

VARIATION AMONG POPULATIONS OF *CLARKIA* *UNGUICULATA* (ONAGRACEAE) ALONG ALTITUDINAL AND LATITUDINAL GRADIENTS¹

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We investigated phenotypic variation in 15 traits in greenhouse-grown plants from 16 populations of *Clarkia unguiculata* from three elevational habitats and six latitudinal transects. Populations from the lowest and highest elevations were geographically and ecologically marginal within the species' range. We (1) describe patterns of trait variation with elevation and latitude; (2) compare latitudinal variation between marginal and central areas of the species' range; and (3) compare patterns of variation within *C. unguiculata* to interspecific patterns within the genus. Although there was some evidence that traits varied clinally (i.e., increased/decreased monotonically) along environmental gradients, interaction effects between altitude and latitude dominated patterns of variation. For most traits, latitudinal trends at the low-elevation margin of the species' range differed from trends at mid- and high-elevation areas. Based on interspecific comparisons, populations at the hotter, more arid ends of both environmental gradients were expected to have rapid development, small flowers and vegetative size, low levels of herkogamy and protandry, and high rates of gas exchange. Instead, we found that while some traits were correlated with one gradient in the expected way (e.g., development time with elevation, gas-exchange physiology with latitude), all traits were not consistently associated with each other along both gradients, and intraspecific patterns of variation differed from interspecific patterns.

Key words: altitude; *Clarkia unguiculata*; elevation; floral traits; geographic variation; marginal and central populations; morphology; Onagraceae; phenology; physiology.

The study of natural variation in ecologically important traits has a long history in evolutionary biology (Turesson, 1922; Ford, 1954; Clausen, Keck, and Hiesey, 1948; see Endler, 1977, 1986; Linhart and Grant, 1996). The primary motivation for studies of this nature is to further our understanding of the roles of natural selection, gene flow, and genetic drift in shaping levels of adaptation and in affecting the distribution and abundance of species.

In plants, studies have shown that populations are often genetically differentiated with respect to life history, morphology, and physiology, at both small and large spatial scales (Turesson, 1922; Clausen, Keck, and Hiesey, 1948; Hiesey and Milner, 1965; Langlet, 1971; Briggs and Walters, 1984; Linhart and Grant, 1996). Studies of variation at geographic scales have focused on two broad areas of inquiry. First, what are the patterns and causes of variation in ecologically important traits in relation to environmental gradients, such as latitude or elevation? Second, what are the patterns and causes of trait variation between populations at the center vs. the margin of a species' geographic range?

There is extensive documentation of intraspecific variation in ecologically important traits along environmental gradients (see references in Stebbins, 1950; Endler, 1977, 1986; Briggs and Walters, 1984). In many cases,

patterns of trait variation across environmental gradients have suggested hypotheses concerning their adaptive significance. Adaptive explanations become more convincing (a) when the same pattern of trait variation in relation to an environmental gradient is found in different parts of a species' range, (b) when functionally related traits vary in coordinated fashion across an environmental gradient, or (c) when intra- and interspecific patterns of trait variation in relation to an environmental gradient are similar. It is rare, however, that researchers document character variation along replicate transects paralleling the same environmental gradient throughout a species' range, as most studies are confined to variation along a single transect (but see Reinartz, 1984a, b; Thorpe and Baez, 1987; Nevo, Carver, and Beiles, 1991; Endler, 1995). Furthermore, many studies of character variation within species along environmental gradients focus on one or a few traits (e.g., Lacey, 1988; Winn and Gross, 1993; but see Reinartz, 1984a, b). Lastly, it is not often that intraspecific variation can be compared to patterns of interspecific variation.

Geographic range margins are often thought to represent ecologically marginal environments for a species (Mayr, 1963; Lewontin, 1974; Antonovics, 1976; Lewis and Lewis, 1955). As such, they provide an important arena for empirical and theoretical studies on the limits to adaptation (Mayr, 1963; Antonovics, 1976; Hoffmann and Parsons, 1991; Geber and Dawson, 1993; Lewis and Lewis, 1955). Thus, researchers have attempted to identify the environmental factors that demarcate range margins (Connell, 1961; Gill and Hawksworth, 1961; Woodward and Williams, 1987; Root, 1993), and to pinpoint the traits that may be important in limiting species' distributions at margins (St. Clair and Gregory, 1990; Shuter and Post, 1990; Loik and Nobel, 1993; see Lewis and

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Lewis, 1955). In addition, comparisons have been made of levels of genetic variation between marginal and central populations because marginal populations are predicted to be depauperate in variation as a result of genetic drift, inbreeding, or strong selection (Lewontin, 1974; Brussard, 1984; Ohlson, 1989; Hoffmann and Parsons, 1991; Rice and Mack, 1991a; Blows and Hoffmann, 1993; Johansson, 1994; Stewart and Nilsen, 1995). Theoreticians have also modeled the interplay between selection and gene flow in shaping adaptation to ecological and/or geographical margins (Garcia-Ramos and Kirkpatrick, 1997; Kirkpatrick and Barton, 1997), and empirical work has suggested that gene flow between ecologically favorable and unfavorable habitats may swamp adaptation to marginal environments (Rice and Mack, 1991b; Stanton and Galen, 1997). Lastly, marginal populations have been considered for their value in conservation efforts because they may harbor unusual phenotypes and genotypes (Millar and Libby, 1991; Lesica and Allendorf, 1994).

In this study, we characterized geographic variation in ecologically important traits across latitudes and between marginal and central populations in the annual plant *Clarkia unguiculata* Lindl. (Onagraceae), as part of a broader investigation of patterns and causes of the limits to adaptation in this species. *Clarkia unguiculata* is a primarily outcrossing endemic to California. It is highly variable in morphology and phenology, but typically germinates with the onset of winter rains and flowers in early summer (Lewis and Lewis, 1955).

The species has a U-shaped geographic distribution in the mountains that ring the San Joaquin Valley, from Mendocino, Butte, and Plumas Counties in the North, to Los Angeles County in the South (Fig. 1). It occurs along the coastal mountains to the west, and the Sierra Nevada to the east, but is not found in the San Joaquin Valley proper. Several disjunct populations also occur in San Diego County (Lewis and Lewis, 1955). *Clarkia unguiculata* typically grows in fairly discrete populations, on slopes in oak or oak–Gray pine woodland, and occasionally in chaparral. At low-elevation arid regions, populations occur in grassland and oak savanna habitat with sparse or no tree cover (Lewis and Lewis, 1955; Jonas, 1997).

In species with a U-shaped distribution, there are not only high- and low-latitudinal range margins, but there are also interior and exterior margins along the inner and outer edges of the U. For *C. unguiculata*, the interior margin in the Sierra Nevada coincides with low-elevation foothills at the edge the San Joaquin Valley, while the outer margin corresponds to a high-elevation limit on the western slopes of the mountains. *Clarkia unguiculata* reaches its highest abundance, both in terms of population numbers and size, at mid-elevations in the Sierra Nevada; at low- and high-elevation margins, populations are sparser and smaller (Jonas, 1997). The pattern of declining abundance from the “center” toward the periphery of the range is typical of many species (Brown, 1984; Lawton, 1993).

On the western slopes of the Sierra Nevada, precipitation increases, while temperature and potential evapotranspiration decrease, with elevation and latitude. The elevational gradient in climate has been of particular in-

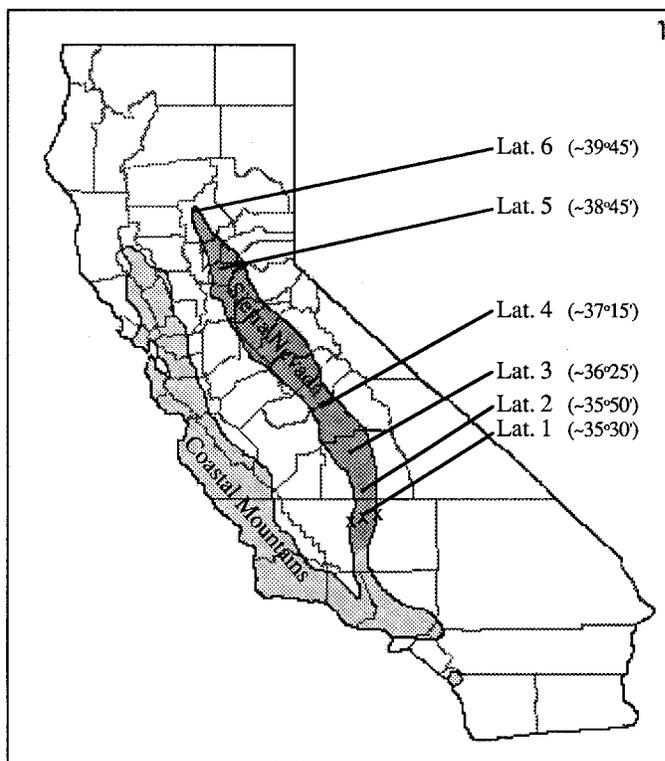


Fig. 1. Map of California, showing the U-shaped geographic range of *Clarkia unguiculata* (light shading) and area of this study (dark shading). The locations of the elevational transects at six latitudes are shown. In the four southernmost transects, one population was sampled from low-, mid-, and high-elevation habitats (x). At the two northernmost transects, only populations from mid- and high-elevation habitats were sampled. In all transects the low- and high-elevation populations were located at the margin of the species range and the mid-elevation population was located in the central region of highest abundance.

terest in studies of character evolution within the section *Phaeostoma* of the genus *Clarkia*, of which *C. unguiculata* is a member. Several species in *Phaeostoma* occur in or beyond the low-elevation margins of *C. unguiculata* habitat, where the growing season is shortened by the early onset of summer drought (Lewis and Lewis, 1955; Vasek, 1964, 1968). Comparisons among species of *Phaeostoma* have suggested that low-elevation arid habitats are associated with earlier reproduction, smaller vegetative and floral size, and increased rates of self-fertilization due to reduced herkogamy and protandry (Vasek, 1964; Vasek and Sauer, 1971). In addition, common garden studies of two *C. unguiculata* populations have suggested that, within the species, populations from lower elevations flower earlier (Vasek, 1964, 1971). Based on these associations, early flowering has been interpreted as an adaptation to avoid the early onset of summer drought at low elevations, both among species and within *C. unguiculata*. However, the extent to which the differences found between the two populations of *C. unguiculata* represent a consistent pattern of clinal variation within the species is unknown. It is also unclear whether the other traits that are associated with hotter, drier environments interspecifically (small vegetative and floral size, reduced herkogamy, and protandry) are associated in this way

TABLE 1. Latitude and elevation of the 16 study populations of *Clarkia unguiculata*.

Transect	Habitat	Latitude	Elevation (m)	Location
Lat. 1	LOW	35°25'	270	Lower Kern River Canyon, Kern Co.
	MID	35°32'	600	Old Kern River Canyon Rd., Kern Co.
	HIGH	35°32'	850	Old Kern River Canyon Rd., Kern Co.
Lat. 2	LOW	35°50'	270	Old Springs Rd., Tulare Co.
	MID	35°52'	490	Deer Creek Rd., Tulare Co.
	HIGH	35°50'	1220	CA Hot Sprigs, Tulare Co.
Lat. 3	LOW	36°20'	140	Lemoncove, Tulare Co.
	MID	36°25'	760	Mineral King Rd., Tulare Co.
	HIGH	36°30'	1370	General's Hwy, Tulare Co.
Lat. 4	LOW	37°40'	150	Willms Rd., Stanislaus Co.
	MID	37°	460	Pittman Hill Rd., Fresno Co.
	HIGH	37°	790	Tollhouse Rd., Fresno Co.
Lat. 5	MID	38°43'	200	Salmon Falls Rd., El Dorado Co.
	HIGH	38°48'	400	Hwy 49, El Dorado Co.
Lat. 6	MID	39°35'	300	Cherokee Rd., Butte Co.
	HIGH	39°55'	600	Tobin, Plumas Co.

with *C. unguiculata*. Lastly, it is not known whether north–south gradients in latitude and high–low gradients in elevation result in similar patterns of character variation and association among populations of *C. unguiculata*.

We characterized variation in phenology, floral and vegetative morphology, and gas-exchange physiology among populations of *C. unguiculata* from three elevational habitats at six latitudes representing most of the species' range in the Sierra Nevada (Fig. 1). This design allowed us to compare patterns of trait variation along replicate environmental gradients. Using “common garden” experiments, we examined population differentiation in the context of (1) describing patterns of trait variation with elevation and latitude; (2) comparing patterns of trait variation across latitudes between marginal and central populations; and (3) comparing patterns of trait variation along environmental gradients within *C. unguiculata* to interspecific patterns of variation.

MATERIALS AND METHODS

Study populations—During the summer of 1995, we collected seed from populations along six elevational transects in the Sierra Nevada spanning a latitudinal range from Kern County in the South, to Plumas County in the North (Fig. 1, Table 1). At the four southernmost transects (latitudes 1–4), we collected seed from one population in each of three habitat types: (1) low-elevation oak savanna sites had no or widely spaced tree cover (usually *Quercus douglasii*) and an understory dominated by grasses; (2) mid-elevation oak woodland sites were characterized by relatively open cover of *Q. douglasii* and *Q. wislizenii* and some scattered California buckeye (*Aesculus californica*) and Gray pine (*Pinus sabiniana*); (3) high-elevation oak woodland sites were characterized by a similar species assemblage, but the overstory contained a higher proportion of evergreen species (for a description of elevational gradients in California oak woodland, see Griffin [1977]). At all four latitudes, the low- and high-elevation populations were from the lowest and highest elevations, respectively, at which *C. unguiculata* could be located after an extensive search. They therefore represent the low- and high-elevation margins (both geographic and ecological) of the species' range in the Sierra Nevada. Mid-elevation sites were chosen in the

TABLE 2. Traits scored on *Clarkia unguiculata* individuals grown in a common garden.

Life history
Days to germination (d)
Days from germination to first flower (d)
Floral traits
Petal length (mm)
Petal width at widest point (mm)
Style length (mm)
Length of long stamen (mm)
Herkogamy ^a (mm)
Protandry (d)
Vegetative development and morphology
Node of first flower
Average internode length ^a (mm)
Total number of nodes at reproductive maturity
Height at reproductive maturity (cm)
Area of largest leaf (cm ²)
Physiology
Maximum photosynthetic rate (A_{max}) ($\mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) ^b
Stomatal conductance (g) ($\text{mmol H}_2\text{O}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) ^b

^a Traits calculated from primary measurements (see text).

^b Traits measured on plants from the four southernmost latitudes only.

central area of highest abundance. *Clarkia unguiculata* did not occur in the low-elevation habitat type at the two northernmost transects (latitudes 5–6). Consequently, only the mid- and high-habitat types are represented in these two transects. The distance between populations within an elevational transect was at least 5 km.

Study populations contained >300 individuals each, and collections were made when >95% of the plants in a given population had produced at least one seed capsule (dates of 95% maturity ranged from late June to early August). In each upright capsule, a few to hundreds of seeds may develop; in the field, the seeds disperse passively as the capsule dehisces in mid-late summer. We collected at least one mature but unopened capsule from the main stem of 100 individuals in each population. Individuals were 1 m apart on a transect placed through the middle of the population. If one transect did not yield capsules from 100 plants, we sampled plants from a second transect perpendicular to the first. Seeds were stored dry in coin envelopes for 2 mo until the beginning of the greenhouse study.

Climate information—There is a predictable gradient of temperature, precipitation, and potential evapotranspiration (potE) along the elevational cline through *C. unguiculata*'s range in the Sierra Nevada. Major (1977) reported climes in long-term averages of these three abiotic parameters along West-to-East transects at five latitudes in the southern Sierra from Kern Canyon (35°30'N) in the South, to the hills above Stockton (38°N) in the North. At each latitude, temperature decreased with increasing elevation at average rates of –0.35 to –0.65° C/100 m. Precipitation increased at a rate of +94 to +208 mm/100 m, and potE decreased at –13 to –36 mm/100 m. Ten-year (1986–1995) monthly averages of precipitation from weather stations positioned along the elevational gradient at latitude 3 of this study support this trend (Fig. 2, data from California Department of Water Resources, Division of Flood Management). Vasek and Sauer (1971) also found that, at lowland *C. unguiculata* sites in Kern County, soil drying occurred more rapidly and earlier in the season, and average temperatures were higher than at higher elevation populations.

Latitudinal gradients in climatic factors in this region of California are less well documented. However, Major (1977) presented evidence of increasing annual precipitation and decreasing temperatures with latitude at grassland elevations and at 500 and 1000 m. Data from precipitation stations ~200 m below/above our high-elevation sites at latitudes

TABLE 3. Analyses of covariance of phenological, morphological, and physiological traits in *Clarkia unguiculata*. Latitude refers to the north-south positions of the six elevational transects; habitat refers to the low-, mid-, and high-elevation locations of populations within transects. Nonsignificant interaction terms were dropped for the final analyses. Contrasts of latitudinal variation among elevations were restricted to populations from the four southernmost latitudes (see text).

Source	Days to germination		Days to flower		Petal length		Petal width		Style length		Stamen length	
	df	F	df	F	df	F	df	F	df	F	df	F
Block		1.40		1.63		1.48		0.83		1.30		2.03
Seed mass	11	6.10	11	7.39	11	3.88	11	2.14	11	3.32	11	2.15
Latitude	1	12.40*	1	20.74*	1	6.66*	1	30.10*	1	44.02*	1	32.76*
Habitat	3	28.62*	3	31.94*	3	3.46	3	0.17	3	5.14	3	6.18
Latitude × habitat	1	4.40*	1	15.27*	1	5.11*	1	13.32*	1	17.10*	1	12.72*
Block × latitude	8	—	8	—	8	—	8	—	8	—	8	—
Block × habitat	—	—	—	—	—	—	—	—	—	—	—	—
Block × seed mass	—	—	—	1.99	—	—	—	—	—	—	—	—
Habitat × seed mass	—	—	11	—	—	—	—	—	—	—	—	—
Latitude × seed mass	—	—	—	—	—	—	—	—	—	—	—	—
Model R ²	—	0.41	—	0.60	—	0.47	—	0.60	—	0.60	—	0.52
Latitudinal contrasts												
High vs. mid		8.89*		11.60*		2.43		6.96*		5.89*		3.03
Contrast R ²	3	0.11	3	0.15	3	0.04	3	0.10	3	0.08	3	0.04
Low vs. (high and mid)		1.74		15.87*		8.63*		22.98*		32.68*		23.51*
Contrast R ²	3	0.03	3	0.21	3	0.13	3	0.28	3	0.36	3	0.28

* Significant based on sequential Bonferroni test at a tablewide significance level $\alpha = 0.05$ (see text).

1, 2, and 4–6 suggest that the trend is similar at these elevations (Fig. 3).

Common garden study—In October 1995, 24 plants were randomly selected from the 100 seed plants sampled at each study population for use in the common garden experiment. Five seeds from each plant were planted together directly into tube-shaped pots (655.48 cm³; Deepots[®], Stuewe & Sons, Inc., Corvallis, Oregon) filled with fritted clay (for a description of the properties of fritted clay, see van Bavel, Lascano, and Wilson [1978]). A small plug of Metro-Mix soil was placed at the top of each pot to prevent seeds from falling down between clay particles. Pots were arranged in a randomized block design, with two pots from each population in each of 12 blocks. Each pot was 6.35 cm from its nearest neighbor. This spacing was maintained for the duration of the study.

At the outset, plants were kept in a controlled environment chamber with diurnally ramped temperatures (10°C night, 22°C day) and 10 h of light provided by two 1000-W high-pressure sodium bulbs, and were watered evenly with a mist nozzle two times daily. Pots were observed daily for germination. Ninety-nine percent of pots had at least one emergent individual. After 8 d in the chamber, plants were moved into the greenhouse, where they were grown under natural light for 6 d, after which time each block was positioned directly below a 400-W high-pressure sodium bulb. Plants were fertilized once per wk with a 125-ppm solution of EXCEL (15-5-15, plus micronutrients) beginning 10 d after planting. Greenhouse temperatures ranged between 18°C and 32°C. Plants were watered at least once per d, with extra watering when needed. At 17 d after planting, seedlings were thinned to one per pot, leaving the tallest individual in all cases. The germination date for the remaining individual was assumed to be the date of first germination for its pot. During the course of the experiment, 56 plants developed striking morphological abnormalities due to an apparent viral infection. These plants were not included in the analysis.

Each individual was scored for 15 traits (Table 2). Flowering time was scored as the number of days from germination to petal opening of the first flower. All flower measurements were made on the first flower using electronic calipers (Mitutoyo Digimatic, Japan). *Clarkia unguiculata* has two sets of stamens. Measurements were done on the larger set, which has anthers that dehiscence later (closer to the time of

stigma receptivity). Stamen length was measured on the first day of flower opening, and petal and style lengths were measured on the first day of stigma receptivity. Herkogamy was calculated as the difference between style and stamen lengths. Protandry was scored as the number of days from first flower opening (when the pair of short anthers begin to dehiscence) to stigma receptivity.

The phyllotaxis of *C. unguiculata* is generally alternate, but early leaves are oppositely arranged. Data from a subset of individuals indicated that there were no consistent differences among populations in the node at which the switch to alternate leaf arrangement occurs. Therefore, for traits based on node number, each node was counted once in this study, regardless of leaf arrangement at that node. Average internode length was calculated by dividing height to first flowering node by the number of nodes to first flower. Total number of nodes and plant height were measured on the first day of stigma receptivity of the first flower. Height was measured from the base of the plant to the apical meristem of the main stem. Leaf area was measured using a LI-COR 3000 leaf area meter (LI-COR, Lincoln, Nebraska). Plants were grown for 4 mo, at which time flowering had finished and plants had begun to senesce.

Instantaneous rates of gas exchange were measured on a leaf area basis using a CIRAS-1 portable open gas-exchange system at ambient levels of CO₂ (PP Systems, Herts, UK). Measurements were done on one block per day between 1000 and 1400, as this was determined to be the period of greatest gas-exchange activity based on several days of diurnal measurements (C. Jonas, Cornell University, unpublished data). All measurements were made on the newest fully expanded leaf of each individual, just before most plants began flowering. Leaves were allowed to acclimate to conditions within the cuvette until the photosynthesis curve reached a plateau. Light levels were 1500–1900 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ photosynthetic photon flux density (PPFD) (the range was <100 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PPFD within blocks), provided by a supplemental source within the CIRAS-1 cuvette. Leaf temperatures ranged from 22.7° to 28.9° during measurements. Calculations of photosynthetic rate (A_{max}) and stomatal conductance (g) were based on equations of von Caemmerer and Farquhar (1981). Measurements were made only on populations from the four southern transects, where all three elevational habitats were represented.

Differences among plants grown in a common environment reflect

TABLE 3. Extended.

Herkogamy		Protandry		Node of first flower		Average internode length		Total number of nodes		Height		Leaf size		A_{max}		g	
df	<i>F</i>	df	<i>F</i>	df	<i>F</i>	df	<i>F</i>	df	<i>F</i>	df	<i>F</i>	df	<i>F</i>	df	<i>F</i>	df	<i>F</i>
11	0.52	11	1.91	11	1.35	11	3.62	11	1.70	11	7.74*	11	0.05	11	2.28	11	7.09*
1	0.10	1	0.16	1	1.98	1	0.14	1	0.30	1	1.61	1	0.05	1	5.12	1	2.45
3	5.21*	3	32.68*	3	31.54*	3	8.39*	5	21.41*	3	21.95*	3	4.53*	3	13.05*	3	11.79*
1	5.26	1	0.17	1	6.54	1	1.23	2	6.52	1	8.20	1	3.15	2	8.40*	2	3.15
8	4.29*	8	2.84*	8	4.54*	8	16.72*	—	—	8	10.37*	8	6.12*	—	—	—	—
55	1.46	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
22	2.39*	—	—	—	—	—	—	—	1.72	—	—	22	1.72	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2	3.08	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	2.47	—	—	5	2.47	—	—	—	—
—	0.56	—	0.36	—	0.49	—	0.48	—	0.52	—	0.50	—	0.52	—	0.33	—	0.42
3	1.28	3	1.28	3	0.04	3	8.67*	—	—	3	10.41*	3	0.88	—	—	—	—
—	0.02	—	0.02	—	0.15	—	0.13	—	—	—	0.16	—	0.01	—	—	—	—
3	5.50*	3	5.50*	3	2.75	3	24.41*	—	—	3	12.31*	3	10.15*	—	—	—	—
—	0.07	—	0.07	—	0.05	—	0.28	—	—	—	0.16	—	0.15	—	—	—	—

some combination of effects due to the genotype of the study individual and the genotype and growth environment of the maternal plant. In studies like this one, where the main goal is to examine genetically-based differences among populations, some care must be taken to factor out maternal effects. Seed size is the best documented route by which maternal genotype and environment can affect offspring traits in plants (Roach and Wulff, 1987). Maternal effects have been shown to influence germination, survivorship, seedling biomass, adult plant size, and competitive ability through effects on seed size (see references in Schaal, 1984; Roach and Wulff, 1987). To control as much as possible for maternal effects on the traits of interest, maternal seed mass was used as a covariate in all analyses. Five seeds from each maternal capsule were weighed on a electronic microbalance (XM1000 P, Sartorius Instruments, McGaw Park, Illinois) for an estimate of average seed mass.

Data analysis—Traits were analyzed using a mixed-model ANCOVA (JMP, SAS Institute, Inc., Cary, North Carolina) of the form: trait = seed mass + latitude + habitat + block + interaction terms + error. Block was a random effect. Three- and four-way and nonsignificant two-way interaction terms (at $\alpha = 0.1$) were dropped from the model for the final analyses. Several traits were analyzed using transformed data to correct for heterogeneity of variances in the original data set (residuals were tested using Levene's test for homogeneity of variances). Days to germination, protandry, and node of first flower were log transformed, largest leaf size was square-root-transformed, and stomatal conductance (g) was squared for the final analysis. Homogeneity of variances was improved in all cases, however, the hypothesis of equal variances was rejected by Levene's test for transformed values of days to germination, leaf size, and g . Normal probability plots of the residuals from the ANCOVA analyses for all traits indicated normal distributions.

Main effects and interactions were tested for significance by a sequential Bonferroni procedure at an overall $\alpha = 0.05$ (Rice, 1989). For each main effect or interaction effect, traits were ranked in order of P values obtained from the ANCOVA analysis, from smallest (P_1) to largest (P_k). For each trait of rank i , the significance of the effect was tested at an α level of $0.05/(1 + k - i)$.

For traits showing a significant latitude by habitat effect, we used a series of contrasts designed to partition the interaction effect SS into parts due (1) to differences between mid- and high-elevation popula-

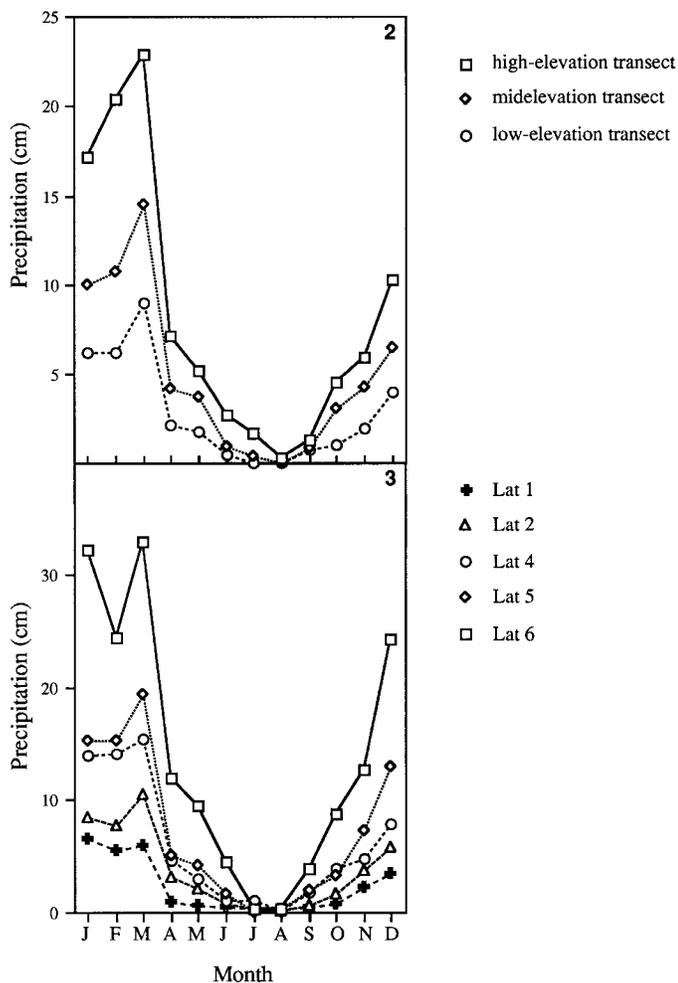
tions across latitudes, and (2) to differences between low- vs. mid- and high-elevation populations across latitudes (C. McCulloch, Cornell University, personal communication). For these contrasts, we used data from the four southernmost transects only, where all three elevations were represented. F values obtained for each trait were tested for significance by a sequential Bonferroni procedure at a "tablewide" level of $\alpha = 0.05$ within each contrast (Rice, 1989).

To examine whether traits exhibited clinal variation (i.e., monotonic increasing or decreasing) across elevational habitats, we computed the Spearman rank correlation between the population mean values for each trait and habitat (ranked 1–3 from low- to high-elevation habitats). All 16 populations were included in the calculation of the correlation between a trait and elevational habitat, because, in spite of the often significant latitude by habitat interaction effect on a trait (see Results), there were simply too few populations to calculate a separate correlation at each latitude. To examine whether traits exhibited clinal variation across latitudes, we computed the Spearman rank correlation between the population mean values for each trait and latitude, including all 16 populations, and then separately for populations from low-, mid-, and high-elevational habitats. This method of examining clinal variation does not adjust for correlation between traits among populations. Traits that are correlated among populations will show similar patterns of variation across elevation or latitude.

RESULTS

Effects of seed mass on trait variation—Seed mass, which is a potential source of maternal influence on trait variation, had no significant effect on any life history, floral, vegetative, or physiological trait, based on the sequential Bonferroni analysis. Because seed mass was a covariate in all analyses, differences among populations in trait values most likely represent true genetic differentiation.

Patterns of trait variation—There were significant differences among elevational habitats in days to germination, days to first flower, and A_{max} and among latitudes in all traits (Table 3). Thus, traits varied more widely across



Figs. 2–3. Monthly precipitation averaged over the years 1986–1995 (data from California Department of Water Resources). 2. At high, mid, and low elevations along a transect at Latitude 3 of this study. 3. At five stations near high-elevation populations at five latitudes.

latitudes than across elevations, as might be expected from the greater variation in precipitation across latitudes than across elevations (Figs. 2, 3), and from the greater distance between elevational transects.

Spearman rank correlations indicated that the following traits showed clinal (i.e., monotonically increasing/decreasing) variation with elevation across all populations combined: days to germination and flowering, and node of first flower increased with elevation, while there was a tendency for petal size to decrease with elevation (Table 4). Clinal variation with latitude across all populations combined was found for petal, style, and stamen lengths, node of first flower, total number of nodes, A_{\max} , and g (Table 4, latitude, all populations). The morphological characters increased in value with latitude, while physiological traits decreased with latitude. These clinal patterns were often not statistically significant when correlations were calculated from the smaller number of populations at a single elevation, but they were of the same direction (see Table 4). For a few traits, significant clinal variation across latitude was found at one or more

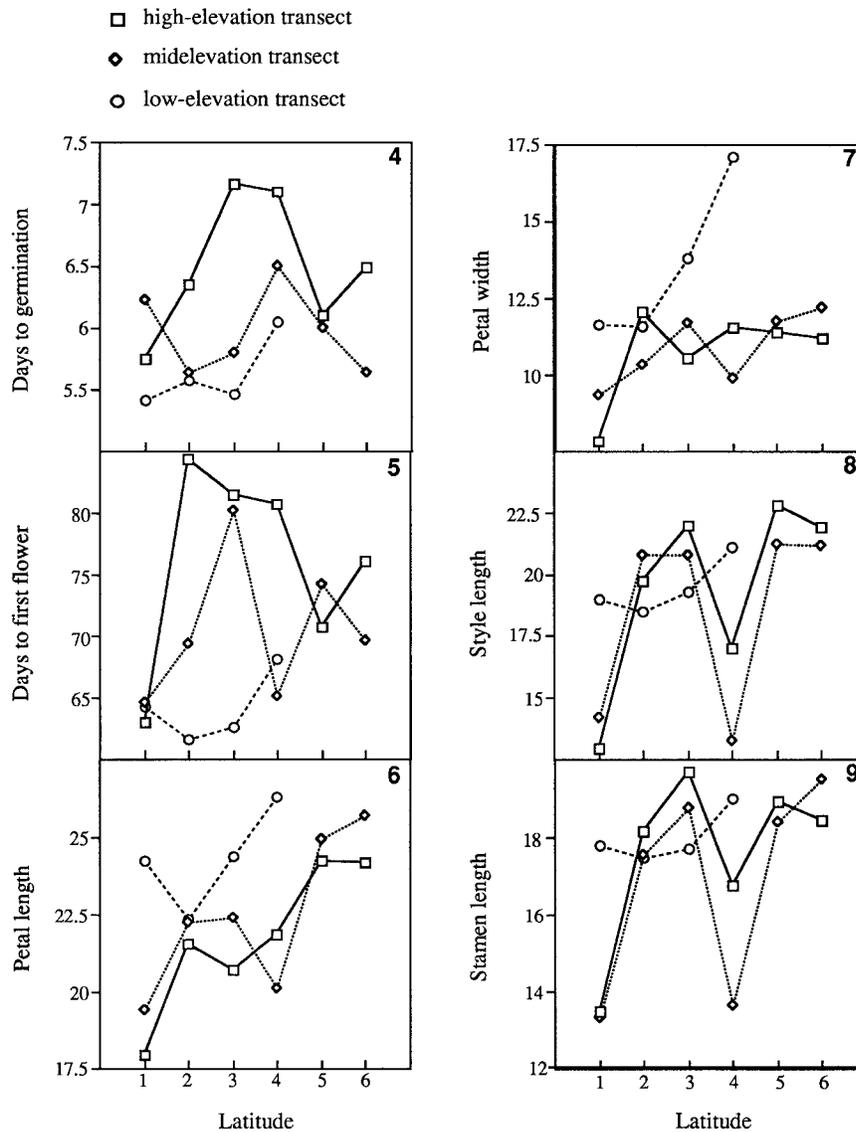
TABLE 4. Spearman rank correlations between populations mean values for each trait and (a) latitude and (b) habitat (= elevation). Separate correlations were calculated for all populations ($N = 16$), and for populations at high- ($N = 6$), mid- ($N = 6$), and low-elevation ($N = 4$) habitats across latitudes. Correlations in bold type are statistically significant at $P < 0.05$; underlined correlations are significant at $P < 0.1$.

Trait	Latitude				Habitat (all populations)
	All populations	High	Mid	Low	
Days to germination	0.33	0.31	-0.20	0.63	0.70
Days to flowering	0.41	-0.09	0.49	0.40	0.67
Petal length	0.56	0.89	0.83	0.80	-0.48
Petal width	0.33	0.20	0.83	0.80	<u>-0.46</u>
Style length	0.63	0.60	0.60	0.80	0.21
Stamen length	0.57	0.49	0.71	0.40	0.08
Herkogamy	<u>0.44</u>	0.71	-0.03	1.00	0.15
Protandry	0.75	0.71	0.37	1.00	0.15
Node of first flower	0.56	0.54	0.26	1.00	0.55
Internode length	-0.32	-0.20	0.03	-1.00	-0.34
Total nodes	0.75	0.81	0.60	0.80	0.28
Total height	0.04	-0.26	0.09	0.00	0.31
Area of largest leaf	0.38	0.54	0.43	-0.40	0.01
A_{\max}	-0.76	-1.00	-0.40	-1.00	-0.03
g	-0.89	-0.80	-1.00	-1.00	0.18

elevations but not for all populations combined (e.g., petal width, internode length).

In general, traits showing clinal variation with latitude differed from those showing clinal variation with elevation, except for node of first flower. In the case of flower size, clinal patterns across latitude appeared to be in the opposite direction to clinal patterns across elevations. Latitudinal and elevational trends appeared to be quite different for traits related to the propensity for selfing (style, stamen lengths, herkogamy, and protandry), and for gas-exchange physiology.

For all traits except number of nodes, A_{\max} , and g , there was a highly significant latitude by habitat interaction, indicating that the pattern of trait variation across latitudes differed among low-, mid-, and high-elevation populations. Contrasts of trait variation between mid- and high-elevation populations across latitude were significant for days to germination, days to first flower, petal width, style length, internode length, and plant height (i.e., 6 out of 12 traits; Table 3). Contrasts between low vs. mid and high transects were significant for all traits except days to germination and node of first flower (i.e., 10 out of 12 traits; Table 3). The first set of contrasts accounted for a lower fraction of the interaction variance than the second set, as judged by the coefficients of partial determination for the contrasts (Table 3). Thus, mid- and high-elevation populations varied more nearly in parallel with each other across latitudes than they did with the low-elevation populations (Figs. 4–18). The closer parallelism in trait variation between mid- and high-elevation populations was most obvious for leaf size, style length, stamen length, and herkogamy, all of which decreased at mid-latitudes (latitude 3 and/or 4) relative to neighboring latitudes (2–3, 5) at both elevations (Figs. 4, 8–10, 16).



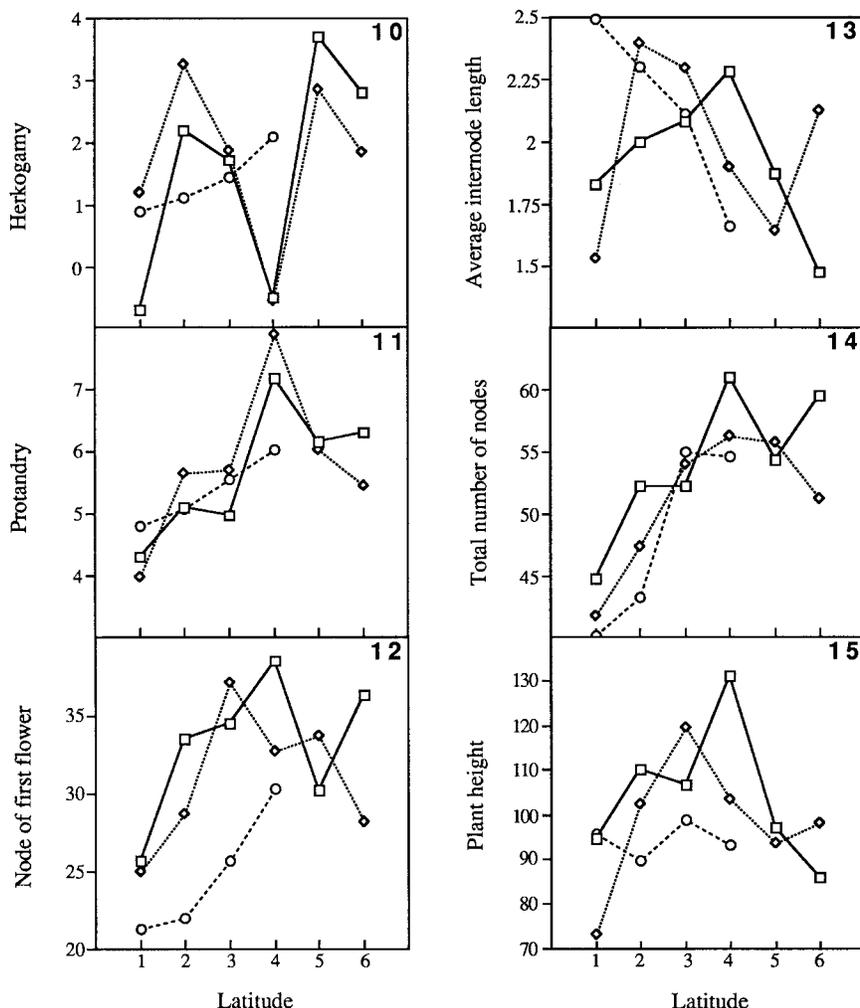
Figs. 4–18. Least squares mean character values for high-, mid-, and low-elevation populations at six latitudinal transects. **4.** Days to germination (d). **5.** Days from germination to opening of first flower (d). **6.** Petal length (mm). **7.** Petal width (mm). **8.** Style length (mm). **9.** Stamen length (mm). **10.** Herkogamy (mm). **11.** Protandry (d). **12.** Node of first flower. **13.** Average internode length (mm). **14.** Total number of nodes. **15.** Plant height (cm). **16.** Area of largest leaf (cm²). **17.** A_{max} ($\mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). **18.** g ($\text{mmol H}_2\text{O}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). (Values reported for Figs. 11, 12, 16, and 18 are back-transformed least squares means.)

DISCUSSION

Environmental gradients and intra- vs. interspecific comparisons—Elevational gradients are thought to have played a large role in interspecific differentiation within the genus *Clarkia*. In the section *Phaeostoma*, early onset of flowering has been interpreted as an adaptive mechanism to avoid the heat and desiccation stress of early summer drought at low elevations. Studies of reproductive timing in these annuals have focused on comparisons between the protandrous, primarily outcrossing *C. unguiculata* and several closely related species that tend to occur in or beyond the low-elevation margins of *C. unguiculata* habitat. These other species, *C. exilis*, *C. springvillensis*, and *C. tembloriensis*, differ from *C. unguiculata* in that they flower earlier, have smaller leaves and floral

parts, lack pubescence on the ovary and calyx, and have less separation between anthers and receptive stigma in time (protandry) and in space (herkogamy) (Lewis and Lewis, 1955; Vasek, 1964, 1968). Within *Phaeostoma*, protandry and herkogamy are highly correlated with outcrossing rate (Moore and Lewis, 1965; Holtsford and Ellstrand, 1992). Thus, among species in the section, there is a suite of traits related to life history, morphology, and breeding system that is associated with the short season of low-elevation habitats.

The association of a self-fertilizing breeding system and early flowering with drier habitats is seen in several other genera as well and has led to the hypothesis that self-fertilization could evolve from outcrossing as a result of selection for rapid development in drought-stressed en-



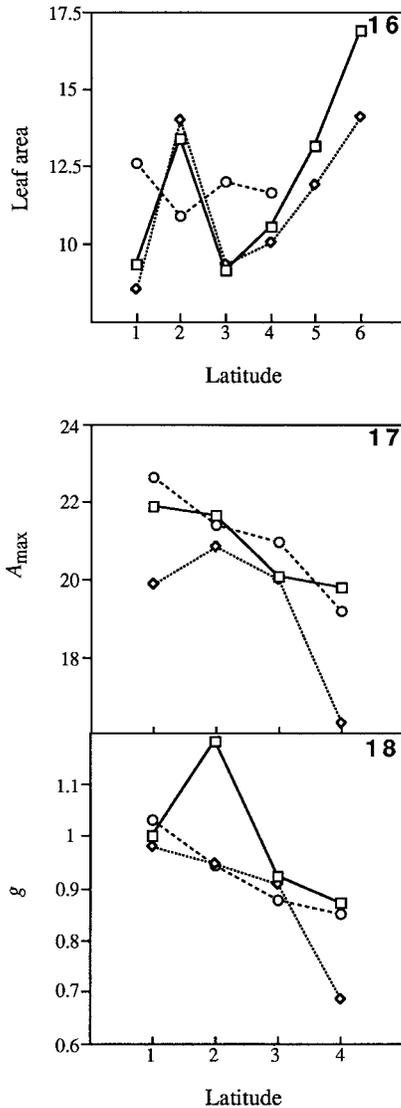
Figs. 4–18. Continued.

vironments (Guerrant, 1984; Diggle, 1992; Eckhart, Geber, and Jonas, 1996). In this scenario, selection for rapid reproduction leads to truncated morphological development resulting in small flowers and, because of allometric relationships, reduced stigma–anther separation. To the extent that plants achieve rapid development by faster growth and an increase in metabolic rate, physiological rates such as photosynthesis and stomatal conductance are also expected to be higher in plants selected for early flowering (Geber and Dawson, 1990; Ehleringer, 1993; Jonas, 1997).

Previous studies of life history and morphology based on a smaller region of *C. unguiculata*'s range have suggested that population differentiation within the species follows the elevational pattern seen among species in *Phaeostoma*. In the Caliente Hills of Kern County, a low-elevation population (305 m) flowered earlier than a high-elevation population (790 m) both in the field and in a greenhouse (Vasek, 1971, 1977; Vasek and Sauer, 1971), and had reduced protandry and a nonsignificant trend toward smaller reproductive parts in the greenhouse (Vasek, 1971, 1977). In a companion to the present study, leaf carbon isotope analysis of greenhouse-grown *C. ungui-*

culata from populations at latitudes 1 and 2 suggested that rates of physiology were negatively correlated with development time and with elevation (Jonas, 1997).

By contrast, the results of this study indicate that early flowering, small vegetative and floral morphology, selfing, and high physiological rates are not always associated in a clinal way in *C. unguiculata*. Low-elevation populations do tend to germinate and flower earlier and to flower at an earlier node than higher elevation populations (Figs. 4, 5, and 12; Table 4), but the elevational pattern is not repeated at all latitudes (as indicated by significant latitude by habitat interaction effects, Table 3). Thus, though there is evidence that some populations from the hottest, most arid habitat have faster development, this trend does not hold in all latitudinal regions of the species' range. There is also no evidence of smaller floral or vegetative size at lower elevations. In fact, petals tend to be larger at lower elevations (see Table 4, Figs. 6–7). Finally, there is no indication that low-elevation populations have reduced herkogamy or protandry, or higher rates of photosynthesis and stomatal conductance (Table 4, Figs. 10–11, 17–18). If interspecific patterns are indeed a product of selection for early summer drought



Figs. 4–18. Continued.

avoidance, the results of our study suggest that the same evolutionary processes have not acted inter- and intra-specifically to shape this suite of traits.

Based on interspecific comparisons along gradients of temperature and aridity, we expected latitude to be negatively correlated with rates of development and photosynthesis and positively correlated with floral and vegetative size in *C. unguiculata*. The evidence for such correlations is equivocal. Spearman rank correlations indicate that node of first flower and flower size (petal, style, and stamen length) decrease, and that gas-exchange rates increase at lower latitudes for all populations combined (Table 4). There are also nonsignificant trends of earlier germination and flowering and reduced herkogamy and protandry at lower latitudes. However, these associations are not always reflected among populations at a single elevation.

In sum, this study found no strong evidence for a consistent association among rapid development, small floral and vegetative size, reduced herkogamy and protandry,

and increased physiological rates at the hotter, more arid ends of latitudinal or altitudinal gradients. Furthermore, while latitudinal and elevational gradients present similar clines in temperature and precipitation, these are not reflected in congruent patterns of character variation in *C. unguiculata*. Lastly, intra- and interspecific patterns of trait variation differ across elevations.

Central and marginal populations and latitude by habitat interaction—We found it visually striking that trait means from mid- and high-elevation populations seemed to vary more nearly in parallel across latitudes compared to low-elevation populations (Figs. 4–16). Contrasts designed to test this observation indicated that, although mid- and high-elevation populations differ significantly in latitudinal patterns of variation for many traits, there is a greater difference between low-elevation populations and populations from the two higher elevations for all traits except days to germination (Table 3).

High- and mid-elevation populations share several unusual patterns of variation that account for part of their statistical divergence from low-elevation populations. At latitude 4, high- and mid-elevation populations have unexpectedly small styles, stamens, and herkogamy, together with unusually high protandry (Figs. 8–11). This pattern of trait association is surprising in that herkogamy and protandry are otherwise positively correlated within and among other populations of *C. unguiculata*, and among other members of the genus (Moore and Lewis, 1965; Holtsford and Ellstrand, 1992; C. Jonas and M. Geber, Cornell University, unpublished data). These populations also share several other floral traits that are unique to this area of *C. unguiculata*'s range. Petals are darker red than in other regions, buds are globose, and sepals separate completely when they reflex at flower opening (C. Jonas, Cornell University, personal observation). At latitude 2, high- and mid-elevation populations have unexpectedly large leaves (Fig. 16). These were the only two sites that had a high frequency of fog cover during the summer of 1995 (C. Jonas, Cornell University, personal observation).

The greater overall divergence in trait values between low- vs. mid- and high-elevation populations may be related to greater divergence in habitat. The low-elevation region of *C. unguiculata*'s range is characterized by a sparse or absent overstory and a grass-dominated understorey, in contrast to well-developed woody overstories and similar understorey species compositions in the upper and central regions. Thus, latitudinal environmental variation may be qualitatively different and lead to different patterns of selection on ecologically important traits between low vs. central and high regions of the species' range. At present, however, we cannot say whether differences in selection history or in levels of gene flow or genetic drift account for the differentiation of low-elevation populations.

Peripheral populations of widespread species are often targeted for conservation effort with the intention of preserving the among-population component of genetic diversity (Lesica and Allendorf, 1994). Despite similar degrees of isolation and population size (C. Jonas, Cornell University, personal observation) and similar elevational distance from the center of *C. unguiculata*'s range, pop-

ulations from high and low margins showed different amounts of similarity to central populations in patterns of trait variation. To the extent that phenotypic divergence reflects genetic divergence, all peripheral populations of *C. unguiculata* may not be equally valuable to the conservation of diversity within species, and divergence among marginal and central populations may correspond to habitat differences.

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