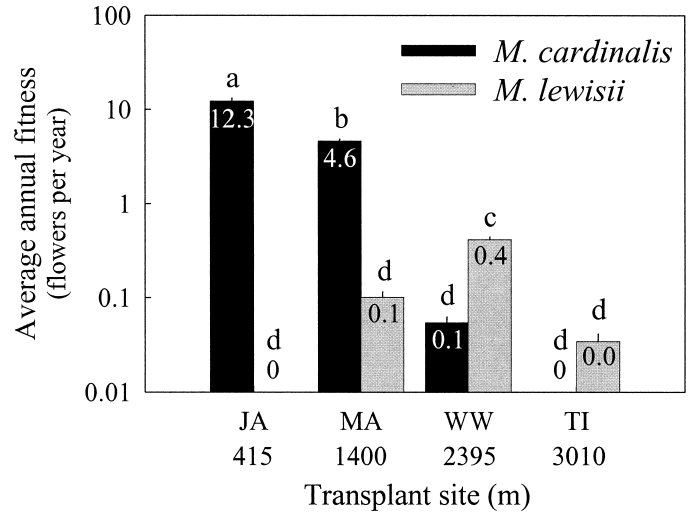


FIG. 4. Species' average annual fitness (in units of flowers per year) + SE at each transplant site (mean values given within each bar). Means sharing the same letter are not significantly different based on Tukey-Kramer adjusted comparisons of least square means in generalized linear mixed model analysis. Transplant site abbreviations as in Figure 2.

Although many reciprocal transplants have been conducted between areas within species' ranges, far fewer have transplanted individuals beyond the range (Gaston 2003). However, transplants beyond the range often display reductions in fitness components such that long-term persistence of populations is unlikely (see references in Gaston 2003 and Geber and Eckhart 2005). Several other experiments have demonstrated reduced growth, delayed phenology, and, as a result, reduced fecundity of plant species transplanted beyond their northern or high elevation range margins, as we found for *M. cardinalis* (Prince 1976; Davison 1977; Woodward 1990; Asselin et al. 2003). Analogous patterns of delayed development have been reported for aphids (Gilbert 1980) and butterflies (Crozier 2004) transplanted beyond their latitudinal range limits. In these examples, fitness reductions generally are not due to a single environmental event such as a

TABLE 7. Spearman rank correlation between population average annual fitness and [transplant elevation – population origin elevation].

Site (m)	<i>M. cardinalis</i>		<i>M. lewisii</i>	
	r	Prob > r	r	Prob > r
415	-0.02	0.90	0.03	0.87
1400	0.07	0.69	-0.02	0.90
2395	-0.08	0.64	0.04	0.83
3010	0.01	0.96	0.11	0.53

frost or to a single vulnerable life-history stage, but rather result from the gradual accumulation and cascading effects of fitness reductions at many stages.

In contrast to expectations for northern or upland range limits, it is generally assumed that climate becomes more permissive for most organisms and that biotic interactions become relatively more important in setting southern or lowland distribution limits (MacArthur 1972; Woodward 1975; Sievert and Keith 1985; Hersteinsson and Macdonald 1992; Richter et al. 1997; Scheidel et al. 2003; Cleavitt 2004). Similarly, a recent study of fitness variation across the parapatric ranges of *Clarkia xantiana* subspecies along a west-to-east gradient implicated biotic interactions such as competition, herbivory, and pollination as causes of fitness declines when subspecies were transplanted beyond the range boundary (Geber and Eckhart 2005). Few studies of southern or lowland distributions limits find severe abiotic limitation as we have documented for *M. lewisii* at low elevations. Many plants showed signs of heat stress such as leaf scorching and reduced leaf size, and subsequent growth chamber studies have demonstrated strikingly similar patterns of mortality when *M. lewisii* are grown under the high temperatures characteristic of low elevation (A. Angert, unpubl. data).

Population Variation in Fitness

Although population and population-by-site effects were frequently statistically significant, they were of much smaller magnitude than site effects. We detected differences among *M. cardinalis* populations but not *M. lewisii* populations in survivorship at different elevations. For *M. cardinalis*, the low elevation Mariposa Creek population (590 m) displayed greater survivorship at middle elevation than the midelevation Tenaya Creek population (1210 m), but at high elevation the Tenaya Creek population had greater survivorship than the Mariposa Creek population. The direction of reversal in survivorship is consistent with adaptation of the range margin Tenaya Creek population to higher elevations, but it is not entirely consistent with adaptation to position within the range because of the poor relative performance of the midelevation population at middle elevation. No other differences among populations were significant, indicating that differentiation among populations for survivorship is low.

We detected differences among *M. lewisii* populations but not *M. cardinalis* populations in average annual stem length. Local adaptation of growth traits may take two possible forms. First, populations could exhibit genetically based clinal differences in growth in which populations originating from higher elevations display reduced growth rates or short

stature across all environments (Clausen et al. 1940). Alternatively, populations could show decreasing growth with increasing distance from population origin. We find some slight evidence that the former scenario is true for *M. lewisii*. The population from the highest elevation of origin was significantly smaller than other populations based on differences among levels of the population main effect. Also, populations from the midelevation range margin showed a greater increase in growth at the range center than two high elevation populations. Hiesey et al. (1971) also found some evidence for genetically based clinal growth differences among *M. lewisii* populations. However, because in their study populations were collected from throughout the geographic ranges of both species, the wide latitudinal and longitudinal distances that separated most populations from the transplant sites are not easily separated from the effects of adaptation to elevation.

For both species, we detected variation among populations in reaction norms for average annual fitness versus transplant site, but these differences were not consistent with the hypothesis that populations are adapted to their elevation of origin. For example, at Mather (1400 m), the nearby Tuolumne River populations of both species (1320 m) were not more fit than the distant *M. cardinalis* Mariposa Creek (590 m) or *M. lewisii* Warren Fork (2750 m) populations. The *M. cardinalis* population-by-site interaction resulted from populations differing in the degree of decrease in fitness with increasing elevation. The significant *M. lewisii* population-by-site interaction arose because three populations (Tuolumne River, 1320 m; Tamarack Creek, 1920 m; and Tioga Road seep, 2580 m) displayed significantly increased fitness at 2395 m versus other elevations and three did not (Porcupine Creek, 2400 m; Snow Creek, 2690 m; and Warren Fork, 2750 m). Reaction norms for fitness did not cross, but instead differed in the slope of decrease from the range center to range margins, suggesting that populations do not exhibit symmetrical ‘home’ elevation advantages. This conclusion is supported by the lack of significant correlations between population mean fitness and the difference in elevation between population origin and transplant site.

Gene Flow and Selection

Range limits arise where populations are no longer able to adapt sufficiently to local environmental conditions. Low fitness of both species at their range margin suggests that adaptation to the marginal environment is hindered. Likewise, weak differentiation among populations within each species indicates that populations from the range margin have been unable to adapt to environmental conditions at the range boundary.

A similar lack of strong regional adaptation was observed in a recent study of *Clarkia xantiana* transplanted within and beyond the range boundary, in which populations showed much greater fitness declines when moved beyond the range than when transplanted to a different location within the range (Geber and Eckhart 2005). The weak adaptation to position of origin within the range observed in these studies is striking given the number of documented examples of adaptive differentiation both among populations at geographic scales

(e.g., Clausen et al. 1940; Grant 1963) and within populations at extremely local spatial scales (e.g., Bradshaw 1960; Schemske 1984). Many species display ecotypic variation along elevation gradients (Clausen et al. 1940; Oleksyn et al. 1998; Jonas and Geber 1999). The populations used in the present experiment were sampled along an elevation gradient that imposes variation in several important abiotic environmental variables, including length of growing season and temperature. Species may not be able to adapt to environmental conditions at the range margin if they lack appropriate genetic variation upon which selection can act or if differential natural selection is weak relative to the homogenizing effects of gene flow (Mayr 1963; Kirkpatrick and Barton 1997).

The interplay of gene flow and selection along environmental gradients or between discrete environments is important to several models of range or niche evolution (Holt and Gaines 1992; Kawecki 1995; Kirkpatrick and Barton 1997; Gomulkiewicz et al. 1999; Holt 2003). For example, Kirkpatrick and Barton (1997) modeled the evolution of a quantitative character determining fitness across a one-dimensional environmental gradient. The character evolved under stabilizing selection toward an optimum phenotype that varied with the environmental gradient. Population density in their model depended on dispersal, density-dependent population regulation, and the degree of mismatch between the optimum and population mean phenotypes. Stable range limits arose when gene flow imposed a strong constraint on local adaptation, as when dispersal was high or the environmental gradient was steep.

Although the focus of the Kirkpatrick and Barton model was on the swamping effects of gene flow, it also modeled adaptive trade-offs between environments because no single phenotype was optimal across the entire environmental gradient. Models of niche evolution explicitly consider the role of trade-offs between habitats in limiting species distributions, finding that selection to improve adaptation to environments outside of the niche may be weak due to the demographic asymmetry between habitats within versus outside of the niche (Kawecki 1995; Holt 1996; Gomulkiewicz et al. 1999). In a recent model of range evolution, Holt (2003) explicitly modeled the feedback between the evolution of dispersal and the evolution of habitat specialization (i.e., trade-offs) in a two-habitat model where neither habitat was initially outside of the niche. In this model the evolutionary dynamics of the geographic range depended on the shape of adaptive trade-offs between habitats and the initial habitat distribution of the population. For instance, a species initially specialized to one habitat may evolve habitat generalization if mutations that increase adaptation to a new habitat have little cost to fitness within the present habitat. Conversely, if a linear and symmetrical trade-off in fitness between two habitats exists, evolution will favor increased specialization to whichever habitat the species initially resides in. These models highlight the need to understand the relative roles of dispersal, adaptive trade-offs, and demographic asymmetries between habitats in range evolution. Further work is necessary to understand how these components interact to determine the elevation range limits of *Mimulus cardinalis* and *M. lewisii*.

Dispersal.—Elevation distributions offer a tractable experimental analog to latitudinal distributions at larger spatial scales, because both arise along continuous environmental gradients and encompass multiple populations. The environmental gradient from the center to the edge of elevation and latitude ranges is also similar, with temperature and length of growing season decreasing to the north and at higher elevations, although the rate of change in environmental parameters across space is greater for elevation than for latitude gradients. Indeed, a change of 100–200 m in elevation is roughly equivalent to a change of one degree in latitude (Criddle et al. 1994; Flebbe 1994). Due to the steepness of the environmental gradient across elevation, for a given dispersal distance, individuals encounter a more different environment than if dispersing across latitude, making it more likely that marginal populations may be swamped by centrally adapted phenotypes at elevation range boundaries than at latitudinal range boundaries (Kirkpatrick and Barton 1997).

Little is known about mechanisms of dispersal of *M. cardinalis* and *M. lewisii* seeds. Because both species are found in riparian habitats, it is possible that seed dispersal via downstream currents provides a mechanism for primarily unidirectional long-distance dispersal among populations, setting up an interesting dichotomy between *M. cardinalis* and *M. lewisii* at their shared midelevation range boundary. A net flux of migrants downstream would imply that the *M. lewisii* midelevation range limit may be subject to swamping gene flow from high elevation central populations, but that the *M. cardinalis* midelevation range limit is not. However, gene flow via pollen may show the opposite pattern due to the greater flight distance of hummingbirds, the primary pollinator of *M. cardinalis*, compared to bumblebees, the primary pollinator of *M. lewisii*. Estimations of F_{ST} among populations of each species are in progress to begin to identify patterns of gene flow among central and marginal populations of each species.

Adaptive trade-offs.—Because central and marginal populations of each species display few adaptive differences versus elevation, interspecific comparisons are necessary to understand adaptive trade-offs across the elevation gradient. Since their recent common ancestor, *M. cardinalis* and *M. lewisii* have evolved differences that restrict their distributions to different areas of the complex environmental gradient associated with elevation. Specialization to different elevation ranges suggests that different phenotypes are necessary for fitness at low versus high elevations. Estimation of the strength and direction of selection on phenotypic traits across the elevation gradient, in combination with genetic mapping of quantitative trait loci, will identify traits under selection at high versus low elevation and the underlying genetic architecture of those traits (A. L. Angert, H. D. Bradshaw, and D. W. Schemske, unpubl. data). Experimental evolution of segregating hybrid populations at low and high elevation will also illuminate whether there are fitness costs of specialization to low versus high elevation (A. L. Angert, H. D. Bradshaw, and D. W. Schemske, unpubl. data). Together, these studies will help elucidate mechanisms of adaptive trade-offs between low and high elevation environments. In conjunction with estimates of gene flow between central and

marginal populations, we hope to understand what causes and constrains adaptation to different elevation ranges.

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APPENDIX

Source populations and reciprocal transplant sites. Abbreviations: M, Mariposa county; T, Tuolumne county; YNP, Yosemite National Park; SNF, Stanislaus National Forest; INF, Inyo National Forest; na, not applicable.

Species/Garden	Location (county, nearest landmark)	Waterway	Coordinates	Elevation (m)
<i>M. cardinalis</i>	M, Mariposa	Mariposa Ck.	N 37.4867°, W 119.9690°	590
	M, SNF, Buck Meadows	Moore Ck.	N 37.7770°, W 120.0635°	830
	M, Midpines County Park	Bear Ck.	N 37.5258°, W 119.9185°	860
	M, Triangle Rd. bridge	Snow Ck.	N 37.5171°, W 119.8374°	950
	M, YNP, Yosemite Valley	Tenaya Ck.	N 37.7427°, W 119.5616°	1210
	T, YNP, Carlon Day Use Area	S. Fork Tuolumne R.	N 37.8152°, W 119.8657°	1320
<i>M. lewisii</i>	T, YNP, Carlon Day Use Area	S. Fork Tuolumne R.	N 37.8152°, W 119.8657°	1320
	M, YNP, Tamarack Flat	Tamarack Ck.	N 37.7572°, W 119.7399°	1920
	M, YNP, Porcupine Flat	Porcupine Ck.	N 37.8072°, W 119.5478°	2400
	T, YNP, Tioga Rd.	Unnamed seep	N 37.8129°, W 119.5035°	2580
	M, YNP, May Lake	Snow Ck.	N 37.8365°, W 119.4944°	2690
	Mono, INF, Tioga Pass	Warren Fork Lee Vining R.	N 37.9520°, W 119.2261°	2750
Jamestown	T, Quartz Mountain	na	N 37.9173°, W 120.4212°	415
Mather	T, Camp Mather	na	N 37.8855°, W 119.8553°	1400
White Wolf	T, White Wolf Ranger Station	na	N 37.8718°, W 119.6507°	2395
Timberline	Mono, Saddlebag Lake	na	N 37.9615°, W 119.2808°	3010