

## MICROTOPOGRAPHY OF MICROBIOTIC CRUSTS ON THE COLORADO PLATEAU, AND DISTRIBUTION OF COMPONENT ORGANISMS

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**ABSTRACT.**—We analyzed the microtopography of microbiotic soil crusts at 3 sites on the Colorado Plateau of southern Utah and investigated distributions of cyanobacteria and several lichens in distinctive microhabitats created by this topography. At all 3 sites the long axes of linear soil mounds were oriented nonrandomly in a NNW–SSE direction. The conspicuous and consistent orientation of soil mounds may result from a combination of physical and biotic processes. Subtle differences across sites in mound orientation and organismal distribution suggest that these variables may be useful in comparing disturbance histories of crusts retrospectively.

Differences in colonization frequencies, abundances, and distributions of microorganisms comprising the crusts, as a function of mound aspect or exposure, suggest that these organisms are associated with particular aspects due to distinctive and favorable microhabitats on these exposures. Polysaccharide sheath material, deposited by cyanobacteria, and associated filaments occurred in greater quantities on ENE than WSW mound exposures, and cover by *Collema* spp. lichens exhibited the same pattern. Colonization of mounds by common lichen species occurred significantly more frequently on ENE than WSW mound aspects at 2 of 3 sites. In contrast, the 3 most common lichen species, aside from *Collema* spp., did not exhibit a tendency for greater cover on ENE than WSW mound aspects. Physiological differences between gelatinous cyanolichens and green-algal lichens may explain the different distributional patterns of *Collema* spp. and the 3 other lichens.

*Key words:* microbiotic crusts, cryptobiotic soil, colonization, microtopography, nonrandom orientation, exposure, *Collema*, lichen, cyanobacteria, disturbance history.

Microbiotic crusts (or cryptogamic, cryptobiotic, and microphytic crusts), consisting of cyanobacteria, algae, lichens, fungi, and mosses growing on soil surfaces, provide the predominant cover for many semiarid and arid regions throughout the world (Fig. 1a). Several researchers have reported on ecological services provided by these crusts: substrate stabilization, nutrient enhancement, and, perhaps, increased moisture availability (Harper and Marble 1988, Isichei 1990, West 1990, Metting 1991, Johansen 1993, Eldridge and Greene 1994, Evans and Johansen 1999). The importance of these effects has been highlighted by increasing levels of anthropogenic disturbances which disrupt microbiotic crusts, reduce services provided, and potentially lead to desertification of some semiarid ecosystems (Johansen et al. 1984, Schlesinger et al. 1990, Belnap 1993, Evans and Ehleringer 1993, Johansen 1993).

Estimated recovery times for disturbed crusts in arid and semiarid regions of the Great Basin (Andersen et al. 1982, Johansen et

al. 1984, Johansen and St. Clair 1986) and the Colorado Plateau (Cole 1990, Belnap 1993) vary in relation to soil type, climate, and component organisms, but full recovery of ecosystem services provided by the crusts is generally conceded to be slow. Recovery rates for cyanobacteria (including the widely distributed *Microcoleus vaginatus*), lichens, and mosses have been estimated at 40 yr, 45–85 yr, and 250 yr, respectively (Belnap 1993). Factors prolonging crust recovery remain poorly explored, and elucidation of these factors may require considering both physical and biological processes.

One possible requisite for crust recolonization by particular species may be the creation of new microhabitats by naturally and gradually occurring changes in the microtopography of crusts and underlying soils. On the Colorado Plateau, well-developed microbiotic crusts often exhibit a consistent and distinctive microtopography composed of elliptically shaped pedicellations (mounds) with short and long axes (Fig. 1a). Pedicellated mounds are small,

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Fig. 1. a, High percent cover by linear crusts on shallow soils in the Needles District of Canyonlands National Park on the Colorado Plateau (note elliptical mounds); b, close-up view of a pedicellated soil mound.

typically 5–15 cm long and up to 7 cm tall from base to crown (Fig. 1b). Although mounds form perhaps the most visually striking of all soil crusts, the processes producing them remain poorly understood (J. Johansen personal communication). Traditionally, their origins have been attributed to a combination of frost-heaving during freeze-thaw cycles in cooler seasons (West 1990) and selective erosion (Metting 1991, Johansen 1993, and see

below), but such causality has yet to be tested explicitly with empirical evidence. As the microtopography of crusts develops through time, microtopographic heterogeneity increases (Cole 1990). The degree of microtopographic heterogeneity may affect both quality and quantity of microhabitats found on resultant mounds. The gradual development of microtopography could therefore result in new microhabitats that afford “safe sites” for colonization

and establishment of early-arriving species (e.g., van der Valk 1992).

In addition, early-arriving species may somehow modify the environment in ways that favor colonization by species that recruit later in the successional sequence. For example, some of the first colonists in succession on crusts of the Colorado Plateau are nitrogen-fixing species, cyanolichens in the genus *Collema* and epiphytic diazotrophic bacteria associated with *M. vaginatus* (Steppe et al. 1996). Such species may affect both absolute and relative availabilities of nutrients to microorganisms. Moreover, several cyanobacteria, particularly the predominant *M. vaginatus* on the Colorado Plateau (Belnap and Gardner 1993), tend to arrive long before *Collema* lichens (Johansen et al. 1984, Belnap 1993), and they secrete polysaccharide sheaths that are left behind as dry, fibrous remains as the organisms continue growing. By binding strongly to soil particles (Belnap and Gardner 1993), this sheath material may impose structure and stability on mounds, contribute to changes in crust microtopography, and even affect moisture penetration and retention (Harper and Marble 1988, Metting 1991, Johansen 1993, Eldridge and Greene 1994, Williams et al. 1999). A better understanding of successional changes in conditions favoring colonization and growth of soil microorganisms may suggest ways in which assisted natural regeneration could enhance recovery rates of disturbed crusts.

The purpose of our study is to characterize the microtopography of crust-covered mounds on shallow soils of the Colorado Plateau and to examine how this microtopography correlates with recruitment, abundance, and distribution of the microorganisms comprising microbiotic crusts. Toward this end, we first examined whether linear mounds exhibit nonrandom compass directions. After confirming directionality, we then determined whether abundances and/or distributions of microorganisms vary in relation to mound aspect.

#### METHODS

Data were taken at sites established (1) near Pothole Point in the Needles District of Canyonlands National Park (109°48'W, 38°10'N, 1585 m elev), (2) at Behind-the-Rocks (BTR) area, approximately 12 miles south of Moab (109°30'W, 38°25'N, 1675 m), and (3) on the

southern lip of White Canyon, near Cheesebox Butte (16 miles west of the junction of route 95 and the turnoff to Natural Bridges National Monument, 110°10'W, 37°40'N, 1525 m). At each of the 3 sites, pinyon-juniper communities with sparse densities of herbs formed the dominant higher plant cover on shallow, sandy substrates, dissected by exposed bedrock. Data were taken on 4 April 1997 and 1 May 1998 at Pothole, 12 October 1997 at BTR, and 26 March and 1 May 1998 at Cheesebox.

Four kinds of data were taken: (1) compass orientations of linear mounds, (2) amounts of cyanobacterial sheath material on opposing long sides of mounds, (3) relative cover of *Collema* spp. (all sites) and 3 other lichen species (Pothole Point only) on opposing long faces of mounds, and (4) numbers of colonization events of lichens on opposing long and short sides of mounds.

#### Mound Orientation

At each site mound orientation was determined for 20 cyanobacterial mounds (mounds without lichens) and 20 lichen mounds (mounds dominated by *Collema* spp. lichen cover). Mounds were located in areas with a mixture of exposed bedrock and sandy soils, including depressions commonly referred to as potholes. We worked within relatively homogeneous, intershrub habitats where direct sunlight would not have been obscured by trees, shrubs, or topographic features. We chose the first 20 mounds of each type haphazardly, with the following qualifications: First, we avoided mounds that had been trampled by livestock, wildlife, and humans. Second, we required mounds to be lichen-free (cyanobacterial mounds) or predominantly *Collema*-covered (lichen mounds), depending on the type of mound being investigated. Third, we used no more than 2 mounds per pothole or soil outcrop. In addition, we worked within arm's length of slickrock, where we could stand without damaging the crust.

Compass measurements were taken along the long mound axes, and orientations in degrees from North (0°) were recorded for axes present between 0° and 180° (Fig. 2). Declination adjustments corrected compass measurements to true North. Since data sets for both cyanobacterial and lichen mounds met the assumptions of parametric statistics, we used an ANOVA to test continuous compass measurements in each of the 2 data sets for site

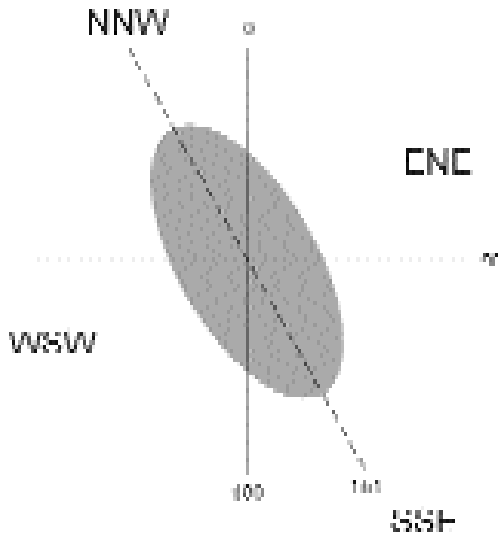


Fig. 2. Diagram demonstrating how microtopographic orientation was determined for elliptical soil mounds (shaded) of microbiotic crusts on the Colorado Plateau.

differences in mean mound orientations. Where significant differences were observed, we employed Tukey pairwise tests to determine which comparisons were responsible for such disparities. Differences in orientations of cyanobacterial and lichen mounds were tested with  $t$  tests independently for each site. Multiple comparisons were taken into account by correcting  $\alpha$  to a tablewise value of 0.05 (Rice 1989).

Subsequently, compass measurements were grouped into a categorical variable with 4 levels (0–45°, 46–90°, 91–135°, 136–180°). A chi-square analysis was used to compare numbers of observations across levels to the expectation, under random orientation, of equal observations per level. Cyanobacterial and lichen mounds were treated separately and for each site independently in these analyses. Multiple comparisons for each mound type required adjustment of critical levels of  $\alpha$  to a tablewise value of  $\alpha = 0.05$  (Rice 1989).

#### Cyanobacterial Sheath Material

Cyanobacterial mounds sampled for mound orientation were subsequently divided in half along their discernible lengthwise axes with a straight edge. After removal of litter, each mound half (substrate and dead and live organic matter) was collected separately until level with the surrounding soil surface. Samples were

placed in appropriately labeled coin envelopes and returned to the lab, where they were dried for approximately 1 wk at 42°C in a Precision oven. Dried filaments and associated sheath material were separated from soil particles (substrate) using progressively finer USA Standard Testing Sieves (1 mm, 710  $\mu\text{m}$ , 600  $\mu\text{m}$ , 500  $\mu\text{m}$ ). Filamentous material that remained after each level of sieving was removed and considered to be cyanobacterial sheath. Material passing completely through all sieves and found in the collection pan was considered to be substrate. (While the substrate fraction assuredly contained some organic matter in addition to substrate, this minor contamination would not have biased our comparisons of mound exposures, and the method's resolution was appropriate to the question we were asking.) Substrate and cyanobacterial material were weighed separately to the nearest 0.01 g for each side of each mound and expressed as a sheath-to-substrate ratio (g of sheath material / g of substrate).

Sheath-to-substrate ratios were analyzed by split-plot ANOVA (to account for paired data) to identify effects of site, exposure, and site-by-exposure interactions. Subsequent multiple pairwise comparisons by the Tukey method determined which sites contributed most strongly to the significant effect of mound exposure. Paired  $t$  tests were used to identify which sites accounted for the significant site-by-exposure interaction. For multiple paired  $t$  tests,  $\alpha$  was corrected to a tablewise value of 0.05 (Rice 1989).

#### Lichen Cover Versus Mound Aspect

The commonness of *Collema* spp., *Placidium squamulosum*, *Psora decipiens*, and *Squammarina lentigera* in preliminary censuses led us to focus on these species in our comparisons of lichen cover in relation to mound aspect. Except for *Collema* spp., which were examined at all 3 sites ( $N = 20$  mounds per site, or 60 mounds in total), these comparisons were made just at Pothole Point ( $N = 20$  mounds per non-*Collema* spp.).

For each of the 4 lichen species independently, we determined visually whether relative cover was greater on either of the opposing long sides. Sampling was restricted to homogeneous intershrub habitat in areas with a mixture of exposed bedrock and shallow,

sandy soils including potholes. We used only mounds oriented in the naturally prevailing compass direction (verified by compass measurements), worked from slickrock on the edges of crusts, and scored a maximum of 2 mounds per pothole or soil outcrop. Mounds were rejected if the species of interest was absent. With these exceptions, we chose the first 20 mounds haphazardly. Excluding mounds used to sample the relative cover of *Collema* spp., those sampled for relative cover were unique and independent of mounds used in other analyses. Mounds sampled for relative cover of *Collema* spp. were scored concurrently for lichen colonization events (see below).

We scored cover as higher on either the ENE or WSW aspect and, depending on sample sizes, analyzed the data by 1 of 2 methods. To determine whether data on *Collema* spp. could be lumped across sites, we compared numbers of mounds with greater *Collema* lichen cover on ENE versus WSW mound exposures across 3 sites using a Fisher's exact test. (Some cell counts were too low for a contingency test.) Site differences were not significant ( $P = 0.835$ ), and we therefore pooled data across sites ( $N = 60$  mounds in total) and used a nonparametric binomial test to evaluate the hypothesis that cover did not differ between the 2 mound exposures. If the numbers of mounds with higher cover on ENE and WSW exposures were equal, then the expected frequency or probability of each outcome under the binomial distribution would be 0.50. We used a  $z$  approximation of the binomial distribution to assess departure of these dichotomous data from expected frequencies of 0.50.

Sample sizes were smaller for non-*Collema* lichens. We therefore used a chi-square test to compare numbers of mounds with greater cover on ENE versus WSW mound faces against the assumption of equal cover on the 2 mound aspects. To correct for multiple comparisons, we adjusted the critical level of  $\alpha$  to a tablewise value of 0.05 (Rice 1989).

#### Lichen Colonization Events

At all 3 sites, lichen colonization events were examined relative to mound aspects for all lichen species encountered. For this study a colonization event was defined as the initialization of growth by lichen on a particular

mound aspect. Because lichens typically grow outward radially from a central point, colonization events could be recognized when thallus surfaces covered a single exposure. When a lichen thallus extended over multiple aspects, it was not evident which exposure had been colonized first. By our definition, colonization might be confused with cases of retracting lichens. However, the observation of radial growth outward from a central point and the absence of senescent thalli consistently indicated colonization rather than retraction.

Twenty mounds were sampled within relatively homogeneous intershrub areas on shallow soils dissected by exposed bedrock. We worked from bedrock at the edges of crusts and imposed 3 additional conditions during selection of mounds. First, no more than 2 mounds were sampled per pothole or soil outcrop. Second, mounds were rejected unless they were aligned in the typical direction (see Results below). Third, in all but the BTR site, where we did not reject any mound, we rejected mounds lacking lichens. Otherwise, we again sampled 20 mounds haphazardly during each site visit (1 visit to BTR and 2 visits to the other sites; see above). To bolster our sample sizes, we pooled all non-*Collema* lichens, which included *Psora decipiens*, *Psora tuckermanii*, *Fulgensia* spp., *Placidium squamulosum*, *Diplochistes* sp., *Toninia* sp., *Squammarina lentigera*, and *Heppia* sp., as well as the moss *Tortula ruralis*. A chi-square test was used to test for equality of observed colonization events between exposures with similar total surface areas (NNW vs. SSE, and ENE vs. WSW).

## RESULTS

### Mound Orientation

ANOVAs demonstrated highly significant differences in mound orientations among the 3 sites for cyanobacterial mounds ( $F_{2,57} = 5.692$ ,  $P = 0.006$ ) but not for lichen mounds ( $F_{2,57} = 0.009$ ,  $P = 0.991$ ; Fig. 3). For the former, subsequent Tukey pairwise comparisons indicated a significant difference between orientations at Cheesebox and BTR, and a marginal difference between Cheesebox and Pothole Point (Table 1). Long axes of cyanobacterial mounds at Cheesebox are oriented more closely to the E-W axis, on average, than are those at BTR and Pothole (by  $17^\circ$  and  $12^\circ$ ,

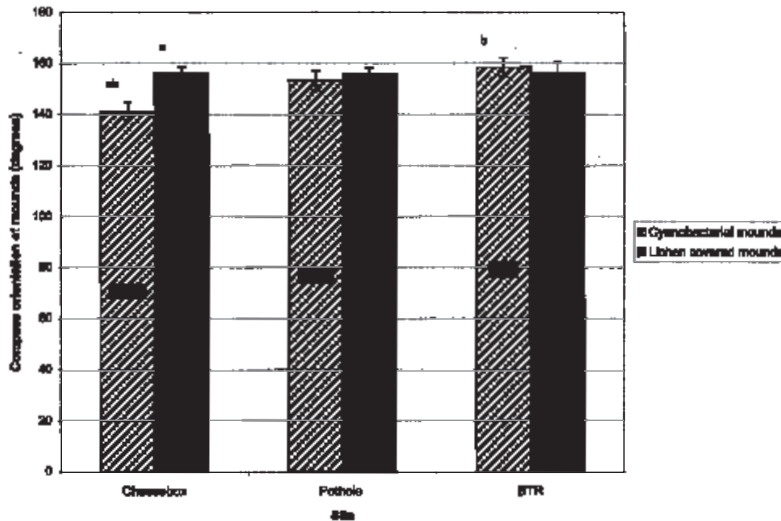


Fig. 3. Mean orientations (degrees from North) of elliptical soil mounds in microbiotic crusts at 3 sites on the Colorado Plateau in southeastern Utah. Data compare cyanobacterial crusts lacking lichen and mounds with abundant *Collema* spp. lichen. Each column represents data from 20 mounds. Vertical bars represent standard error of the mean orientation. The same letter above 2 columns indicates a statistically significant difference.

respectively). They are also farther from mean orientations of lichen mounds at all sites, and they face more toward the east than do the long axes of lichen mounds at Cheesebox ( $t = -3.295$ ,  $df = 38$ ,  $P = 0.001$ ), but not at the other sites (Pothole Point:  $t = -.459$ ,  $df = 38$ ,  $P = .324$ ; BTR:  $t = -.384$ ,  $df = 38$ ,  $P = .351$ ; Fig. 3).

In chi-square analyses at each of the 3 sites, orientations of both cyanobacterial and lichen mounds were highly directional (Fig. 4a, cyanobacterial mounds: Cheesebox:  $\chi^2 = 23.6$ ,  $df = 3$ ,  $P = 3.03E-5$ ; Pothole Point:  $\chi^2 = 45.6$ ,  $df = 3$ ,  $P = 6.9E-10$ ; BTR:  $\chi^2 = 52.4$ ,  $df = 3$ ,  $P = 2.46E-11$ ; Fig. 4b, lichen mounds: Cheesebox:  $\chi^2 = 52.4$ ,  $df = 3$ ,  $P = 2.46E-11$ ; Pothole Point:  $\chi^2 = 52.4$ ,  $df = 3$ ,  $P = 2.46E-11$ ; BTR:  $\chi^2 = 39.6$ ,  $df = 3$ ,  $P = 1.3E-8$ ). For both types of mounds, the 4th level ( $136^\circ$ – $180^\circ$ ) received the overwhelming majority of observations at each of the 3 sites.

#### Cyanobacterial Sheath Material

In the split-plot ANOVA, mean sheath-to-substrate ratios differed significantly among the 3 sites ( $F_{2,57} = 78.51$ ,  $P < 0.000$ ). ENE exposure exhibited a significantly higher ratio than did WSW exposure ( $F_{2,57} = 18.48$ ,  $P <$

$0.000$ ). The interaction between site and exposure was significant ( $F_{2,57} = 2.40$ ,  $P = 0.037$ ; Fig. 5). Subsequent paired  $t$  tests demonstrated that average cyanobacterial sheath-to-substrate ratio was greater on the ENE than WSW aspect for 2 of 3 sites (Table 2). The comparison was not significant at the 3rd site, Cheesebox, though the difference lay in the same direction.

#### Lichen Cover Versus Mound Aspect

As determined by the binomial test, the ENE exposure exhibited greater *Collema* cover than did the WSW exposure (Table 3). We were unable to reject the null hypothesis of equal cover on the 2 opposing aspects for any of the 3 other species examined at Pothole Point (*Psora decipiens*:  $\chi^2 = 0.059$ ,  $df = 1$ ,  $P = 0.808$ ; *Squamarina lentigera*:  $\chi^2 = 1.143$ ,  $df = 1$ ,  $P = 0.285$ ; *Placidium squamulosum*:  $\chi^2 = 0.692$ ,  $df = 1$ ,  $P = 0.405$ ).

#### Lichen Colonization Events

For pooled non-*Collema* lichens and moss (listed above) at 2 sites, chi-square analysis of colonization events detected significantly more events on the ENE than WSW aspect (BTR:  $\chi^2 = 2.37$ ,  $df = 1$ ,  $P = 0.002$ ; Pothole Point:  $\chi^2 =$

TABLE 1. Differences in mean orientation of cyanobacterial mounds at 3 sites in southeastern Utah. Twenty mounds were sampled at each site.<sup>a</sup>

Site 1	Site 2	Mean difference between sites (Site 1–Site 2)	Standard error <sup>b</sup>	P	95% confidence interval	
					Lower bound	Upper bound
BTR	Cheesebox	17.2	5.2	.005	4.6	29.7
BTR	Pothole	5.1	5.2	.601	-7.5	17.6
Pothole	Cheesebox	12.1	5.2	.062	-5	24.7

<sup>a</sup>Multiple pairwise comparisons using the Tukey procedure

<sup>b</sup>Pooled standard error of the mean difference

= 11.21,  $df = 1$ ,  $P = 0.0008$ ). Although the comparison for Cheesebox was in the same direction, the result was not significant ( $\chi^2 = 3.07$ ,  $df = 1$ ,  $P = 0.080$ ). Comparison of the NNW against SSE aspect revealed no significant differences at any site. Our ability to detect strong patterns in the NNW versus SSE comparison may have been reduced due to the very small surface areas of these exposures (Fig. 2).

## DISCUSSION

### Mound Formation and Directionality

Pedicellation of soil mounds in microbiotic crusts of southeastern Utah appears to produce distinctive microhabitats to which components of these crusts respond. What factors might account for mound formation and directionality and for variation in microhabitat favorability? To date, no specific studies have focused on the formation of crust-covered mounds, but it is commonly held that both physical and biological forces play a role in the development of mound microtopography (Harper and Marble 1988, West 1990, Metting 1991, Belnap and Gardner 1993, Johansen 1993). West (1990) highlights the physical forces of needle ice and frost-heaving for areas that receive much of their precipitation during cold seasons. Physical forces like wind erosion and deposition may also shape the microtopography of crusts. For example, on the Colorado Plateau, where predominant winds are from the west (NW in cooler seasons and SW in warmer months), we noted that our soil mounds often gave the appearance of being heavily eroded or “sand-blasted” on their western exposures.

These physical factors may interact with biotic factors to influence substrate microtopography and microhabitat differentiation, as illustrated, e.g., by soil hummocking beneath

some desert vascular plants. Biotic effects on the microtopography of soil crusts are perhaps best documented by Belnap's (1993) study of the recovery of intentionally scalped crusts in southeastern Utah. There, plots inoculated with scalped material developed greater pedicellation more quickly than did plots receiving no inoculum. Substrate binding properties of the predominant cyanobacterium, *M. vaginatus*, almost certainly play a major role in determining microtopography of crusts (Harper and Marble 1988, Metting 1991, Belnap 1993, Belnap and Gardner 1993, Johansen 1993, etc.). Using electron microscopy, Belnap and Gardner (1993) demonstrated the effectiveness with which soil is bound by *M. vaginatus*. By growing prolifically inside an envelope of secreted polysaccharide and leaving this material behind as dry sheath, *M. vaginatus* cements the upper mound surface into less erodible aggregates of substrate (Harper and Marble 1988, Belnap and Gardner 1993, Johansen 1993). Cementation, coupled with physical processes like erosion (see above), substrate deposition, and frost-heaving (e.g., Cole 1990), has been suggested as the reason for the rugose microtopography of soil crusts (Metting 1991, Johansen 1993).

Interactive effects of physical and biological factors in mound formation likely vary with mound aspect, due to a combination of wind directionality and microhabitat effects on the growth of microorganisms (see below). Winds may deposit sediments differentially on the windward (westerly) exposures, possibly covering slow-growing lichens (D. Davidson and colleagues unpublished data). Alternatively, or in addition, they may erode lichens or prevent their colonization and establishment. If such moisture differentials exist, they could contribute to better performances of *M. vaginatus* and *Collema* on ENE than WSW exposures of soil mounds. We discuss determinants for these performance differences below and note here

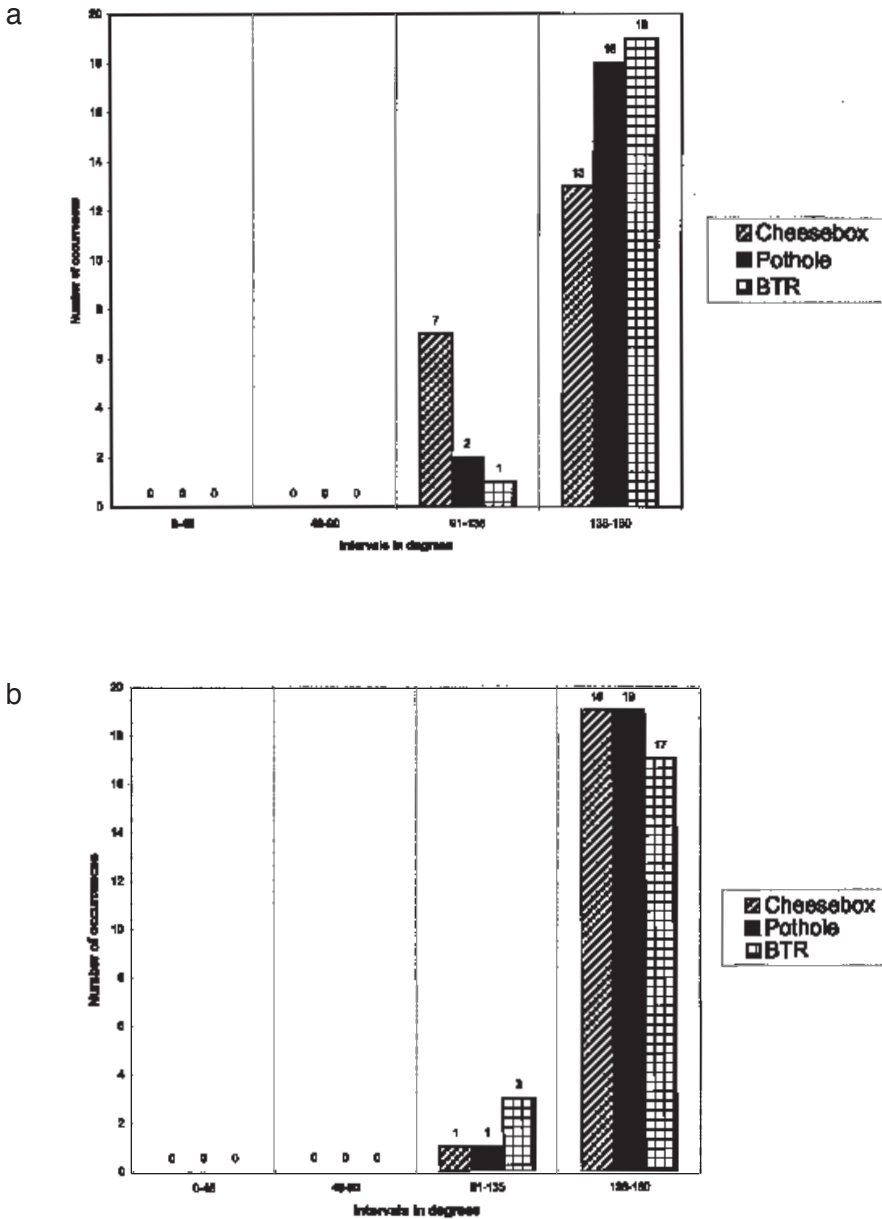


Fig. 4. Orientations of elliptical soil mounds dominated by cyanobacteria (a) and *Collema* spp. lichen (b) in microbiotic crusts at 3 sites on the Colorado Plateau in southeastern Utah. Histograms depict numbers of observations falling into each of 4 equal compass intervals between 0 and 180 degrees.

only that stronger performances of cyanobacteria and lichens on ENE mound exposures could produce greater substrate binding and perhaps nutrient binding on those exposures. Ultimately, this combination of physical and biological processes could produce elongation along the NNW–SSE axis.

#### Responses of Microorganisms to Mound Microhabitats

Some constituent species of the crust appear to respond to microtopography typical of crusts on the Colorado Plateau. As evidenced by measures of cyanobacterial material and lichen cover, respectively, early successional



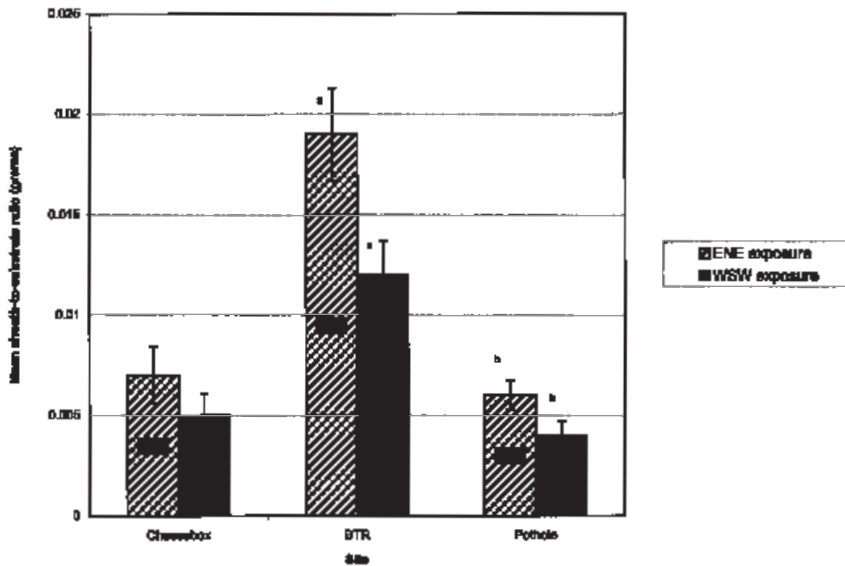


Fig. 5. Mean sheath-to-substrate ratios for ENE and WSW exposures of soil crust mounds at 3 sites on the Colorado Plateau. Vertical bars represent standard errors of the mean sheath-to-substrate ratios. The same letter above 2 columns indicates a statistically significant difference.

cyanobacteria and *Collema* spp. lichens exhibited greater growth and/or higher survivorship on ENE mound aspects than on WSW exposures. (Although dormancy during unfavorable conditions might limit mortality due to some factors, e.g., drought, differential erosion on the 2 sides [see below] could affect survivorship.) In addition, both *Collema* spp. lichens and later successional lichens and mosses colonized with greater frequencies on the former than on the latter mound aspect.

In contrast, cover by non-*Collema* lichens was not disproportionately high on ENE mound faces, and we can only speculate as to why. First, it is possible that differences are artifacts of disparities in sample size ( $N = 60$  for *Collema* spp. and just 20 for each of the other lichen species), which influences the statistical power of the test. If differences are real, one possible explanation is that these later successional species colonize after the environment has been substantially altered in ways that diminish distinctiveness of microhabitat on ENE and WSW mound exposures. For example, although *Collema* spp. might grow more rapidly on ENE faces due to greater representation of soil-stabilizing and/or moisture-enhancing cyanobacteria there, soil stability and moisture may not vary significantly as a function of

mound exposure once *Collema* spp. have colonized all mound faces. That is, erosion of mounds by predominantly southwest winds may be less important later in succession.

An alternative explanation may involve differences in physical conditions favoring photosynthesis by gelatinous cyanolichens (i.e., *Collema* spp.) and green-algal lichens included in our study. These 2 types of lichen appear to specialize in using different moisture sources, the distribution of which varies seasonally in different ways (Lange et al. 1998, Lange in press). The very high compensation points of the gelatinous cyanolichens in the genus *Collema* leave them poorly adapted to use water vapor or dew (even if available) as a source of moisture for photosynthesis. In addition, their relatively high optimal temperatures for photosynthesis make it unlikely that they benefit significantly from moisture made available from snowmelt. Lange et al. (1998) consider these lichens to be "extreme-sun" species, limited in their geographic distributions to areas where sufficient moisture is available from summer rain showers. Although *Collema* lichens respond more slowly to summer storms than do green-algal species, due in large part to a depression in photosynthesis at high degrees of hydration, they are able to

TABLE 2. Comparison of sheath-to-substrate ratios for ENE and WSW exposures of cyanobacterial mounds at 3 sites in southeastern Utah.<sup>a</sup>

Site	<i>t</i>	df	<i>P</i> -value (1-tailed)	Mean difference (ENE–WSW)	95% confidence interval of the difference	
					Lower	Upper
Cheesebox	1.346	19	.0971	1.73E-03	–9.60E-04	4.42E-03
BTR	3.166	19	.0025	6.95E-03	2.36E-03	1.16E-02
Pothole Point	2.958	19	.0040	2.29E-03	6.69E-04	3.90E-03

<sup>a</sup>One-sample *t* tests were used on paired data (ENE vs. WSW).

store more water. Larger storage capacity makes moisture available over longer time periods. Monsoonal summer showers on the Colorado Plateau tend to occur during afternoons, and ENE mound exposures would be somewhat shielded from direct sunlight at this time. Given these 2 facts, our data are consistent with the hypothesis that *Collema* spp. are able to store and use water over longer time periods on ENE faces of the mounds. Some stored moisture may even allow photosynthesis the following morning, when direct irradiation on ENE mound exposures would provide sufficient photosynthetic photon flux density (PPFD—a measure of light intensity in photosynthetic wavelengths) to fund the unusually high rates of photosynthesis of which *Collema* species are capable (Lange et al. 1998). Both temperature optima and light requirements of *Collema tenax* are much higher than those of green-algal species with which it coexists.

In contrast to gelatinous, cyanobacterial *Collema* lichens, green-algal species, such as the 3 examined in our study, tend to lose moisture more quickly after rainfall. However, they are better able to use dew and water vapor as a moisture source, and their lower temperature optima for photosynthesis may enable them to benefit more than do *Collema* spp. from snowmelt during winter (Lange et al. 1998). Also, unlike gelatinous species, green-algal species do not suffer a depression of photosynthesis at high levels of hydration. This fact, coupled with rapid dry down after wetting, might mean that they benefit only briefly from summer monsoonal storms. Also, with photosynthesis saturating at lower levels of PPFD than in *Collema* spp., gross photosynthesis, and perhaps also net photosynthesis, might be more or less equivalent on ENE and WSW mound faces. Winter frontal rains are less well correlated than are convective sum-

mer thunderstorms with time of day, and the same may be true of snowmelt. Thus, it is difficult to predict whether these moisture sources might affect growth differentially on the 2 mound exposures. Finally, dew and water vapor are not likely to be important water sources for lichens on the arid Colorado Plateau (Lange et al. 1998). In summary, physiological constraints of moisture acquisition for gelatinous cyanolichens may subject them more strongly to abiotic selective regimes imposed by different mound exposures. In addition, the greater diversity of seasonal water sources used by green-algal species may make it less likely that these lichens will exhibit the same patterns as do *Collema* species in their relative abundances across mound faces.

#### Site-specific Differences

Data from the Cheesebox site stood out in a number of ways from those for the other 2 sites. First, although orientation of cyanobacterial mounds was nonrandom at all sites, mean mound orientation differed significantly between Cheesebox and BTR and marginally between Cheesebox and Pothole Point (Table 1, Fig. 3), but not between BTR and Pothole Point. This was so despite no differences among sites in orientations of lichen mounds. Second, only at Cheesebox did compass orientations of cyanobacterial mounds differ from those of lichen mounds. Because lichens colonize later in succession than do cyanobacteria (Johansen et al. 1984, Belnap 1993), cyanobacterial mounds should be younger than lichen mounds on average. If one assumes that directionality of mounds develops gradually over time since disturbance, the most parsimonious and plausible explanation for the discrepancies between cyanobacterial mounds and lichen mounds at Cheesebox would be more recent and/or locally intense disturbance there than at the

TABLE 3. Comparison of relative cover of the *Collema* spp. lichens on ENE and WSW exposures of mounds at 3 sites in southeastern Utah.<sup>a</sup>

Exposure	N	Observed prop.	Test prop.	P < (2-tailed)
WSW	11	.22	.50	.000
ENE	39	.78		
Total	50	1.00		

<sup>a</sup>As determined by a binomial test

other 2 sites. We noticed that the Cheesebox area was visually more disturbed than were the other sites. Situated 100–200 m from a major highway, our study area lies near a vehicle pull-off area that is frequented by campers and hikers. In contrast, study sites at Pothole Point and BTR were potentially more protected from disturbance, as consequences of national park status and remoteness, respectively.

If mounds are indeed younger on average at Cheesebox, this, coupled with the slightly different compass orientation of mounds, might help explain 2 other distinctions in data from this site. Although both lichen colonization events and cyanobacterial sheath material were better represented on ENE than WSW exposures at all sites, patterns were not significant at Cheesebox. Early in mound formation, differential representation of cyanobacterial fiber on ENE and WSW exposures may not yet have had an opportunity to develop. Moreover, in comparing both cyanobacterial sheath material and lichen colonization events, we sampled mounds oriented in the “typical” direction at each site. Since the “typical” direction differed slightly between Cheesebox and the other sites, so did exposures on which we sampled. If organisms responded to these subtle differences in exposure, this could have affected the results of our comparisons.

If interpretations given here are correct (and they do need to be verified by explicit tests), several of our results may be useful in evaluating disturbance histories of soil crusts. Across areas with similar climates and exposures, more recent and more frequent disturbances should be associated with greater disparities in orientations of cyanobacterial and *Collema* mounds, and less pronounced discrepancies in both lichen colonization events and cyanobacterial sheath-to-substrate ratios on opposing long sides of mounds.

## SUMMARY

In summary, specific microhabitats created by topography of soil mounds appear to be particularly conducive to prolific growth of *M. vaginatus* and to subsequent lichen recruitment. Relatively slow rates at which mounds form may thus help explain why disturbed and experimentally scalped crusts take so long to recover. Increased understanding of determinants of mound building and mound orientation, as well as effects of microhabitat variation on growth and recruitment of cyanobacteria and lichens, may suggest ways to assist natural regeneration of crusts. Microtopographic patterns in recruitment and growth of microorganisms across mound microhabitats may also prove useful in interpreting biogeographical distributions of component species in soil crusts across landscapes and biogeographic regions.

## ACKNOWLEDGMENTS

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GEOGRAPHIC DISTRIBUTION, MORPHOLOGICAL AND  
MOLECULAR CHARACTERIZATION, AND RELATIONSHIPS OF  
*LATHROCASIS TENERRIMA* (POLEMONIACEAE)

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ABSTRACT.—*Lathrocasis* is a recently recognized genus of Polemoniaceae that circumscribes the species first named *Gilia tenerrima* A. Gray. This species, distributed primarily in the Great Basin and Rocky Mountain floristic regions, has previously escaped thorough taxonomic scrutiny. Surveys of herbarium specimens and living material show that some features of this species have been inaccurately characterized in the past, while other characteristics have not been previously considered in assessing its relationships. *Lathrocasis* possesses a distinct suite of morphological features that, considered as a whole, distinguish this taxon at the generic level. This suite of characters includes the mostly entire, non-mucronate leaves, effuse branching with diverging to retrorse and threadlike pedicels, uniformity of short stipitate glands throughout, uniovulate locules, spiriliferous seeds with verrucate seed coats, minute funnellform flowers with simple vasculature, and stamens equally inserted approximately mid-tube. Parsimony analyses of ITS, *trnL*, and *matK* genes recover similar trees that place *Lathrocasis* in Gilieae with possible sister relationships to *Gilia*, a group composed of *Allophyllum*, *Collomia*, and *Navarretia*, or both of these groups combined. A detailed description of *L. tenerrima*, a review of its taxonomic history, and notes on the type collection are presented.

*Key words:* Lathrocasis, Polemoniaceae, *Gilia*, taxonomy, phylogeny, geographic distribution.

*Gilia tenerrima* A. Gray is a small-flowered, delicately statured annual species of mid-elevations distributed in the Great Basin and Rocky Mountain floristic regions of western United States. As with many inconspicuous species, *G. tenerrima* has not received thorough systematic study, and its relationship to other Polemoniaceae typically has been inferred without critical examination. *Gilia tenerrima* was described during a period when Gray's view of diagnostic characters for genera of North American Polemoniaceae was principally confined to staminal features and their relationship to the corolla (Gray 1870). Gray's *Gilia* was admittedly polymorphous and included most temperate Polemoniaceae with the exception of *Phlox*, *Polemonium*, and a few disparate species referred to *Collomia*. Gray (1870) placed *G. tenerrima* in section *Microgilia*, a taxon erected by Bentham (1845) to house *G. minutiflora* Benth., which, like *G. tenerrima*, has single-seeded locules. Subsequent workers rejected Gray's generic circumscriptions and emphasized combinations of characters, rather than single characters, for generic recognition in Polemoniaceae (Mason 1945). As a consequence, the circumscription

of *Gilia* has incrementally narrowed during the 20th century as natural groups previously housed in this genus received independent taxonomic recognition (Milliken 1904, Grant and Grant 1955, Grant 1956, Porter 1998a, 1998b).

Students of Polemoniaceae through the 1940s generally followed Gray regarding the relationships of *Gilia tenerrima*. Brand (1907) provided a more detailed Latin description of this species than Gray, and placed it and *G. minutiflora* with species now referred to *Microsteris* and *Allophyllum* in his section *Phlogastrum*. Rydberg (1917) placed *G. tenerrima* with *G. minutiflora* and *G. sinistra* M.E. Jones in his informal "Minutiflorae." Several important contributions to Polemoniaceae taxonomy were restricted to the Californian flora (Milliken 1904, Jepson 1925, Munz 1959) and thus did not treat this species because it remained unknown in that state until the late 1950s (*Hardham* 2356 RSA). Mason and Grant (1948, 1951) placed *G. tenerrima* in their new subgenus *Kelloggia* with *G. minutiflora*, *G. leptalea* E. Greene, and *G. capillaris* Kellogg—a group comparable in composition to Rydberg's "Minutiflora" considering modern synonymy and the different geographic ranges considered

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by these authors. Although following earlier workers in describing the leaves of *G. tenerrima* as entire (Mason and Grant 1948), Mason and Grant (1951) selected an illustration depicting lobed leaves occasionally produced by this species.

Grant and Grant (1954) were the first to disassociate *G. tenerrima* from *G. minutiflora* and discounted relationship with *G. leptalea* and *G. capillaris* by placing the latter 2 species in their section *Saltugilia*. Because *G. tenerrima* was not the focus of their work, they indicated only that its affinities were probably in the direction of subgenus *Campanulastrum* (*G. campanulata* A. Gray and relatives), whereas *G. minutiflora* was referred to subgenus *Ipomopsis*. Grant (1959) reconsidered this decision, in part, and included *G. tenerrima* in section *Saltugilia* without comment. In a regional flora of the Intermountain region of the western United States, Cronquist (1984) provided a somewhat detailed gross description of *G. tenerrima* and again associated it with *G. minutiflora* (Cronquist also recognized *Gilia* more broadly than Grant [1959] or Munz [1959] by retaining *Ipomopsis* and *Allophyllum* within *Gilia*). Day (1993a), in formally recognizing section *Kelloggia* (based on *G. capillaris*), referred *G. tenerrima* to section *Giliastrum*, a polymorphous taxon as defined by Grant (1959) that included species showing affinities to *G. rigidula* Benth. as well as species recognized earlier in subgenus *Campanulastrum*. Recent treatments attempting to deal specifically with the relationships of *G. tenerrima* first referred this species to *Allophyllum* (Grant 1998) and then *Tintinabulum* (Grant and Day 1998). These publications concur with the removal of *G. tenerrima* from *Gilia* as discussed by Johnson and Porter (1998), but inadequately consider the full body of evidence in determining its affinities.

Paralleling its obscurity in the field, few published comparative studies of character diversity in Polemoniaceae have included *Gilia tenerrima*. Broad investigations in this family of pollen morphology (Stuchlik 1967, Taylor and Levin 1975), pollen-ovule ratios (Plittman and Levin 1990), and flavonoid chemistry (Smith et al. 1977, Harborne and Smith 1978) favored other species to represent Grant's (1959) section *Saltugilia*. Pollen morphology was recently discussed for this species (Grant and Day 1998), but many morphological features

for *G. tenerrima* relative to other Polemoniaceae either are not available in the literature or, in some instances, have been inaccurately described. DNA sequence investigations (Johnson and Soltis 1995, Johnson et al. 1996, Porter 1996) have included *G. tenerrima*, and the inferences therein provided the stimulus to critically examine the biology and affinities of this taxon. As a consequence of in-depth study, Johnson (in Porter and Johnson 2000) established a new genus, *Lathrocasis*, to house this enigmatic species. Here, we elaborate the rationale behind this taxonomic shift. We document the geographic distribution of *Lathrocasis tenerrima*, describe its morphological attributes, and infer its phylogenetic relationships. The classification of Porter and Johnson (2000), which encompasses several new combinations for Polemoniaceae in addition to the formal description of *Lathrocasis*, is followed in the remainder of this paper.

## MATERIALS AND METHODS

### Morphology and Biogeography

We obtained gross morphological observations, large-scale measurements, and locality data from a survey of 450 specimens of *Lathrocasis tenerrima* representing 202 unique accessions from 18 herbaria (BRY, CIC, GH, IDS, MONT, MONTU, NY, OSC, POM, RENO, RM, RSA, SRP, UC, UNLV, UTC, UW, and WILLU). Additional data from specimens housed at CAS, but not seen by us, were kindly provided by A. Day (California Academy of Sciences, personal communication). Destructive observations, for example electron microscopy of pollen grains, pollen ovule ratios, and internal flower measurements, were taken from 10–25 samples haphazardly chosen to represent the geographic range of all specimens while also encompassing the range of size variation at the whole-flower level. We made all reproductive measurements from pressed material rehydrated in Pohl's solution (Pohl 1965). Pohl's solution was also used to rehydrate young anthers for pollen counts. After rehydration, anthers were momentarily placed in saffranin before dissection in a small drop of 3:1 lactic acid:glycerol where all grains per anther could be counted. Gland morphology was observed on dried specimens and rehydrated material cleared in NaOH and chloral hydrate (Ruzin 1999).

The broad geographic sampling provided by herbarium specimens was supplemented with observations and measurements made on living material grown from seed collected in 1993 from Mono County, California (Johnson 93-103 WS). These observations included aspects of seed germination, phenology, anatomy, and morphology.

Comparative observations with other species were made from first-hand examination of specimens housed at BRY, NCSC, RSA, WS, and the first author's personal collection, or from literature descriptions.

#### DNA Sequence Analysis

DNA sequences were compiled from 3 gene regions: nuclear ribosomal DNA internal transcribed spacer regions 1 and 2 (ITS; Baldwin et al. 1995); chloroplast *trnL* intron-*trnF* spacer regions (*trnL*; Taberlet et al. 1991); and the 5' two-thirds of the chloroplast *matK* gene (*matK*; Johnson and Soltis 1995). The ITS and *trnL* sequences were generated specifically for this project for 9 populations of *L. tenerrima* (following Johnson et al. 1999 and using the primers of White et al. 1990 or Taberlet et al. 1991). Sequences for 23 additional species were generated previously or in tandem for various ongoing investigations (Johnson 1996, Johnson et al. 1996, L. Johnson unpublished, J.M. Porter unpublished). All sequences have been deposited in GenBank (Table 1).

Taxonomic representation between the 3 DNA data sets is comparable but not identical. This is not problematic inasmuch as species representation was based on results of prior analyses (Johnson and Soltis 1995, Johnson et al. 1996, Porter 1996) and a growing body of unpublished sequence data that span the entire family (L. Johnson unpublished, J.M. Porter unpublished). That is, species analyzed here were selected from larger matrices to illustrate what we have discovered about the genetic relationships of *L. tenerrima* in a much larger, and densely sampled, taxonomic context. The representative sampling presented here provides an unbiased view of results obtained from these larger analyses insofar as placement of *L. tenerrima* is concerned. Multiple populations of *L. tenerrima*, representing the geographic range of this species, were sampled to assess molecular variation within this species and increase confidence in

relationships inferred through analyses of these data.

Sequence alignment for all 3 regions was accomplished by eye using a much larger sampling of sequences to aid in homology assessments. In general, alignments in all regions were straightforward. A few poly-A, poly-T, or poly-AT strings in the *trnL* region provided less sure alignments, and nucleotides in those areas were positioned to minimize character change. Gaps were treated as missing data (i.e., "?") rather than a 5th state. When alignments were unambiguous and gapped characters were not autapomorphic, we coded gaps as binary characters appended to the data matrices, regardless of their length (Baldwin 1992). While inclusion of these gap-coded characters in analyses had minimal or no effect on topologies recovered from parsimony analyses, it did provide additional support for groups recovered on the basis of base-substitutions alone. All parsimony and data set congruence analyses were conducted with PAUP\* 4.0b2 (Swofford 1999) following Johnson et al. (1996) and Johnson and Soltis (1998).

## RESULTS AND DISCUSSION

### Biogeography, Ecology, and Phenology

*Lathrocasis tenerrima* is distributed in portions of the Great Basin and Rocky Mountain floristic provinces of western United States (Takhtajan 1986). Its range extends north from California, Nevada, and Utah (latitude 38°20'N) into Oregon, Idaho, Wyoming, and Montana (latitude 46°50'N), and from Wyoming (longitude 106°50'W) west to the Cascades of Oregon (longitude 120°40'W) and the Sweetwater Mountains of Mono County, California (Fig. 1; Appendix). Although not seen by us, *L. tenerrima* is expected in northern Colorado as well.

This geographic range overlaps with a number of Polemoniaceae species but is unique compared to the closest relatives of *L. tenerrima*. That is, several genera such as *Aliciella*, *Collomia*, *Gymnopteris*, *Ipomopsis*, *Navarretia*, *Linanthus*, and *Microsteris* contain species with large geographic ranges that largely or wholly encompass the distribution of *L. tenerrima*. Yet, the more closely related *Saltugilia*, restricted to the mountains and adjacent valleys of southern California and Baja California,

TABLE 1. Voucher and GenBank accessions for DNA sequences used in parsimony analyses. Information is ordered: species; collector & number; herbarium; ITS, *trnL*, *matK* Genbank accession number. "NS" indicates gene not sequenced for that particular collection. For some species, sequences were derived from different collections as indicated. For *Lathrocasis tenerrima*, a population acronym is also provided in boldface type.

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*Aliciella hutchinsifolia* (Rydb.) J.M. Porter; *Johnson 93-069*, WS: AF208193, NS, L34186; *Tommerup 301*, RSA: NS, AF208164, NS.

*Aliciella latifolia* (S. Watson) J.M. Porter; *Johnson 93-018*, WS: AF208194, NS, L48578; *Porter & Machen 10253*, RSA: NS, AF208165, NS.

*Aliciella leptomeria* (A. Gray) J.M. Porter; *Johnson 93-008*, WS: AF208195, NS, L34196.

*Aliciella triodon* (Eastw.) Brand; *Porter & Heil 7341*, RSA: AF208196, AF208166, NS.

*Allophyllum divaricatum* (Nutt.) A.D. Grant & V.E. Grant; *Johnson 96-009*, BRY: AF208197, AF208167, NS.

*Allophyllum glutinosum* (Benth.) A.D. Grant & V.E. Grant; *Johnson 93-032*, WS: AF208198, AF208168, L48564.

*Allophyllum integrifolium* (Brand) A.D. Grant & V.E. Grant; *Johnson 93-111*, WS: AF208199, AF208169, L48563.

*Collomia linearis* Nutt.; *Johnson 92-045*, WS: AF208200, AF208170, L34188.

*Collomia rausoniana* E. Greene; *Patterson s. n.*, WS: AF208201, AF208171, L48571.

*Gilia angelensis* V.E. Grant; *Johnson 93-029*, BRY: AF208202, NS, L34177.

*Gilia brecciarum* M.E. Jones; *Johnson 93-049*, WS: AF208203, NS, AF208191.

*Gilia cana* (M.E. Jones) A.A. Heller; *Johnson 93-016*, WS: AF208204, NS, L48577.

*Gilia capitata* Sims; *Johnson 92-015*, WS: AF208206, NS, L34182.

*Gilia laciniata* Ruiz & Pav.; *Morrell 403*, RSA: AF208208, AF208175, NS.

*Gilia scopulorum* M.E. Jones; *Johnson 304*, WS: AF208209, AF208176, L34190.

*Gilia stellata* A.A. Heller; *Johnson 93-059*, WS: AF208212, AF208179, L34199.

*Lathrocasis tenerrima* (A. Gray) L.A. Johnson;

CA = *Johnson 93-103*, WS: AF208213, AF208180, L34192;

ID-c = *Holmgren & Holmgren 5924*, BRY: AF208214, AF208181, NS;

ID-v = *Grimes & Packard 1807*, BRY: AF208215, AF208182, NS;

MT = *Lesica 3466*, MONTU: AF208216, AF208183, NS;

NV = *Tiehm & Crisafulli 11814*; RSA: AF208217, AF208184, NS;

OR = *Ertter 4364*, BRY: AF208218, AF208185, NS;

UT = *Welsh 19600*, BRY: AF208219, AF208186, NS;

WY-c = *Goodding 110*, RSA: AF208220, AF208187, NS;

WY-t = *Goodrich 24955*, BRY: AF208221, AF208188, NS.

*Linanthus campanulatus* (A. Gray) J.M. Porter & L.A. Johnson; *Tommerup 355*, RSA: AF208205, AF208172, NS.

*Linanthus filiformis* (C. Parry ex. A. Gray) J.M. Porter & L.A. Johnson; *Johnson 93-015*, WS: AF067552, NS, L34185; *Porter & Machen 10849*, RSA: NS, AF208174, NS.

*Navarretia breweri* (A. Gray) E. Greene; *Johnson 93-101*, WS: AF208222, AF208189, L48599.

*Navarretia intertexta* (Benth.) Hook.; *Johnson 93-088*, BRY: AF208223, AF208190, NS; *Glazner 9349*, WS: NS, NS, L34202.

*Navarretia sinistra* (M.E. Jones) L.A. Johnson; *Johnson 93-130*, BRY: AF208210, AF208177, AF208192.

*Saltugilia caruifolia* (Abrams) L.A. Johnson; *Johnson 93-096*, WS: AF208207, AF208173, L34183.

*Saltugilia splendens* (Douglas ex Mason & A.D. Grant) L.A. Johnson; *Johnson 93-098*, WS: AF208211, AF208178, L34191.

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Mexico, is entirely allopatric. *Gilia* is also largely Californian in distribution. Although several species inhabit the Great Basin region, none is geographically confluent with the entire range of *L. tenerrima*. It is not known if any *Gilia* species are truly sympatric with *L. tenerrima* at the population level. Few herbarium sheets record other Polemoniaceae as associates. The few species listed or observed personally include *Collomia linearis* Nutt., *Ipomopsis aggregata* (Pursh) V.E. Grant, *Leptosiphon septentrionalis* (H. Mason) J.M. Porter & L.A. Johnson, *Microsteris gracilis* (Douglas ex Hook.) E. Greene, and *Phlox longifolia* Nutt.

Areas of the Great Basin and Rocky Mountain floristic provinces inhabited by *L. tenerrima* are classified at a grand scale as shrub

steppe, cold desert scrub, and western montane coniferous forest vegetation types (Barbour and Christensen 1993). Habitats are typically gravelly slopes and sandy sagebrush scrub to pinyon-juniper zones but vary into more mesic sites framed by aspen or conifers. Precipitation in the Great Basin as a whole is sparse and comes primarily in the form of winter snow, but increased precipitation occurs in the higher elevations and latitudes preferred by *L. tenerrima* (Holmgren 1972). Elevation range for *L. tenerrima* is predominantly 1524–2743 m (5000–9000 ft), although collections records range from 1127 m to 2987 m (3700–9800 ft). At the lowest latitudes, populations generally occur at relatively high elevations (2377–2895 ft). Thus, this species does not appear to



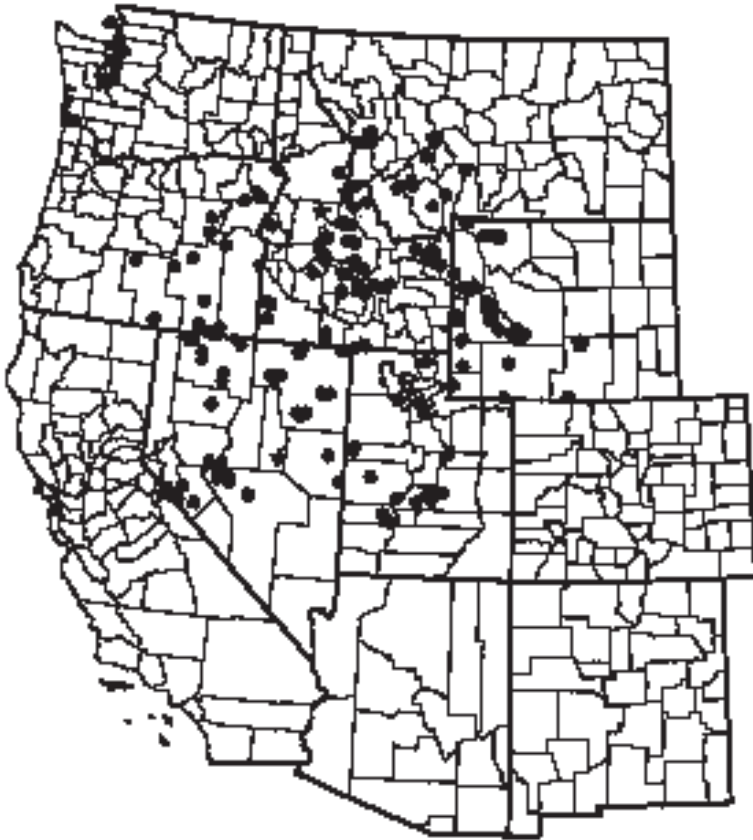


Fig. 1. Geographic distribution of *Lathrocasis tenerrima* indicated by gray dots. Stars indicate samples used in DNA analyses (Table 1). White versus black stars distinguish the 2 major chloroplast haplotypes observed in *trnL* data (see Fig. 3A).

inhabit the warmest and driest portions of its geographic range. These data, combined with surveys of immature herbarium specimens, suggest individuals of *L. tenerrima* germinate in the spring following cold stratification of seeds via extended periods of moist chilling. Anecdotally, seeds of *L. tenerrima*, collected from Mono County, California, in 1993 and stored at room temperature, successfully germinated in 1996 and again in 1998, following 8–10 wk of moist chilling at 4°C. Seeds sown simultaneously and kept at room or greenhouse temperatures failed to germinate even after 6 months. These germination trials, conducted to produce plants rather than to deduce germination cues specifically, lacked a rigorous experimental design. However, the presence or absence of light and the application of treatments intended to stimulate refractory

seeds (Keeley 1984) did not appear to positively affect germination.

Following germination, greenhouse-grown plants required 6 wk to produce their 1st flowers. Anthesis and stigma opening occur more or less simultaneously just prior to opening of corolla lobes. Stigmatic lobes make direct contact with anthers, and all flowers mature at least 2, but most often all 3, ovules. Flowers close by evening, do not open a 2nd day, and are pushed off the plants by the enlarging capsule. Seeds mature approximately 2 wk following anthesis. Flowering takes place predominantly in June and July, but it can occur from May through September.

#### Vegetative Morphology

*Lathrocasis tenerrima* is a diffuse-branching, tap-rooted annual usually <3 dm in height

(Fig. 2A). The 1st nodes are subopposite to alternate and sometimes form a loose rosette. Internodes lengthen above and typically 5–15 nodes are produced before the primary meristem terminates in a single flower. Subsequent growth is predominantly axillary with new sympodial internodes more or less maintaining the linear path of the previous internode and, in the process, pushing each terminal flower to the side. Flowers thus appear leaf-opposed, with the pedicels divergent or retrorse. Branching dichotomies are produced frequently with the branch pairs spreading widely.

Cotyledons are ovate from a short petiole and may persist into flowering but usually wither with age (Fig. 2B). Leaves of the primary stem are mostly entire, narrowly lanceolate to oblanceolate with a tapering base and an elliptic, or sometimes more rounded, apex (Fig. 2C). These lower leaves are usually more or less equivalent in length, increasing or decreasing in size gradually from node to node. Upwards, the higher-order branches produce leaves that gradually to somewhat abruptly reduce in length and width. These upper leaves are borne opposite each flower, or at the base of each diverging branch pair. Lower leaves occasionally bear a single, linear to falcate lobe on 1 or both leaf margins (Fig. 2C–E). These lobes may appear opposite or unpaired and have been observed on plants from throughout the geographic range of this species (*Breedlove* 43710 RSA, *Evert* 16688 POM, *Hitchcock & Muhlick* 14144 RSA, *Jones* 5425 POM, *Jones s. n.* POM 75138, *Stickney* 2915 MONT). Anatomically, lower leaves have 2 layers of palisade parenchyma below the upper epidermis. Vascular tissue is located below these palisade layers, followed by spongy mesophyll to the lower epidermis. Epidermal cells, predominantly sinuate, become long, narrow, and noninterlocking over the midvein of the leaf.

*Lathrocasis tenerrima* bears trichomes more or less throughout the vegetative body. Internodes and pedicels are densely covered, where-

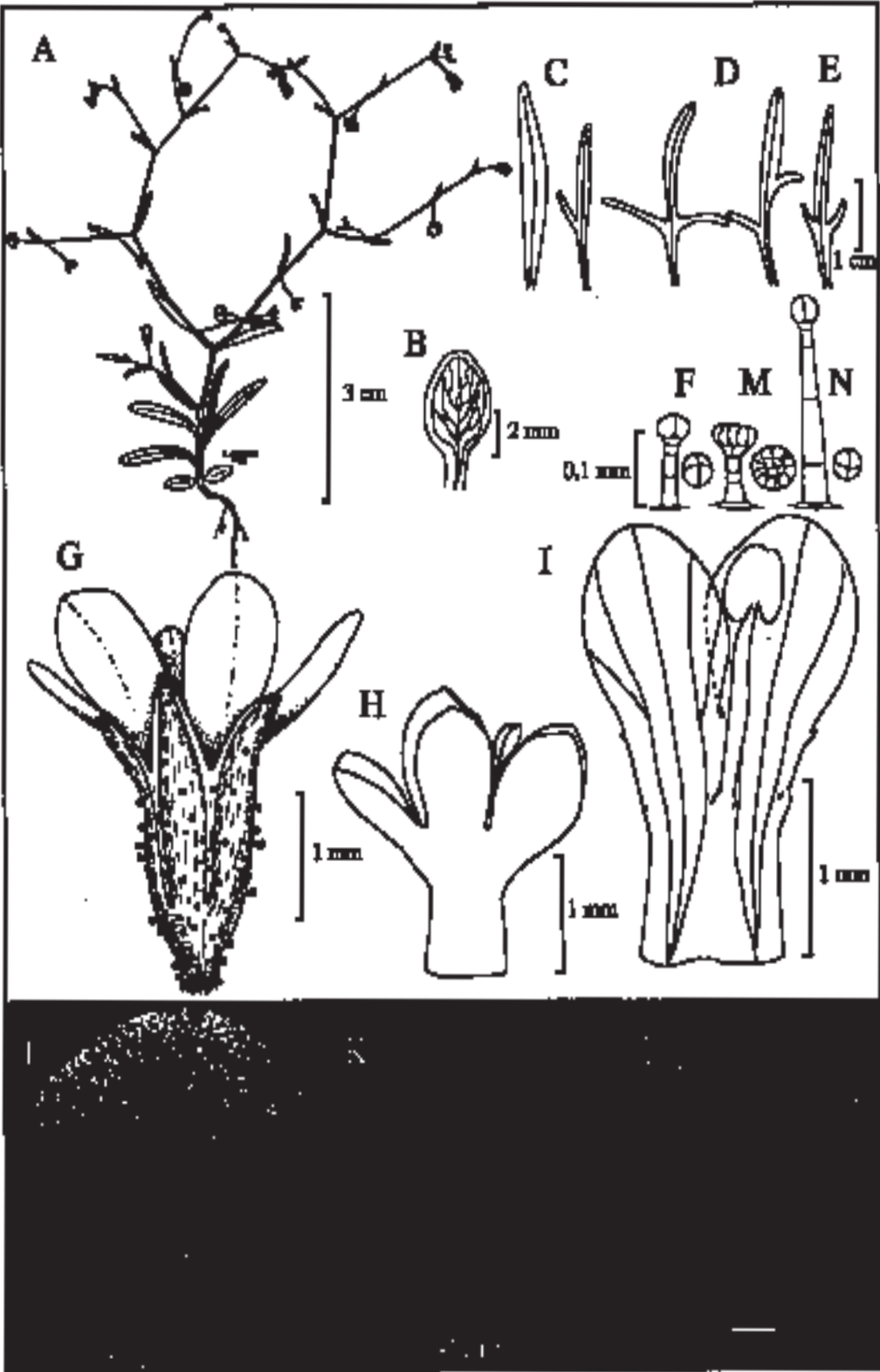
as leaves and calyces (both herbaceous and membranous regions) are less densely covered. The trichomes, all of the same type, are short stipitate with typically 4 translucent cells in the stalk leading to a subglobose to globose cytoplasmic-dense gland composed of 1–4 cells (Fig. 2F). The terminal cell(s), often translucent to yellow on living material, frequently appears black on herbarium mounts. The glands are somewhat odorous and more or less viscid such that they may accumulate sand, insects, or trichomes from other plants.

#### Reproductive Morphology

Flowers of *L. tenerrima* are minute (Fig. 2G), usually no more than 3 mm in length. The campanulate calyces consist of 5 herbaceous, membrane-edged sepals joined by the membrane 3/5 to 4/5 of their length (Fig. 2G). Apices are short acute and nonmucronate. This degree of fusion in the calyx is important to note inasmuch as some taxonomic keys (Day 1993b) require one to specify fusion less than 1/2 to arrive at this species, and some literature descriptions are likewise misleading (Patterson 1989, Grant and Day 1998). Membranes expand slightly but are ultimately torn by the expanding capsule.

Corollas of *L. tenerrima*, frequently described as campanulate, are short funnellform with both a parallel “tube” and more flared “throat” (Fig. 2H). This distinction may be obscure at first glance with typical field magnification, but it is readily observed on herbarium specimens with, or many times even without, the calyx removed. Corollas can exceed the calyx up to twice the calyx length. Corolla lobes are ovate and range from slightly less to greater in length than the fused portion of the corolla. Lobes only half as long as the fused corolla portion (Cronquist 1984) were never observed by us. However, because the lobes flare outward initially from their base, their margins may overlap on pressed specimens, which obscures the precise location of the sinus and may cause the lobes to appear shorter than

Fig. 2. Morphological features of *Lathrocasis tenerrima* and glands from 2 additional genera: A, young plant; B, cotyledon; C–E, lower leaves; F, pedicel gland; G, live flower; H, pressed corolla showing funnellform shape; I, corolla venation and stamen insertion; J, K, pollen grains; L, outer epidermal layer of seed coat covered with verrucae; M, pedicel gland from *Tintinabulum* (= *Linanthus*) *inyoensis*; N, pedicel gland from *Gilia lacinita*. A: *Tiehm & Birdsey* 5134 RENO; B: *Tiehm & Rogers* 4212 UTC; C, G, L: *Johnson* 93-103 BRY; D: *Hitchcock & Muhlick* 14144 UW; E: *Cronquist* 2970 IDS; F, H, I: *Nelson* 2992 RM; J: *Bratz* B386-165 CIC; K: *Welsh* 19600 BRY; M: *Tiehm & Nachlinger* 12432 BRY; N: *Morrell* 403 RSA.



they are. Corolla lobes are white to cream, or tinged blue, lavender, or purple particularly around the vasculature and the outer surface. A yellow spot is located in the fused portion of the corolla beneath each lobe but above the point of stamen insertion. Below this spotted region corollas are invariably white. The yellow spot is obscure and difficult to observe on herbarium specimens. Vascularization of the corolla is simple (Fig. 2I). For each lobe a single trace enters the base of the corolla and immediately diverges into 3 strands (or rarely remains single). These strands do not form anastomoses throughout their length and either do not branch, or branch only simply in or just below the base of corolla lobes. Epidermal cells of adaxial corolla lobes are distinctively papillate. Papillae diminish in size below the lobes but may enlarge once more below the point of stamen insertion.

Stamens are inserted equally just above the midpoint of the fused portion of the corolla, alternate with the lobes (Fig. 2I). Stamen filaments are glabrous, equal in length, and exerted beyond the corolla opening to just less than the length of the corolla lobes. Filaments frequently curve inward, making direct contact with stigmatic lobes. Anthers contain 40–120 white pollen grains each. The number of grains per anther within a single flower can vary by a factor of 2 or 3. Pollen ovule ratios in *L. tenerrima*, even using the lowest pollen-per-anther counts, exceed those of several other self-pollinating species of Polemoniaceae (Plittman and Levin 1990) because the number of ovules is reduced in *L. tenerrima* relative to these same species. Pollen grain morphology is variable. All grains have a striate-reticulate exine with colporate apertures, but distribution of the apertures varies from anomotreme to pantotreme or bizonotreme (Figs. 2J, 2K).

The globose ovary contains a single ovule in each of its 3 locules, rests upon a short nectary disk, and is terminated by an elongate style exerted more or less to the same level as the anthers and bearing 3 stigmatic lobes. The ovary and style are glabrous, the style is deciduous, and the stigma papillae are distinctively long. Capsules are subglobose, somewhat broader than long, and loculicidal. The dehiscent valves separate to their base and may persist or detach from the plant. Mature seeds are ovate and slightly flattened with a chestnut brown seed coat enclosing a straight, chloro-

phyllous embryo embedded in abundant endosperm. Upon immersion in water the outer cell wall layer of the seed coat separates into 1 or a few large sheets by the expansion of conspicuous hygroscopic spiracles clustered in helical coils. Numerous minute verrucae can be observed on the surface of each cell of this separated epidermal layer under magnification (Fig. 2L).

#### Chromosome Number

Chromosome counts from 2 populations of *L. tenerrima*, both from Mono County, California, have been conducted (A. Day, California Academy of Sciences, personal communication; *Breedlove* 43710, 43601 CAS, RSA). The counts, from meiotic pollen mother cells, show these populations of *L. tenerrima* to be tetraploid ( $2n = 36$ ) based on  $x = 9$  as the base chromosome number in Polemoniaceae.

#### DNA Sequence Variation

Levels of nucleotide variation among 9 populations of *L. tenerrima* are comparable in the nuclear ITS and chloroplast *trnL* regions. In the combined ITS-1 and ITS-2 regions, 5 of 462 nucleotide sites showed base substitutions. Two of these sites were autapomorphic, and no indels were observed. Three additional sites in a single sequence were polymorphic. In all, 6 unique ITS sequences were identified. In comparison, sequences of the *trnL* region ranged from 1191 to 1209 bp in length and required 10 indels of 1 to 11 bp for sequence alignment. Nine nucleotide sites showed base substitutions, and 1 of these was autapomorphic. In all, 5 unique *trnL* sequences were identified. Separate parsimony analyses of these 2 regions each recovered a single, homoplasy-free topology (Fig. 3A) with some polytomies attributable to low levels of base substitutions. The 2 topologies are largely, but not entirely, compatible. The *trnL* topology distinguishes 2 main groups that are well separated by 6 base substitutions and 7 indels. The ITS topology differs from this in placing the Montana population in a different primary group compared to *trnL* sequences, and in uniting Utah and Carbon County, Wyoming, sequences that are placed in different subgroups in the *trnL* topology (Fig. 3A). Thirteen differences in the *trnL* region that distinguish the 2 primary population groups are substantial relative to levels of variation observed between species

within several genera elsewhere in Polemoniaceae (data not shown). These 2 major chloroplast groups (haplotypes) are more or less intermixed across the geographic range (Fig. 1). Because only a single individual per population was sampled, both haplotypes may be sympatric. Nevertheless, the number of differences between haplotypes and their wide geographic distribution suggest that most nucleotide divergence in *trnL* occurred prior to the widespread migration of haplotypes across the landscape. Further work is needed to assess the significance, if any, of this molecular variation.

Comparisons of ITS, *trnL*, and *matK* sequences of *L. tenerrima* (Johnson 93-103 WS) with a variety of other Polemoniaceae representing *Gilia*, species recently segregated from *Gilia*, and historically distinct genera reveal levels of divergence most similar to those observed between, rather than within, other genera (Table 2). In addition to nucleotide sequence variation, all 9 sampled *L. tenerrima* populations have a 5-base insertion and a 17-base deletion in the *trnL* region that distinguish this taxon from all other Polemoniaceae surveyed to date (J.M. Porter and L. Johnson unpublished data).

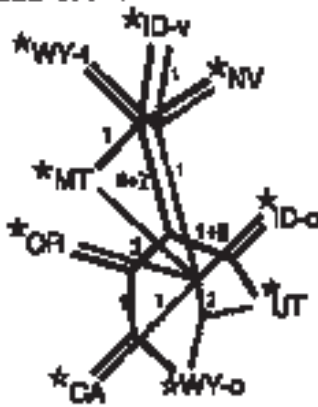
#### Generic Relationships

Morphological and molecular variation presented above differentiates *Lathrocasis* clearly from all other genera of Polemoniaceae and provides a suite of characters useful for diagnosing this taxon that are summarized below. In considering generic relationships of *Lathrocasis*, it is worth reiterating that *L. tenerrima* (as *Gilia tenerrima*) was described at a time when generic boundaries of *Gilia* encompassed all but the most distinctive elements of temperate Polemoniaceae (Gray 1870). Although limits of *Gilia* have since narrowed, this genus has remained the depository for any species of uncertain taxonomic affinity (Wherry 1940, Patterson 1989). The taxonomic shuffling without discussion of *L. tenerrima* within *Gilia* (reviewed above) indicates the uncertainty workers have faced in positioning this species on the basis of incompletely described morphology. Several students of Polemoniaceae over the past 20 yr have considered the polymorphic nature of *Gilia* (Smith et al. 1977, Patterson 1989), but only with the inclusion of *L. tenerrima* in the sequence analyses of Johnson and Soltis (1995), Johnson et al. (1996),

and Porter (1996) did the possibility of removing this element from *Gilia* gain serious consideration. The recent taxonomic reassignments of *Gilia tenerrima* to *Allophyllum* (Grant 1998) and *Tintinabulum* (Grant and Day 1998), while agreeing in principle with the removal of this species from *Gilia*, are not supported by comparative morphology or cladistic analysis of DNA sequences. Of these 2 classes of data, the latter are considered here first.

Parsimony analyses of ITS, *trnL*, and *matK* DNA sequence data sets individually reveal similar phylogenetic inferences regarding *L. tenerrima*. Analyses of ITS data recover 6 minimal length trees of 372 steps (CI = 0.67, RI = 0.77; Fig. 3B). Two of these trees weakly place *L. tenerrima* as sister to a clade composed of *Allophyllum*, *Collomia*, *Gilia*, and *Navarretia* (21% bootstrap), whereas the other 4 trees weakly place *L. tenerrima* as sister only to *Gilia* (48% bootstrap). Analyses of *trnL* data recover 2 minimal length trees of 217 steps (CI = 0.85, RI = 0.89; Fig. 3C). One of these trees weakly places *L. tenerrima* as sister to the *Allophyllum*, *Collomia*, *Navarretia* clade (39% bootstrap), and the other tree weakly places *L. tenerrima* as sister to *Gilia* (51% bootstrap). Analyses of the *matK* data recover 3 minimal length trees of 227 steps each (CI = 0.88, RI = 0.92; Fig. 3D) that place *L. tenerrima* with minimal support (69% bootstrap) as sister to *Gilia*. Partition homogeneity tests (Farris et al. 1995, Johnson and Soltis 1998) show that differences in placement of *L. tenerrima* among analyses are insignificant and individual gene data may be combined into a single matrix without greatly increasing phylogenetic conflict ( $P = 1.00$ ). Analyses of a combined data matrix recover a single tree of 703 steps (CI = 0.83; RI = 0.80; Fig. 3E) that places *L. tenerrima* as sister to *Gilia*, again with only minimal support (62% bootstrap). Overall, these data place *L. tenerrima* unambiguously in Gilieae, as do larger analyses with more thorough sampling of Polemoniaceae diversity (Johnson et al. 1996, Porter 1996). However, the precise sister relationship of *L. tenerrima* within Gilieae remains weakly supported. The best current inference is that *Saltugilia* is sister to remaining Gilieae, which comprises 3 additional lineages that are more or less equivocally resolved relative to each other: *Gilia*, *Lathrocasis*, and a group composed of *Allophyllum*, *Collomia*, and *Navarretia* (see also

A. ITS & *trnL*



B. ITS



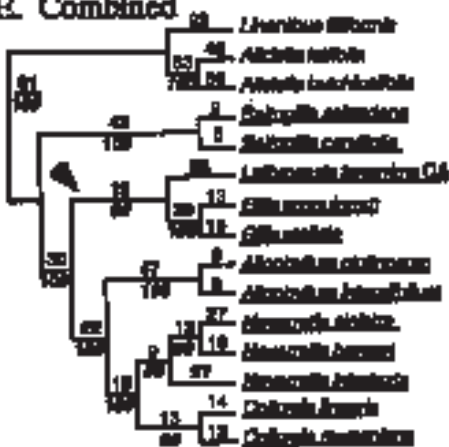
C. *trnL*



D. *mtD*



E. Combined



Johnson et al. 1996, Porter 1996, Porter and Johnson 2000).

DNA sequence analyses also show a large number of base substitutions reconstructed on the branch leading to *L. tenerrima*, and very few homoplasmy-free putative synapomorphies uniting this taxon with a sister group (Figs. 3B–E). This substantive molecular change in *L. tenerrima* offers insights into the historically difficult task of assessing relationships of this species. That is, divergence levels in morphological features similar to those observed in the DNA sequences may exist that have obscured relationships. Modification of synapomorphies once shared with its sister group and the development of autapomorphies either unique relative to, or convergent with, states observed in other genera could have occurred. We are coding a morphological data set for explicitly distinguishing between synapomorphy and homoplasmy in features that characterize *L. tenerrima* and other Gilieae, but the scope of that species-extensive project precludes its presentation here. Nevertheless, examination of a broad range of morphological features has been useful in assessing the systematic position of this taxon.

At a gross morphological level, the effuse, sympodial branching system is a distinctive feature of *Lathrocasis tenerrima* (Fig. 2A). Most Polemoniaceae have cymose inflorescences, and in many species branching is sympodial, albeit less conspicuously so because their pedicels usually are not retrorse as they are in *L. tenerrima*. Widespread distribution of this basic branching pattern provides little information regarding affinities of *Lathrocasis*. Grant and Day (1998) suggest the spreading habit, slender stems, and solitary flowers of *L. tenerrima* are similar to the condition found in Grant's (1998) *Tintinabulum*. Differences in

growth forms of these 2 genera are distinguishable, and similarities of equal magnitude are found also in *Linanthus* and *Aliciella*. *Tintinabulum* sensu Grant (1998) circumscribes the historical "Gilia campanulata complex," including *Tintinabulum filiforme* (Parry ex A. Gray) Rydberg (holotype GH!), *T. campanulatum* (A. Gray) V.E. Grant (holotype GH!), and *T. inyoensis* (I.M. Johnston) V.E. Grant (holotype GH!). These 3 species were transferred to *Linanthus* by Porter and Johnson (2000) but are referred to here as *Tintinabulum* for clarity of discussion. *Tintinabulum* may develop several shoots as primary axes of growth from the lower nodes giving rise to a "spreading" habit, but the direction of growth for shoots, subsequent branches, and pedicels is generally ascending, rather than strongly diverging. Also, leaf-opposed terminal flowers in *Tintinabulum* are predominantly, if not always, paired rather than solitary. *Aliciella micromeria* (A. Gray) J.M. Porter, with pedicels typically at 90° to the axis of growth, approaches *L. tenerrima* in gross morphology most closely. These 2 species are superficially similar, and *A. micromeria* is mistaken for *L. tenerrima* more frequently on herbarium sheets than any other species. Even Gray, who named both species, confused these taxa on herbarium sheets (*Cusick s. n.* GH). *Aliciella*, including *A. micromeria*, differs importantly from *L. tenerrima* in pollen morphology, lacking strongly mucilaginous seeds, usually producing more than 1 ovule per locule, having several lobed leaves with mucronate leaf and calyx lobes, and having the stamen insertion point located in the sinus of the corolla lobes.

*Gilia*, *Aliciella*, and *Saltugilia* predominantly have pinnately to tripinnately divided leaves with mucronate leaf and calyx lobes. *Lathrocasis tenerrima* differs in lacking mucros on its

Fig. 3. Minimum length trees recovered from parsimony analyses of DNA sequence data: A: Single minimum length unrooted topologies from analysis of 9 populations of *Lathrocasis* for ITS (gray) and *trnL* (black). Plain numbers represent base substitutions reconstructed on branches; underlined numbers represent indels reconstructed on branches. White versus black stars indicate the 2 major chloroplast haplotypes. B–E: Numbers above branches represent reconstructed changes (base substitutions + indels); numbers below branches represent bootstrap values. Arrows designate the branch uniting *Lathrocasis* with its inferred sister group. Numbers inside arrows indicate changes reconstructed on that branch that are free of homoplasmy (i.e., CI = 1). Broken lines indicate branches not found in all minimal length trees (i.e., branches that would collapse on the strict consensus of these trees). Underlined species names designate tribe Gilieae; the remaining taxa represent species formerly circumscribed in *Gilia* but now placed in other tribes. B, 1 of 6 minimum length trees recovered from analyses of ITS data; C, 1 of 2 minimum length trees recovered from analyses of *trnL* data; D, 1 of 3 minimum length trees recovered from analyses of *matK* data with a topology identical to the strict consensus tree for this data set; E, single minimum length topology from analysis of a combined data set for the species present in all 3 of the DNA data sets (i.e., ITS, *trnL*, and *matK*).

TABLE 2. Pairwise comparison of nucleotide differences between species from the aligned data matrix used in the combined parsimony analysis of all 3 genes (ITS, trnL, matK). Intra-generic comparisons are italicized.

Table with columns: Species, Lite, Gsc, Gst, Ssp, Sca, Agl, Ain, Cra, Cli, Nbr, Nin, Nsi, Ala, Ahu. Rows list species like Lathrocasis tenerina, Gilia scopulorum-ITS, etc., with corresponding nucleotide difference counts.



mostly entire leaves and calyx lobes. Even when lobed leaves occur in *L. tenerrima*, lobes are restricted to only 1 per edge, and only a few of many leaves on each plant will bear lobes. *Allophyllum* and *Collomia* also have species with nonmucronate leaves that are either entire or few lobed. Like *L. tenerrima*, these genera are more or less leafy throughout with leaves that either do not reduce, or only gradually reduce, in size upwards. They differ in a number of features including characteristics of cotyledons, calyx, trichomes, and seed. The leafy stem habit is a characteristic also shared by *Gilia* section *Gilia*, and *Tintinabulum*. Calyx lobes and entire to few lobed leaves of *Tintinabulum*, like *Gilia*, are mucronate.

The terminal gland of *Lathrocasis* trichomes is composed of 4 or fewer cells (Fig. 2F). Four-celled glands, which appear as a developmental stage in several Polemoniaceae, are found also as the end product of development in some *Gilia*, such as in the inflorescence of *Gilia laciniata* Ruíz & Pavón (Fig. 2N). *Gilia* species invariably have more than one type of trichome, however, whereas trichomes of *L. tenerrima* are uniform. Trichomes in *Allophyllum* can also be of 2 types, have flat-topped multicellular terminal glands, and some, at least, are >0.5 mm, whereas those in *L. tenerrima* remain <0.15 mm. Trichomes in *Tintinabulum* also differ from *Lathrocasis*. *Tintinabulum filiforme* is almost glabrous, but its few trichomes consist of only 1 or 2 shortened stalk cells capped by a large, cup-shaped multicellular gland. *Tintinabulum campanulatum* and *T. inyoensis* are similar to one another in possessing glandular trichomes capped with 16 cells on the ultimate layer (Fig. 2M), as well as eglandular hairs on leaves and calyces. These differences extend beyond structure to color. The glands of *Tintinabulum* are amber rather than black as indicated by Grant and Day (1998). Darkness in glands of *T. inyoensis* and *T. campanulatum*, red in color with magnification, is located in the penultimate layer of gland cells. Glands in *Lathrocasis*, though cytoplasmically dense, are translucent on living plants and darken to amber or black upon drying.

Flower reduction has occurred in many different genera of Polemoniaceae, and species with reduced vascularization can be found in *Navarretia*, *Aliciella*, and *Linanthus* (Crampton 1954, Day and Moran 1986). Corollas of

small-flowered autogamous *Gilia* species, in contrast, generally remain >4 mm, and veins form anastomoses in the corolla lobes. The funnellform corolla shape, though diminutive in *L. tenerrima*, is widespread in Gilieae. This shape is also common in *Aliciella* but contrasts with the distinctly campanulate corollas of *Tintinabulum*. *Tintinabulum* is also characterized by having stamens inserted at or near the base of the corolla. *Lathrocasis*, with stamens inserted approximately mid-tube, differs in this condition, and from *Gilia* and *Saltugilia*, which typically have stamens inserted at or near the sinus of the corolla lobes. *Allophyllum*, *Collomia*, and *Navarretia* are variable in stamen insertion, from equal to unequal and from near the base to at the sinus of the lobes. The yellow-spotted corolla throat in *L. tenerrima* is shared by many *Gilia* and several disparate species from throughout the family. The calyx of *Lathrocasis* is fused beyond mid-length as is common in Polemoniaceae. This contrasts with calyces of *Tintinabulum*, which have membrane-margined costae that are fused less than 1/2 their length. The inner surface of the intercostal membrane in *Tintinabulum* is also distinctly papillate under magnification, which is not the case for *Lathrocasis* or other Gilieae.

Most *Gilia*, *Saltugilia*, and species in a number of genera such as *Aliciella*, *Collomia*, *Eriastrum*, *Ipomopsis*, and *Tintinabulum* possess distinctive zonocolporate pollen grains with lirae radiating from the apertures like lines of magnetic field (i.e., *Gilia* I type, Stuchlik 1967). The sexine in *L. tenerrima* differs from this in being striate with some lirae running parallel to the longest axis of the colpi, and some at right angles to them, similar to the condition described by Stuchlik (1967) for *Gilia capitata* Sims. Furthermore, the colporate apertures in *Gilia capitata* are anomotreme, but vary to pantotreme or zontotreme. In *Lathrocasis* colporate apertures vary from anomotreme to pantotreme or bizonotreme (Fig. 9). This latter distribution of apertures is rare elsewhere in Polemoniaceae. *Collomia* and *Navarretia* contain several disparate types of pollen grains, some which approach *Gilia* I type, but none identical to *L. tenerrima* (Chuang et al. 1978, Spencer and Porter 1997). The pertectate, pantoporate pollen grains of *Allophyllum* are also quite different from *L. tenerrima* (Grant 1998, Grant and Day 1998).

Brand (1907) described 4 types of seeds in Polemoniaceae depending on the nature of the seed coat and mucilage produced upon wetting. *Aliciella* produces no or only slight mucilage (spiricles) upon wetting, whereas *Microsteris* produces copious mucilage that appears to be truly and wholly mucilaginous in origin rather than the product of spiricle expansion. In all members of Gilieae, conspicuous secondary wall thickenings in the epidermis (i.e., spiricles or fibrils; Schnepf and Deichgräber 1983) expand in water to produce a mucilaginous layer. As the spiricles expand, the outer cell wall layer of the seed coat is shed as a “skin” or sheet. In *Lathrocasis* and *Saltugilia*, cell wall boundaries on this “skin” are difficult to observe, but the surface of each cell is densely covered with minute verrucae (Fig. 2L). In other Gilieae cell wall boundaries are apparent on this “skin,” which is otherwise smooth and void of verrucae. Shevock and Day (1998) describe the testa of *Gilia yorkii* Shevock & A.G. Day as being verrucate, but this must be in reference to a large-scale, general wartiness of the seed coat. The outer epidermal wall layer of this species, like other *Gilia*, lacks the verrucae described above for *Lathrocasis* and *Saltugilia*. *Tintinabulum* also possess verrucae, but cell wall boundaries are also apparent and the spiricles are much finer in texture so as to make individual spiricles difficult to discern at equivalent levels of magnification. The general seed coat color in *L. tenerrima* is darker than that of *Gilia*, *Saltugilia*, or *Tintinabulum*, but lighter than that of *Allophyllum*. It approaches most closely the medium chestnut brown of some *Collomia* and *Navarretia*.

As illustrated above, *L. tenerrima* possesses some unique features and shares others with a wide range of genera. Emphasis on any single feature could therefore provide misleading indications of relationships. Morphologically, *L. tenerrima* is readily distinguished from *Gilia* despite their close relationship inferred by DNA sequences and similarities in several morphological features. *Lathrocasis* is also readily distinguished from other genera of Polemoniaceae. It possesses a distinct suite of morphological features that, considered as a whole, characterize this taxon at the generic level. This suite of characters includes the mostly entire, nonmucronate leaves, effuse branching with diverging to retrorse and

threadlike pedicels, uniformity of short stipitate glands throughout, uniovulate locules, conspicuously spiriferous seeds with verrucate seed coats, minute funnellform flowers with simple vasculature, and stamens equally inserted approximately mid-tube.

The origin of *Lathrocasis* appears to lie in the early radiation of tribe Gilieae, possibly as early as the middle Eocene (Lott et al. 1998), following the derivation of ancestral *Saltugilia*. Verrucate seed coats and funnellform, spotted corollas may represent ancestral traits, whereas the reduced flower with simple vasculature and effuse branching system with retrorse pedicels was likely derived within the *Lathrocasis* lineage. Reproductive isolation may have been conferred instantaneously via polyploidization. The lack of species diversity within *Lathrocasis* may reflect extinction, polyploidy, or the autogamous habit of *L. tenerrima*. The latter 2 conditions have been considered evolutionary dead ends (Stebbins 1950). Hauffler (1987) noted, however, that rather than simply buffering against genetic change, polyploidy provides latent pools of genetic diversity that offer opportunities for speciation given time and expanded geographic ranges. Whether *L. tenerrima* represents such a latent pool or a species depauperate of meaningful genetic variation remains unexplored.

#### SYSTEMATIC TREATMENT

*Lathrocasis* L.A. Johnson, *Aliso* 19:67. 2000.

One species.

*Lathrocasis tenerrima* (A. Gray) L.A. Johnson, *Aliso* 19:67. 2000.

Basionym: *Gilia tenerrima* A. Gray, *Proc. Amer. Acad. Arts* 8: 277. 1870.—Type: USA, Utah [Wyoming]: Evanston, July 1869, Watson 922. (Holotype: GH!; isotypes: NY, YU xerox!). Synonyms: *Navarretia tenerrima* (A. Gray) Kuntze, *Revis. Gen. Pl.* 2: 433. 1891. *Allophyllum tenerrimum* (A. Gray) V.E. Grant, *Phytologia* 84: 79. 1998 [1999]. *Tintinabulum tenerrimum* (A. Gray) A.G. Day & V.E. Grant, *Phytologia* 84: 377. 1998 [1999]. Common name: Delicate *Gilia*.

Plants erect or more commonly spreading, (3)–6–30(–35) cm tall and often as wide; stem branching profusely above and eventually from axils of lower nodes. First nodes above cotyledons subopposite to alternate, internodes to 10 mm, elongating above to (2)–10–25(–40) mm; 5–15 nodes produced before the primary apical meristem terminates in a single flower. Branching predominantly sympodial from leaf

axils, or dichotomous at 1–3(–7) node intervals, divergent, branch pairs spreading 45°–110°. Plants ± stipitate glandular throughout, stalks uniseriate (3–)4(–5) cells long, capped with a rounded, cytoplasmic-dense terminal gland composed of 1–4 cells, the gland darkening with age; glands ± dense on stems and pedicels, less dense on leaves and calyces including the membranous portion, absent on corolla, androecium, and gynoecium; ± 0.1 mm long. Cotyledons with ovate blades to 5 mm long and 3.5 mm wide, extending from a narrow petiole ± 1 mm wide and ± 1.5 mm long, persistent into flowering but becoming obscure or withering with age. Lower cauline leaves (5–)10–28(–40) mm long, narrowly lanceolate to oblanceolate (or short ovate on younger plants) from a tapering base and ± elliptic or blunt-acute apex, occasional plants with infrequent lobed leaves, the lobes linear to falcate, 1–12 mm long, borne singly on each side (and then usually, but not necessarily, opposed) or on 1 side only. Upper cauline leaves gradually to abruptly reduced in size, 1–10(–20) mm long, 0.5–3(–5) mm wide, linear-lanceolate to oblanceolate, flower opposed or subtending dichotomous branch pairs. Inflorescence cymose, diffuse, distinctly sympodial. Pedicels threadlike, ± 0.2 mm wide, 2–7(–12) mm long, usually divergent or retrorse at a 90–140(–160°) angle. Flowers minute, 2–3(–3.8) mm long, corolla 1.25–2.3X the calyx; 5-merous calyx, corolla, and androecium, 3 carpellate gynoecium. Calyx campanulate, 1.1–2.1 mm long, 0.4–0.8X the length of the entire flower; ± 1 mm wide (costae ± 0.4 mm wide), membrane margined to apex, the membrane fused 0.6–0.8X of the calyx length, convex in outline along the free portion of the calyx lobes; lobes soft to apex, lacking mucros. Corolla funnelform, 1.6–3.5 mm long; tube (the ± parallel portion of the fused corolla) white, 0.4–1.0 mm long and 0.6–0.9 mm wide, slightly narrowed at junction with throat; throat (the flared portion of the fused corolla) 0.4–0.7 mm long, 1.3–1.7 mm wide at sinus of corolla lobes, with yellow spots alternate with the stamens; corolla lobes white or tinged lavender, purple, or blue, 1.0–1.8 mm long, 0.6–1.3 mm wide, ovate, 0.9–1.2X the length of the fused portion of the corolla. Stamens equally inserted just above the mid-point of the fused (0.6–0.7X) portion of the corolla, equally exerted to 7/8 the length of the

corolla lobes; filaments glabrous, 1.2–1.7 mm long, curving inward; anther 0.4–0.5 mm long, 0.3–0.4 mm wide, with mostly 40–120 pollen grains each. Pollen grains white, 25–35 µm diameter; anomotreme to pantotreme or rarely bizonotreme, apertures colporate, exine striate-reticulate. Nectary disk present at base of ovary; ovary globose to subglobose, 0.5–0.6 mm long, 0.5–0.7 mm wide, tri-ovulate, glabrous. Style 1.5–2.0 mm long, glabrous, exerted to ± level of stamens; stigmas three, 0.3–0.6 mm long, papillate. Capsules compressed globular, 1.3–2.3 mm long, 1.6–2.9 mm wide with loculicidal dehiscence to base; valves persistent to deciduous. Seeds ovoid, 1 per locule, slightly flattened, mostly 0.7–0.8 mm wide and 1–1.3 mm long, appearing mucilaginous when wetted due to the expansion of helical secondary wall thickenings (spiracles), and germinating following extended periods of moist chilling (8–10 wk at 4°C). Seed coat chestnut brown, the outer cell wall layer of the testa clear and each cell of this layer densely covered with minute verrucae, the entire layer separating into 1 or a few large sheets when wetted. Spiracles white (or apparently so), few per cell, retaining a helical shape upon expansion.  $2n = 36$ ; presumably an autopolyploid. Typical ITS sequences = GenBank AF208213–AF208221; *trnL* sequences = GenBank AF208180–AF208188. Flowering (May–)June–July(–September); elevation (1127–)1524–2743(–2987) m.

E.T. Wherry annotated a specimen bearing occasionally lobed leaves "*Gilia tenerrima* ssp. *serrata*" (Cronquist 2970 IDS). The haphazard occurrence of this feature throughout the geographic range of this species indicates, as Wherry undoubtedly realized, the dubious taxonomic value of this feature at the subspecific rank.

#### Type Specimens and Locality

Three accessions of collection number 922 were distributed by Watson that bear 2 locality descriptions. Watson used the same number to indicate collections he regarded conspecific during the King Expedition, regardless of the date or location of their collection (Tiehm 1985). Following Tiehm (1985), taxa described by Gray would seem logically typified by specimens deposited at GH, and the GH specimen was indicated the holotype by

Cronquist (1984). The specimen deposited at GH is a robust plant approximately 23 cm tall and 29 cm wide, devoid of basal leaves (through loss) and well past flowering—only a few intact capsules remain among many dehisced fruit. It is, nonetheless, a well enough preserved specimen to distinguish this taxon from other Polemoniaceae. The label, affixed in the lower left corner, is annotated in handwriting among printed words (the latter in brackets): “[U. S. Geological Exploration of the 40th Parallel under Clarence King, U. S. Geologist], [No.] 922, *G. tenerrima* Gray, [Hab.] Evanston [Utah], July [1869], [Alt.] 6000 ft.” Watson worked with Gray (Tiehm 1985), and it may be from that association that Gray (1870) was able to supply the following additional information: “Utah, on hills above Bear River, near Evanston . . .” The YU and NY specimens are similar in size, maturity, and condition to the GH specimen and bear identical printed labels, but they differ in handwriting (other than possibly the collection number) and in the handwritten information. Both are inscribed “Bear River Valley:” for the location and exclude the month of collection. The inclusion of “Evanston” and “July” in both the protologue and specimen label support the designation of the GH specimen as the holotype. The Bear River Valley (NY, YU) and Evanston (GH) collections may represent separate locations, or the labels may simply reflect different precision in authorship following distribution of the specimens. Neither location is of great enough precision to exclude the other, and the similarity in specimen maturity is suggestive of a single collection. This conclusion is reinforced by comparing the size and maturity of other collections from similar locations made on different dates, and different locations made on similar dates. We follow Welsh (1982) and Tiehm (1985) in considering the NY and YU specimens isotypes.

Evanston, as we know it today, was established in late 1868 to early 1869 along the banks of the Bear River just 4 mi east of the Utah-Wyoming border. This border was established in 1868, a year prior to Watson’s collection, when Wyoming was established as a territory with the area in question acquired from the Utah territory. It is possible that Watson, having been with the King’s Expedition since 1867, considered the general area “Utah” despite the recent change in political boundaries,

or that he used an imprecise working definition of where this new boundary existed such as the Bear River itself. “Near Evanston” and “Bear River Valley” are sufficiently general reference points to include present-day Utah, as the printed labels indicate. However, “hills above Bear River” suggests proximity closer than 4 mi, as if the river were in sight. Though open to interpretation, the type locality is probably in present day Wyoming (Uinta County) rather than Utah.

#### Etymology

*Lathrocasis* is derived from the combination of the Greek *lathro-* (hidden, secret) and *kasis* (sister), in recognition of the obscurity in relationship accorded this taxon, beginning with its initial description. True to its name, it is not clear presently whether *Lathrocasis* is sister to *Gilia*, a group composed of *Allophyl-lum*, *Collomia*, and *Navarretia*, or both of these groups combined. The specific epithet chosen by Gray (1870) is derived from the latin *tener* meaning “soft” or “delicate,” apparently in reference to the fine, threadlike branches and pedicels of this species.

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- APPENDIX. Representative specimens.
- U.S.A. —California, Mono Co.: Sweetwater Mtns, headwaters of Swauger Ck, 27 Jun 1957, *Hardham* 2356 (RSA); steep-walled cyn on NE side of Wheeler Peak above Sweetwater, 10 Jun 1978, *Breedlove* 43601 (CAS, RSA); steep-walled cyn on NE side of Wheeler Peak above Sweetwater, 24 May 1979, *Breedlove* 43710 (CAS, RSA); 2.9 mi into Toiyabe National Forest on Rd 046 near Success Mine, 30 Jun 1993, *Johnson* 93-103 (BRY, WS). —Idaho, Blaine Co.: rocky granitic slope among open lodgepole pine near W edge of Alturas Lake, 22 Jun 1941, *Cronquist* 2601 (GH, IDS, UTC). Boise Co.: 1.5 mi N Elk Lake, Sawtooth Primitive Area, headwaters of S Fk Payette River above Sacajawea Hot Spr, 11-12 Jul 1944, *Hitchcock & Muhlick* 9838 (NY, RM, UW, UTC). Butte Co.: on small bluff on S side of Cedar Butte, S of Atomic City, T1N R30E S35, 10 Jun 1980, *Grimes, Packard, Smithman, & Smithman* 1629 (CIC, NY, UTC, UW). Camas Co.: about 13 mi SE of Fairfield, 1.5 mi S of Sheep Lake, T2S R16E S26 SE1/4 NE1/4, 1 Jul 1984, *Patton & Patton* 1266 (NY). Cassia Co.: Silent City of Rocks (Albion Mtns) just SE of Roads Summit, 13 airline mi SE of Oakley, T15S R23E S26, 15 Jun 1972, *Holmgren & Holmgren* 5924 (BRY, MONTU, NY, RENO, UTC, UW). Clark Co.: U.S. Sheep Experiment Station, enc 1, sec. 35, T10N R36E S35, 16 Jun 1935, *Pechanec s. n.* (RM). Custer Co.: along Morgan Ck about 15 mi from mouth, 29 Jun 1946, *Hitchcock & Muhlick* 14144 (NY, RM, UC, UTC, UW); hillside above Mill Creek, 12 mi W of Challis, 8 Jul 1941, *Cronquist* 2970 (GH, IDS, UTC). Elmore Co.: roadcut about 4 mi NW of Rocky Bar on FS Rd 156, Boise Mountains, T4N R9E S1, 6 Jul 1980, *Ertter & Strachan* 3817 (MONTU, NY, UTC, UW). Fremont Co.: ridge about 0.5 mi NW of Blue Ck Reservoir, about 16 mi NNW of Ashton, T11N R41E S34, 19 Jun 1993, *Evert* 25052 (RM). Idaho Co.: Selway River Cyn adjacent to Steep Gulch, 2 mi N of Haystack Mtn, 34 mi SW of Darby, MT, T28N R14E S29 NE1/4, 26 Jun 1972, *Stickney* 2724 (MONT). Lemhi Co.: shale bank 3 mi up Porphyry Ck, 30 Jun 1946, *Hitchcock & Muhlick* 14202 (NY, RM, UC, UW). Owyhee Co.: ridge extending W from Hayden Mtn, Silver City Range, 2 Jul 1946, *Maguire & Holmgren* 26651 (GH, NY, UC, UTC, UW); Democrat Summit, Reynolds Creek watershed, T4S R4W S14 SW1/4, 4 Jul 1964, *Bratz* B386-165 (CIC). Twin Falls Co.: rd to Monument Spring, 9.1 mi S of Rogerson-Murphy Hot Springs Rd, 15.5 mi WSW of Rogerson, T15S R14E S20, 4 Jun 1972, *Holmgren & Holmgren* 5763 (NY, OSC). Valley Co.: SW-facing hillside above West End Ck, a tributary to Sugar Ck, T18N R9E S2 NE1/4, 11 Jul 1980, *Grimes & Packard* 1807 (BRY, CIC, NY). Washington Co.: Seven Devil Mtns, 5 Aug 1899, *Jones s. n.* (GH, OSC). —Montana, Beaverhead Co.: Pioneer Mtns, S-facing slope above kilns on Canyon Ck, T2S R10W S8, 15 Jun 1989, *Lesica & Shelley* 4838 (MONTU, NY). Gallatin Co.: Spanish Basin, 24 Jun 1897, *Rydberg & Bessey* 4820 (NY). Lewis & Clark Co.: Big Belt Mtns at base of E-facing slopes above Hunters Gulch just above road crossing, T12N R2W S2, 30 Jun 1985, *Lesica* 3466 (MONTU, OSC, RM). Maddison Co.: Highland Mountains on E-facing slopes above Second Ck, T2S R6W S7, 1 Jul 1992, *Lesica* 5756 (MONTU, NY). Missoula Co.: Lolo Nat'l Forest, Sapphire Range, Plant Ck watershed near second sharp switchback, 10.5 mi SSE of Missoula, road cut, T11N R18W S7 NE1/4, 15 Jun 1973, *Stickney* 2915 (MONT). Park Co.: Suksdorf's Gulch, 9 mi NW of Wilsall, 8 Aug 1921, *Suksdorf* 704 (GH, UW). Ravalli Co.: S-facing slopes above a side drainage of Grayhorse Ck, about 9 mi NE of Stevensville, T9N R18W S6, 24 May 1986, *Lesica & De Bolt* 3728 (MONTU, NY). Silver Bow Co.: trail cut along Moose Ck near its confluence with small tributary, T1S R8W S8 SW1/4, 31 Jul 1979, *Lowry* 2740 (MONT). —Nevada, Elko Co.: 0.5 mi above Thomas Cyn Camp Ground, Lamoille Cyn, 15 Jun 1941, *Holmgren* 1131 (BRY, NY, UC, UTC); Independence Mtns, Warm Creek, 3.2 air mi W of the Saval Ranch, T39N R53E S2, 20 Jun 1979, *Tiehm & Birdsey* 5134 (NY, RENO, RSA, UTC). Eureka Co.: Fish Ck Range, Prospect Peak area SSW of Eureka, 0.7 road mi S of peak, T18N R53E, 26 Jun 1988, *Tiehm & Crisafulli* 11814 (BRY, NY, OSC, RENO RM, UNLV, UTC). Humboldt Co.: Santa Rosa Range, Buckskin Mtn N of Windy Gap, S side of

mtn, T45N R39E S14, 28 Jun 1987, *Tiehm 11374* (BRY, IDS, MONTU, NY, OSC, RENO, RM, UNLV); SE side Sage Hen Hills, 11.7 air mi NW of Range HQ Duffurena Ranch, T46N R24E S2, 19 May 1978, *Tiehm & Rogers 4212* (NY, RENO, UTC, UW). Lander Co.: Carroll Summit, Desatoya Mtns, 10 Jun 1941, *Mason 12427* (GH, NY, OSC, RM, UC, UTC, UW). Lyon Co.: ridge on N edge Sweetwater Mtns 2 mi SE of Desert Ck, 30 May 1983, *Breedlove 58768* (GH, NY). Mineral Co.: Agnes D. Mine Cyn, S fork of Cottonwood Cyn near Murray Placer Camp, N slope of Mt Grant, 5 Jul 1940, *Train 4245* (NY, RENO). Nye Co.: Toiyabe Range, R.F. Stewart Ck 20 mi & 305° from town of Round Mtn, N38°53'7" W117°21'57", 17 Jul 1979, *Goodrich 13497* (BRY, NY, RENO, RM, UTC). Pershing Co.: N end of the West Humboldt Mtns, 5.5 air mi SSW of Imlay, NW of Star Peak, T31N R34E S7, 11 Jun 1978, *Tiehm & Williams 4343* (NY, RENO, UNLV, UTC). Washoe Co.: Bald Mtn Ridge, 1.5 air mi W of refuge sub-HQ, T45N R21E S7 NE1/4, 30 May 1978, *Rogers & Tiehm 909* (NY, RENO, UTC, UW). White Pine Co.: Lehman Ck Cyn, Snake Range, 17 Jun 1941, *Maguire 20810* (BRY, NY, UTC, UW); Aurum, 6 Jun 1893, *Jones s. n.* (POM 75138). —Oregon, Grant Co.: Dixie Butte, Blue Mtns, 2 Jul 1910, *Cusick 3507* (OSC, WILLU). Harney Co.: Western Trout Ck Mtns, main ridge rd SW of headwaters of Little Wildhorse Ck, 3/4 mi NW of rd on ridge S of headwaters, near small reservoir an springs, T40S R38E S28 SE1/4, 3 Jul 1981, *Ertter 4364* (BRY, CIC, NY, RENO, RM, UTC, UW). Lake Co.: lava craters 2 mi east of Green Mountain Lookout, NE of Fort Rock, T25S R17E S28 & 33, 7 Jun 1978, *Crosby 1943* (OSC). Malheur Co.: Trout Ck Mtns, mahogany grove E of Mud Spring, T38S R40E S28, 29 Jun 1984, *Wright 1745* (OSC). Owyhee Co.: Malheur Divide near Road Cyn, sandy slopes, 31 May 1896, *Leiberg 2175* (GH, NY, OSC, POM, UC). Union Co.: white stoney hillside, Thief Valley, no date, *Cusick s. n.* (OSC). Wallowa Co.: near summit of Imnaha-Snake Divide, 24 mi above Imnaha, 12 Jul 1933, *Peck 17608* (NY, WILLU). —Utah, Beaver Co.: Tushar Mtns, Beaver River Cyn below Skull Flat, T29S R6W S23, 28 Jul 1984, *Taye 2954* (BRY, UTC). Cache Co.: Spring Hollow, W ridge, 2 Jun 1936, *Maguire 13755* (NY, UTC). Carbon Co.: Scofield, 24 Jun 1904, *Jones s. n.* (POM 75140). Juab Co.: Deep Ck Range, Indian Farm Ck drainage, 14.5 km (9 mi) air distance WSW of Callao, T11S R18W S22 SW1/4, 18 Jul 1995, *Holmgren & Windham 12411* (BRY, NY). Millard Co.: Pavant Mt. Cold Spring about 12 mi SE on Second Ck Rd, T24S R5W S23, 30 May 1986, *Thorne & Nelson 4671* (BRY, NY). Salt Lake Co.: Salt Lake City, City Ck Cyn, 11 Jun 1880, *Jones 1768* (NY, RM, UC, UTC). Sevier Co.: about 23 mi due E of Salina, T23S R4E S36 SW1/4, 14 Jun 1980, *Welch 19600* (BRY, NY, RM); [G?]eland's Ranch, head of Salina Cyn, 15 Jun 1894, *Jones 5425* (NY, POM, RM, UC). —Wyoming, Carbon Co.: The Chimneys, Pedro Mtns, 25 Jun 1901, *Goodding 110* (GH, MONT, NY, RENO, RM, UC). Fremont Co.: W slope Wind River Range, SW face of Wildcat Butte, about 50 air mi SE of Pinedale, T30N R102W S21, 22, & 28, 13 Jun 1991, *Fertig 7724* (RM). Lincoln Co.: Salt River Range, dry ck about 1.75 mi E of cyn mouth, about 3.5 air mi SE of Afton, T31N R118W S9, 4 Jun 1987, *Harrison 471* (RM). Park Co.: ridge S of Middle Ck about 2 mi W of east entrance and 0.25 mi S of Hwy 14, 16, & 20, T52N R109W S18, 13 Jun 1989, *Evert 16688* (RM); along a rd, Undine Falls, 18 Jul 1899, *Nelson & Nelson 5953* (BRY, GH, NY, RM, UC, UW). Sublette Co.: W slope of the Wind River Range, E of Pinedale near Fremont Lake, 11 Jul 1967, *Porter & Porter 10427* (GH, NY, RM, UC, UW). Sweetwater Co.: Cedar Cyn, T22N R103W S8, 25 Jun 1978, *Dorn 3088* (RM). Teton Co.: S-facing slopes below "Warrior Ridge" rock formation in Teton Cyn, Targhee Nat'l Forest, 11 mi E of Driggs, ID, 2 Jun 1956, *Anderson 264* (NY, RM, UC, UTC, UW); Bridger-Teton Nat'l Forest, Gros Ventre Range, Gros Ventre drainage, slopes N of Slide Lake, T43N R114W S33 & 34, 20 Jun 1995, *Goodrich 24955* (BRY). Uinta Co.: Evanston, 29 May 1897, *Nelson 2992* (NY, RM, UTC); Meadow Draw Quadrangle, South Haystack Coal Site, T17N R117W S29 NE1/4, 7 Jun 1978, *Moore, Mayer, & Reardon 525* (RM).

## FACILITATION OF *YUCCA BREVIFOLIA* RECRUITMENT BY MOJAVE DESERT SHRUBS

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**ABSTRACT.**—Patterns of recruitment for *Yucca brevifolia* (Joshua tree) were investigated on 3 elevational transects, 1000–2000 m, in the Spring and Sheep Mountain ranges of southern Nevada. *Yucca brevifolia* is distributed throughout a broad range of plant communities dominated by *Larrea tridentata* and *Ambrosia dumosa* at low elevations, *Coleogyne ramosissima* at middle elevations, and an *Artemisia-Pinus-Juniperus* community at upper elevations. The density of *Y. brevifolia* gradually increased from the lowest elevations, peaked at 1600 m, and remained at intermediate levels at high elevations until reaching an abrupt upper elevational limit at 2000 m. Open substrate dominated the study areas; however, a large majority of *Y. brevifolia* seedlings were found growing under the canopy of other woody shrubs. This pattern of recruitment did not vary by site or elevation. Thirty-five species of perennial shrubs were identified in the study areas, 16 of which were found in association with at least 1 *Y. brevifolia* seedling. However, 4 shrubs were found in a nurse plant relationship with *Y. brevifolia* above the frequency predicted by either their canopy area or numerical dominance. Seedlings exhibited significant variation in aspect, relative to the center of the nurse shrub. In Lee and Lucky Strike canyons, recruitment occurred predominantly on the east and west sides of nurse shrubs, indicating the importance of specific microhabitats. Local presence of specific perennial shrubs resulted in higher levels of recruitment, causing a distinct pattern of community development, presumably through amelioration of abiotic stresses.

*Key words:* *Yucca brevifolia*, nurse plant, Mojave Desert, southern Nevada, desert recruitment, Spring Mountain Range.

Within the Mojave Desert, as in other severe environments, germination and survival of seedlings are rare events, and recruitment of perennial plants most often occurs within the protected microhabitats of established shrub canopies (Smith and Nowak 1990). Since Phillips (1909) reported that seedlings of *Pinus monophylla* (pinyon pine) were found predominantly under the canopy of *Artemisia tridentata* (sagebrush) and rarely in the open, strong correlations have been found between the distribution of stress-tolerant species and less tolerant species unable to regenerate on open substrates. In North American deserts stress-tolerant perennials such as *Ambrosia* spp. often are the initial colonists of open or disturbed sites (McAuliffe 1988). These colonists then apparently modify microhabitats, allowing subsequent recruitment and establishment of species that are less stress tolerant. Survival of perennials beneath the canopies of other plants is an important process in structuring arid and semiarid vegetation (McAuliffe 1988, Franco and Nobel 1989, Silvertown and Wilson 1994). The greater the abiotic stress within an environment, the greater the potential importance

of facilitation (a positive interaction) between plants (Callaway and Walker 1997). Any amelioration of stresses such as cold, heat, salinity, or herbivory is likely to foster survival and growth. Conversely, in environments with low stress and the potential for rapid resource acquisition, competition between plants becomes a dominant interaction. The importance of facilitation therefore appears to increase with increasing stress.

Plants that ameliorate a stressful environment for seedlings of other plants are termed nurse plants. McAuliffe (1988) found that in the Mojave Desert, 88–95% of the landscape is open substrate. However, 67–85% of *Larrea tridentata* (creosote bush) seedlings are preferentially associated with *Ambrosia* spp. shrubs, which account for only 3–6% of the landscape cover. In the northern Sonoran Desert, low-density *Ambrosia* spp. commonly act as nurse plants for seedlings of *Cercidium microphyllum* (paloverde; McAuliffe 1986). Suzan et al. (1996) noted that seedlings of various species in the Sonoran Desert are found under the canopy of the nurse plant *Olneya tesota* in much greater proportion than their canopy area

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would suggest. Such strong nurse preferences have not been consistently documented by all researchers. Callaway (1995) found *Carnegia gigantea* (saguaro) primarily under *C. microphyllum*, but noted that *C. gigantea* seedlings were common under various perennial shrubs. In turn, seedlings of *C. microphyllum* are themselves associated with canopies of several other shrubs (McAuliffe 1986), further reinforcing the concept that facilitation is a major factor in the community structure of arid regions. Turner et al. (1966) delineated 15 different shrubs found in association with *C. gigantea* seedlings that were in proportion to their frequencies. The implication from the literature is that there may be no specific biotic characteristics that determine nurse plant selection, but rather a general alteration of microclimates that produces a more hospitable zone of recruitment.

Nurse plant facilitation mechanisms operate on seedlings directly through amelioration of high temperatures, high light intensity, low soil moisture, and low soil nitrogen typical of arid lands. Facilitation may also operate indirectly through inhibition of competitors, reduction of herbivore pressure, inoculation of the soil with mycorrhizae, and convergence of dispersal processes (Callaway 1995).

Shading appears to be the critical attribute of environmental moderation, allowing greater recruitment and distribution of desert species. Franco and Nobel (1989) found minimum winter soil surface temperatures in the Sonoran Desert were 1.2°C warmer under the canopy of *Ambrosia deltoidea* and summer maximum temperatures 13.5°C cooler at the center of the bunchgrass *Hilaria rigida* than temperatures measured in open areas. Also in the Sonoran Desert, relative to open substrate temperatures, Suzan et al. (1996) reported a 15°C decrease in summer maximum temperatures and an increase in winter minimum temperatures of 3°C under shrubs. Nurse plants may also alter soil moisture. Recent studies at Lucky Strike Canyon, in the Spring Mountain Range within the Mojave Desert, have found that open substrates have lower moisture content during wet and dry periods than soil beneath plant canopies, and that different species have different levels of soil moisture under their canopies. The soil under *Coleogyne ramosissima* (blackbrush) has consistently higher moisture content than *Ambrosia dumosa* and *Larrea tridentata* and it retains greater soil moisture into

the dry months, perhaps due to a higher clay content (Walker et al. in press).

Numerous studies have found nutrient enrichment of the soil beneath shrub canopies via litterfall, nitrogen fixation, nutrient pumping by deeply rooted perennials, and organic debris deposition. Franco and Nobel (1989) found significantly higher nitrogen content under the nurse plants *Ambrosia deltoidea* and *Hilaria rigida* that was correlated to increased dry weight of the nursed *Agave deserti*. In the Mojave Desert, O and A horizon soils are generally absent, while deposition of silt, sand, and organic material beneath shrubs contributes to increased survival rates of seedlings under perennials.

Across a variety of landscapes (e.g., deserts, wetlands, grasslands, high-elevation forests), both facilitation and competition are important factors in the distribution of species and determinants of community structure. Tests of association have consistently found that colonization of stressed environments is not a random process and that seedlings of some species have a high degree of association with mature shrubs. The importance of facilitation varies on a gradient of stress; low-intensity stress allows competitive interactions to dominate and to structure community composition. Highly stressful environments increase the importance of facilitation for recruitment and persistence of species requiring amelioration of open substrate conditions (Holmgren et al. 1997).

The objectives of this research were to determine if seedlings of *Yucca brevifolia* display a nonrandom pattern of recruitment between open substrates and under canopies of perennial shrubs. If recruitment is found primarily under the canopy of another species, are some species associated with *Y. brevifolia* more often than predicted by their canopy area or numerical dominance? And does this association change with elevation or site? Does the aspect of the seedling, relative to the nurse plant central stem, influence survivorship?

#### STUDY SITE

The Mojave Desert, within the Basin and Range geological province, is a region marked by annual weather extremes that support sparse vegetation cover (Appendix A). Regional aridity results from <200 mm yr<sup>-1</sup> precipitation in southern Nevada (at the lowest elevations)

with a potential evapotranspiration of  $>2000$  mm yr<sup>-1</sup> (Smith and Nowak 1990). Most precipitation occurs in the winter, while summer thunderstorms are highly localized and unpredictable. Approximately 42% of the annual precipitation falls during the April–September “growing” season in southern Nevada (Rundel and Gibson 1996).

Edaphic factors often define the vegetative cover that can establish and persist within a region. Lei and Walker (1997) found that Lucky Strike Canyon (Spring Mountain Range, southern Nevada) soils in the open exhibit greater temperature variations than soils beneath shrub canopies, although soils at 15-cm depth showed comparable temperature variation between open and shaded areas.

The Spring and Sheep Mountain ranges, located 65 km north of Las Vegas, Nevada, are major mountain ranges within the Mojave Desert region. They are composed of limestone-dolomite parent material that produce calcareous soils at lower elevations. Charleston Peak (3652 m), within Spring Mountain Range, is the highest point within the Mojave Desert, with extreme elevational and ecological variation. There is a well-defined elevational gradient in vegetation, with *Larrea tridentata* and *Ambrosia dumosa* dominating lower bajadas, *Coleogyne ramosissima* dominating intermediate elevations, and *Artemisia tridentata* dominating upper bajadas (Appendix B). In the Sheep and Spring Mountain ranges of southern Nevada, *Yucca brevifolia* is found in continuous stands at elevations from 1000 m to 2000 m, ranging from the *Ambrosia-Larrea* zone to the *Artemisia* zone. Elevational and ecological variation within a localized area allowed us to test whether the apparent correspondence between *Yucca brevifolia* regeneration and specific plant species could be validated.

#### METHODS

During our study, May 1996 to February 1998, we examined 3 elevational transects, 2 in the Spring Mountain Range and 1 in the Sheep Mountain Range in southern Nevada. The Spring Mountain transects (Lee and Lucky Strike canyons) had a generally northeast exposure and the Sheep Range transect (Corn Creek) a southwest exposure. Along each transect, a 100 × 50-m study site was established

every 200 m in elevation from the lowest (1000 m) to the highest (2000 m) continuous stands of *Yucca brevifolia*. Sixteen study sites were established, 6 in Lee Canyon and 5 each in Lucky Strike and Corn Creek. Study sites were located near major access roads but at least 20 m away from roadways to eliminate road effects. To avoid seedlings derived vegetatively from mature plant root systems, we defined a *Y. brevifolia* seedling as an unbranched stem,  $<50$  cm in height and  $\geq 50$  cm from an adult. All but 3 seedlings were  $>1$  m from an adult. A nurse plant was classified as any perennial plant with a *Y. brevifolia* seedling within its vertical canopy area.

Circular plots (11.3-m radius, 400 m<sup>2</sup>) and nested subplots (4.0-m radius, 50 m<sup>2</sup>) were centered at each *Y. brevifolia* seedling within the 100 × 50-m sites. The 400-m<sup>2</sup> plots ( $n = 174$ ) were surveyed for the number of *Y. brevifolia* adults and seedlings. The 50-m<sup>2</sup> subplots ( $n = 174$ ) were inventoried for the presence of all woody perennials, including secondary *Y. brevifolia* individuals, surrounding each seedling to obtain canopy coverage and the number of individuals of each species of perennial plant. We obtained canopy diameters by multiplying the longest and shortest horizontal dimensions of the plant canopy. Focal seedlings, around which plots and subplots were developed, were seedlings initially encountered, while secondary seedlings were less prominent seedlings found during the intensive inventory, often hidden within the canopy of a shrub.

Seedlings of *Y. brevifolia* were categorized as being located in the open or under the canopy of a shrub. Shrubs containing a *Y. brevifolia* seedling under their canopy were measured for area and height for comparison with conspecifics without seedlings. Seedlings under canopies of shrubs were further categorized by aspect in the 4 cardinal directions relative to the shrub's central stem. Shrub circumference was divided into 4 quadrants to categorize seedling aspect relative to shrub center (north aspect: 315°–45°; east aspect: 45°–135°; south aspect: 135°–225°; and west aspect: 225°–315°). Distance from each *Y. brevifolia* seedling to the nearest adult was measured for all seedlings found within the site. Each species was ranked according to percentage of subplot area covered. The area of each nurse plant was measured and recorded separately to compare

with the average area of its conspecifics. Abundance of plants and their percentage of total plant numbers were categorized by species within subplots. The number of each nurse plant species was compared to canopy area and numerical dominance of all other plant species to see if nurse plant recruitment was based simply upon canopy area or the number of plants, or if there was a selection process. Nomenclature followed Hickman (1993).

One-way analysis of variance (ANOVA) was used to determine if the number of seedlings within 400-m<sup>2</sup> sites differed by elevation. A 3-way analysis of variance (ANOVA) was used to detect differences in site, aspect, and elevation in seedling recruitment relative to potential nurse shrubs. The pattern of establishment of seedlings in open substrate or beneath shrub canopies by site and by elevation was tested with chi-square analysis. Significance was tested at the 5% level.

## RESULTS

We found 277 *Yucca brevifolia* seedlings in sixteen 100 × 50-m sites along 3 transects that spanned a gradient from 1000 to 2000 m elevation. Seedlings were found in an elevational range of 1000–2000 m in Lee Canyon, 1000–1800 m in Lucky Strike Canyon, and 1200–2000 m at Corn Creek. Of 277 *Y. brevifolia* seedlings found, 257 (92.8%) grew within the canopy of other woody shrubs (Fig. 1), even though combined shrub canopy area of all perennial species covered only 20.1% of the area of the 16 sites. Twenty seedlings (7.2%) were found in the open, away from the shade, seed catchment, or fertile island effects of any shrub. This pattern of recruitment under shrubs did not vary by site or by elevation gradient (chi square,  $P = 0.351$ ). Open substrate, consisting of desert pavement, accounted for an average of 80% of the 8700-m<sup>2</sup> area of the intensively surveyed 50-m<sup>2</sup> subplots.

The number of seedlings found within each 400-m<sup>2</sup> plot differed significantly by elevation (1-way ANOVA,  $P < 0.01$ ). The smallest percentage of regeneration was at lowest elevations: 1000 m (1.4%), 1200 m (7.1%); and the highest percentage of regeneration was found at 1600 m (49.8%). Intermediate levels of seedlings were found at 1400 m (15.3%), 1800 m (14.2%), and 2000 m (12.1%).

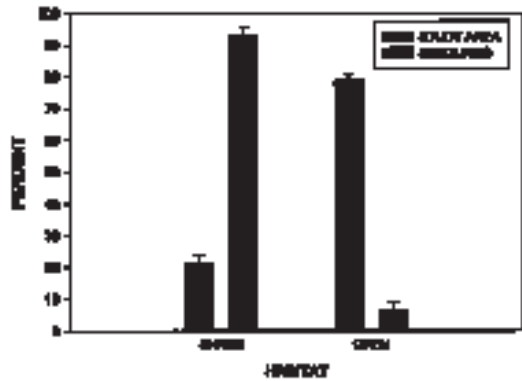


Fig. 1. Percentage of open substrate and area under shrubs within all 50-m<sup>2</sup> subplots and percentage of all seedlings found in both habitats ( $n = 16$  canyon-by-elevation combinations).

Seedling regeneration in the open also varied significantly by elevation (Fig. 2). Intermediate elevations had highest regeneration of *Y. brevifolia* seedlings in the open. Open space within the 50-m<sup>2</sup> subplots ranged from a low of 53% at 1800 m in Lucky Strike Canyon, where there was a dense cover of *Fallugia paradoxa* within a wide, dry wash, to 94% at Corn Creek at 1800 m. Open ground within the 50-m<sup>2</sup> subplots averaged 80% of total area. However, regeneration on open ground accounted for only 7% of all *Y. brevifolia* seedlings (20 seedlings). When all sites were combined, recruitment on open substrate was highest at elevations of 1600 (29%) and 1800 (41%) m. However, density of facilitated seedlings per ha at 1400 and 2000 m was similar to that found at 1800 m, indicating that recruitment in the open was not simply a function of an elevational pattern of establishment (Fig. 2).

Within the 50-m<sup>2</sup> subplots, 10,339 perennial shrubs were identified and measured for canopy area. Thirty-five species were identified, and 16 of them were found to be nurse plants for *Y. brevifolia* seedlings (Fig. 3). Nurse plants accounted for 76% of the total plant area within subplots. *Coleogyne ramosissima* accounted for 44% of the shrub area for combined elevations and canyons, with the remaining 15 nurse species accounting for <10% each. Numerical breakdown of nurse plant species displayed a similar pattern, with *Coleogyne ramosissima* accounting for 57% of all shrubs and remaining shrubs accounting for <10% each. Seedling number per ha was highest at 1600 m

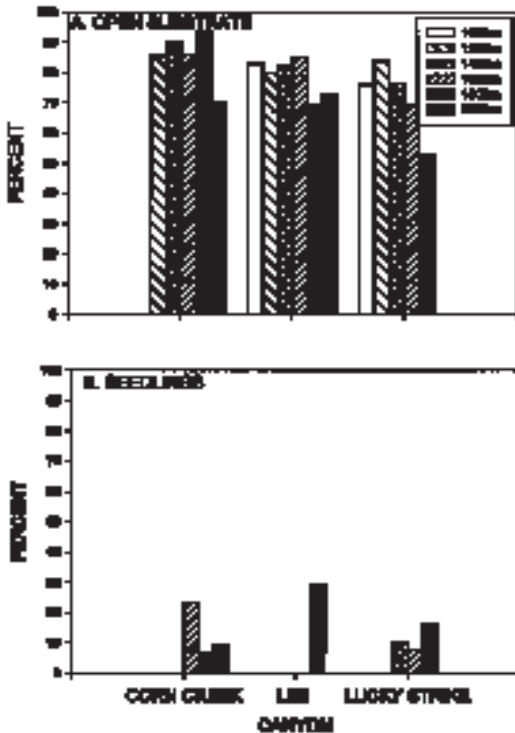


Fig. 2. A, Percentage of area of all 50-m<sup>2</sup> subplots ( $n = 174$  subplots) that was open substrate; B, percentage of seedlings found in the open ( $n = 20$  seedlings).

when all canyons were combined. Similarly, 71% of nursed seedlings (65.5% of all seedlings) were found under the canopy of *Coleogyne*, with 7.2% found in the open. The remaining 15 species had <7% each of all nursed seedlings. However, *Krameria parvifolia*, *Ambrosia dumosa*, and *Grayia spinosa* had higher percentages of *Y. brevifolia* seedlings than expected. Most nurse plant species had *Y. brevifolia* seedlings in lower ratios than their canopy and/or numerical dominance would predict. For example, *Artemisia tridentata* accounted for 9.2% of area and 9.9% of all plants, but it harbored only 7.4% of nursed *Y. brevifolia* seedlings.

The aspect of *Y. brevifolia* seedlings, relative to center stems of nurse plants, varied by site and elevation (3-way ANOVA,  $P < 0.001$ ). A site effect on seedling aspect relative to nurse shrubs was found ( $P < 0.001$ ), with *Y. brevifolia* seedlings found most often on east and west sides of nurse plants (Table 1). The largest variance ( $P = 0.054$ ) in seedling aspect was found between north (15% of total nursed

seedlings) and east (33.5% of total nursed seedlings). An elevational effect on seedling aspect ( $P < 0.001$ ) was found for 1600 m, where a predominance of seedlings was found in the eastern quadrant of nurse shrubs compared to all other elevations. Lee Canyon, with a general northeast aspect, had significantly more seedlings to the east (37%) and west (29.5%) of nurse plants when all elevations were combined. Corn Creek Canyon, with a southwest aspect, had a predominance of seedlings growing in the east (33%) and south (35%) quadrants of nurse shrubs. Most (73%) seedlings within the south quadrant of shrubs in Corn Creek were at 1800–2000 m. More than half (56%) of all Corn Creek (southwest aspect) seedlings were found at 1800 m and 2000 m versus 17% of all seedlings at those elevations within Lee and Lucky Strike canyons (northeast aspect). The remainder of seedlings in Corn Creek grew in the north and west quadrants of nurse shrubs (Table 1).

#### DISCUSSION

The climatic pattern that dominates the Mojave Desert in southern Nevada is responsible for a pattern of vegetation persistence based upon selection to survive a harsh physical environment or ability to take advantage of modified microsites. Perennial shrubs such as *Ambrosia dumosa* at low elevations, *Coleogyne ramosissima* at middle elevations, and *Artemisia tridentata* at higher elevations are able to successfully colonize open substrates and begin to modify conditions under their canopies. This process allows less stress-tolerant species such as *Yucca brevifolia* to establish beneath *Coleogyne* (S. Brittingham personal observation), and *Pinus monophylla* recruitment under *Artemisia* (Phillips 1909). The phenomenon of facilitation, or nurse plant interaction, allows plants to expand their ranges into otherwise inhospitable environments at the margins of their genetic adaptability.

*Yucca brevifolia* appears to be limited at lowest elevations by the fine-grained soil characteristics of basin floors (Hunning and Peterson 1973) and at highest elevations by low temperature constraints (Smith et al. 1983). Recruitment of *Y. brevifolia* in the open occurred between 1600 m and 2000 m in the Corn Creek transect. Corn Creek has an overall southwestern aspect that may have allowed

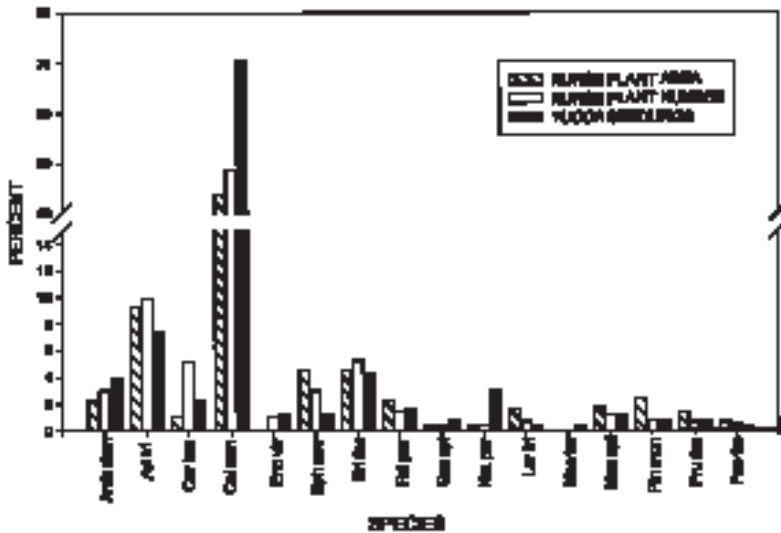


Fig. 3. Percentage of total shrub area occupied by each nurse plant species (total shrub area in all 50-m<sup>2</sup> subplots = 1706 m<sup>2</sup>); percentage of nurse plants ( $n = 7611$  nurse plants); and percentage of all *Yucca brevifolia* seedlings found under nurse plants ( $n = 257$  seedlings). See Appendix A for species abbreviation equivalents.

*Y. brevifolia* seedlings to survive without nurse plants at 2000 m. On the northeastern aspect transects (Lucky Strike and Lee canyons), *Y. brevifolia* seedlings were found in the open only to 1800 m, their upper limit in Lucky Strike Canyon. Franco and Nobel (1989) and Suzan et al. (1996) found that nurse canopies were only 1.2°C to 3.0°C warmer than the surrounding area during seasonal minima. The southwest aspect of Corn Creek may have produced a marginal temperature gain that permitted recruitment at the higher elevation in the open. In Lee Canyon and Lucky Strike Canyon, seedling recruitment on open substrate occurred between 1400 and 1800 m. Soil moisture, soil development, and cooler temperatures increase with altitude, perhaps explaining the lack of open substrate recruitment below 1600 m at Corn Creek and below 1400 m at Lucky Strike Canyon (Fig. 2). Higher elevations may preclude recruitment in the open due to freezing temperatures in winter.

Although a few physiological studies have been conducted on *Y. brevifolia*, little is known about its requirements for reproductive success, persistence within a highly stressful environment, or interactions with other community members. Recruitment of *Y. brevifolia* is largely dependent upon the existence of microclimates that occur under the canopies of perennial shrubs, most importantly *Coleogyne ramosis-*

*sima*. The advantages of germination within the canopy of another plant include higher soil moisture, reduced insolation, reduced surface temperatures, reduced evapotranspirational demand, increased nutrients, reduced herbivory, and reduced wind desiccation. Disadvantages of germination under another plant may include competition for water if the adult plant has a near-surface root system, reduced PAR inhibiting carbon gain, and allelopathy (Franco and Nobel 1989).

Despite similarities in canopy architecture of nurse plants, there appeared to be a selection process for particular species above that predicted by either canopy area or numerical dominance. If the presence of *Y. brevifolia* seedlings beneath a shrub canopy were purely a mechanical process (wind deposition), recruitment would be expected to occur based on total canopy area of each species or their number within the landscape. *Coleogyne ramosissima* was the most numerous plant and had the greatest canopy area when all elevations and sites were combined. Four nurse plants, *Ambrosia*, *Coleogyne*, *Grayia*, and *Krameria*, had a higher percentage of *Y. brevifolia* seedlings (for *G. spinosa* and *K. parvifolia* more than twice) than expected.

Walker et al. (in press) found species differences in soil characteristics under shrubs in Lucky Strike Canyon. Soils under *Coleogyne*

TABLE I. Number of *Yucca brevifolia* seedlings found at each of the 4 cardinal directions from the nurse plant.

Canyon	North	East	South	West	Total
Lee	22	50	23	40	135
Lucky Strike	8	15	15	21	59
Corn Creek	9	21	22	11	63
TOTAL	39	86	60	72	257

maintained higher soil moisture throughout the year than did *Ambrosia* and *Larrea*. The selection mechanism for *Coleogyne* over other nurse species may be more favorable water relations available during the driest period of the year in addition to canopy effects of reduced temperature, solar radiation, wind desiccation, and lower evapotranspiration. Water availability appears to be the primary limitation, with nitrogen becoming a limiting factor only when water is plentiful (Walker et al. in press). However, mortality of seedlings grown in shade versus seedlings grown in the open and supplied with water indicates that shading is more important than water relations for long-term survival of desert seedlings (Valiente-Banuet and Ezcurra 1991).

*Yucca brevifolia* seedling recruitment occurred in distinct directional patterns around nurse shrubs based on the overall aspect of the canyon surveyed. In Lee Canyon east and west quadrants were dominant in seedling recruitment around nurse plants. The southwest aspect in Corn Creek had a predominance of seedlings growing in the east and south quadrants of nurse shrubs. In Corn Creek the majority of seedlings within the south quadrant of nurse shrubs were found at the highest (1800–2000 m) elevations. Perhaps the greater warming, particularly with low winter sun, in the south quadrant of the shrub was the mechanism that allowed more than half of all Corn Creek seedlings to establish at 1800 and 2000 m versus 17% within Lee and Lucky Strike canyons.

*Coleogyne* seedlings had highest mortality on the south side of shrubs in Lucky Strike Canyon (S. Vrooman personal communication). On the east and west sides of shrubs, photosynthesis can occur in the relative coolness of the low, direct morning and late afternoon sun. Morning and late afternoon sunlight produces relatively less heat stress in plant tissues than midday sunlight. Reduced tissue temperature enhances stomatal functioning, maintains

protein and membrane integrity, and lessens photoinhibition in summer months (Singla et al. 1997). Light intensity and heating of tissues may explain the selection of the east quadrant (54.5%) of nurse canopies when the 1000-m and 1200-m elevations of all sites were combined.

Holmgren et al. (1997) reported that dry conditions reduce a plant's tolerance to shade because dry conditions require a greater allocation of carbon to the root system. Reduction of PAR by nurse plant shading would limit productivity of seedlings. However, *Y. brevifolia* light saturates at 25% of midday irradiance (Smith et al. 1983), and higher soil moisture levels found under *Coleogyne* (Walker et al. in press) compensate for reduced light by allowing greater stomatal opening and extending the period of carbon gain into the dry season. Shading also reduces leaf temperature, thereby reducing water vapor concentration within intercellular air spaces.

When all canyons were combined for elevation effects on seedling recruitment, lowest percentages were at 1000 and 1200 m, increasing to a maximum at 1600 m (50%), then decreasing at 1800 and 2000 m (12%). Smith et al. (1983) concluded that low temperatures act as a constraint upon the range of *Y. brevifolia* at high elevations, while high temperatures recorded within the Mojave Desert were within its physiological capability. However, data gathered in the Sheep and Spring Mountain ranges indicate that low elevations did have sparse levels of seedling recruitment, while higher elevations had higher recruitment levels until a physiological point (perhaps a critical temperature) where they no longer occurred.

Highest adult and seedling densities of *Y. brevifolia* at 1600 m suggest optimal conditions for recruitment and persistence exist at this elevation. Maximum seedling growth occurs with a soil temperature of 21°C (Wallace et al. 1970); moderate temperatures produce highest net photosynthesis rates in *Y. brevifolia* (Smith et al. 1983). On an annual

basis the 1600-m elevation, approximately the mid-point of the elevational range of *Y. brevifolia*, would presumably have moderate temperatures between the seasonal minimum and maximum of local bajadas. It would also have high moisture availability during the primary growth period (January–May) while avoiding late-season cold fronts that often result in high mortality of inflorescences at higher elevations as noted in Lee Canyon in April 1997 (S. Brittingham personal observation).

Moderated tissue temperature appears to be the most critical parameter favoring survival of *Y. brevifolia* seedlings. Previous research has found that higher water availability, critical in xeric environments, will increase the life span of plants regenerating on open substrates; however, long-term survival of seedlings is dependent on the presence of shade (Nobel 1980, Valiente-Banuet and Ezcurra 1991, Callaway 1992). Shade reduces temperatures by 13.5°C (Franco and Nobel 1989) to 15°C (Suzan et al. 1996), creating microhabitat temperature and moisture regimes closer to the optima for photosynthesis and maintenance of leaf cell turgor and membrane function. Shade also lowers the water vapor concentration gradient between intercellular spaces and ambient air. Plant architecture can also help maintain a boundary layer of air near the surface, thereby reducing wind desiccation of the soil and diminishing evapotranspiration. Shaded microenvironments provide seedlings with improved water relations, maintenance of carbon gain longer into the dry season, reduced heat and cold damage to tissues, and avoidance of photoinhibition.

The attributes of shade explain the general mechanisms that permit recruitment and persistence of *Y. brevifolia* at higher densities under shrubs than in the open. However, our data also indicate a selection process in which *Coleogyne*, *Krameria*, *Grayia*, and *Ambrosia* are correlated with *Y. brevifolia* seedlings in greater numbers than expected based on their canopy area or density. Aspect selection, relative to the nurse plant, also appears to be influential in successful germination and/or succession. Recruitment of *Y. brevifolia* is based upon microhabitat alterations by specific nurse plants and upon subtle variations in light and shade that have important implications on physiological requirements for germination and survival of *Y. brevifolia*.

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APPENDIX A. Species abundance by canyon: Lee/Lucky Strike/Corn Creek; \* indicates absence of plots at that canyon/ elevation.

	1000 m	1200 m	1400 m	1600 m	1800 m	2000 m
<i>Acamptopappus shockleyi</i> (Aca sho)	0 / 0 / *	27 / 0 / 0	29 / 0 / 0	0 / 0 / 0	0 / 0 / 0	0 / * / 0
<i>Ambrosia dumosa</i> (Amb dum)	56 / 16 / *	66 / 0 / 114	0 / 2 / 0	0 / 0 / 0	0 / 0 / 0	0 / * / 0
<i>Artemisia tridentata</i> (Art tri)	0 / 0 / *	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0	1 / 36 / 1	344 / * / 556
<i>Atriplex canescens</i> (Atr can)	21 / 0 / *	0 / 0 / 0	5 / 1 / 0	103 / 2 / 1	7 / 0 / 5	0 / * / 8
<i>Baileya multiradiata</i> (Bai mul)	0 / 0 / *	0 / 0 / 0	0 / 0 / 0	0 / 0 / 7	0 / 0 / 0	0 / * / 0
<i>Ceratoides lanata</i> (Cer lan)	31 / 12 / *	39 / 1 / 0	247 / 15 / 1	15 / 3 / 0	0 / 0 / 0	0 / * / 0
<i>Chrysothamnus nauseosus</i> (Chr nau)	0 / 0 / *	0 / 0 / 0	0 / 0 / 0	0 / 0 / 1	0 / 0 / 0	0 / * / 5
<i>Coleogyne ramosissima</i> (Col ram)	0 / 0 / *	0 / 47 / 0	23 / 685 / 0	2570 / 1165 / 0	419 / 194 / 503	0 / * / 330
<i>Echinocactus</i> spp. (Ech spp)	0 / 0 / *	0 / 0 / 10	0 / 0 / 0	0 / 0 / 3	0 / 0 / 3	0 / * / 0
<i>Encelia farinosa</i> (Enc far)	0 / 0 / *	0 / 0 / 93	0 / 0 / 0	0 / 0 / 9	0 / 0 / 0	0 / * / 0
<i>Encelia virginensis</i> (Enc vir)	5 / 0 / *	1 / 6 / 122	4 / 14 / 0	0 / 1 / 0	0 / 0 / 0	0 / * / 0
<i>Ephedra nevadensis</i> (Eph nev)	2 / 3 / *	9 / 12 / 1	24 / 70 / 13	109 / 20 / 33	27 / 4 / 1	0 / * / 31
<i>Ephedra viridis</i> (Eph vir)	0 / 0 / *	0 / 0 / 0	0 / 17 / 0	0 / 62 / 0	0 / 13 / 53	0 / * / 37
<i>Eriogonum fasciculatum</i> (Eri fas)	2 / 0 / *	1 / 2 / 0	2 / 1 / 97	0 / 0 / 380	0 / 0 / 0	0 / * / 0
<i>Fallugia paradoxa</i> (Fal par)	0 / 0 / *	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0	7 / 110 / 14	0 / * / 0
<i>Grayia spinosa</i> (Gra spi)	0 / 0 / *	0 / 5 / 0	2 / 0 / 0	47 / 0 / 1	0 / 0 / 0	0 / * / 0
<i>Gutierrezia sarothrae</i> (Gut sar)	0 / 0 / *	0 / 0 / 0	0 / 2 / 0	33 / 1 / 0	29 / 0 / 28	127 / * / 4
<i>Hymenoclea salsola</i> (Hym sal)	0 / 0 / *	0 / 0 / 0	0 / 42 / 0	0 / 0 / 0	0 / 0 / 0	0 / * / 0
<i>Juniperus osteosperma</i> (Jun ost)	0 / 0 / *	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0	4 / * / 2
<i>Krameria parvifolia</i> (Kra par)	4 / 0 / *	4 / 4 / 10	1 / 0 / 3	0 / 0 / 7	0 / 0 / 0	0 / * / 0
<i>Larrea tridentata</i> (Lar tri)	8 / 6 / *	1 / 0 / 31	1 / 0 / 1	0 / 0 / 0	0 / 0 / 0	0 / * / 0
<i>Lycium andersonii</i> (Lyc and)	0 / 23 / *	2 / 1 / 0	12 / 2 / 0	0 / 0 / 0	0 / 0 / 0	0 / * / 0
<i>Machaeranthera tortifolia</i> (Mac tor)	0 / 0 / *	0 / 0 / 0	0 / 0 / 5	0 / 0 / 3	0 / 0 / 0	0 / * / 0
<i>Menodora spinescens</i> (Men spi)	4 / 0 / *	20 / 2 / 17	33 / 0 / 4	0 / 0 / 0	18 / 0 / 1	0 / * / 0
<i>Opuntia</i> spp. (Opu spp)	4 / 2 / *	7 / 10 / 8	7 / 10 / 1	118 / 8 / 2	16 / 43 / 2	6 / * / 18
<i>Pinus monophylla</i> (Pin mon)	0 / 0 / *	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0	0 / 1 / 0	61 / * / 3
<i>Prunus fasciculata</i> (Pru fas)	7 / 0 / *	0 / 1 / 9	7 / 0 / 21	0 / 7 / 0	0 / 2 / 0	0 / * / 0
<i>Psoralea fremontii</i> (Pso fre)	3 / 0 / *	3 / 4 / 13	0 / 0 / 11	0 / 0 / 12	0 / 0 / 0	0 / * / 0



## APPENDIX A. Continued.

	1000 m	1200 m	1400 m	1600 m	1800 m	2000 m
<i>Tetradymia axillaris</i> (Tet axi)	0 / 0 / *	0 / 0 / 0	0 / 0 / 1	41 / 0 / 8	0 / 0 / 0	0 / * / 0
<i>Thamnosma montana</i> (Tha mon)	0 / 0 / *	0 / 0 / 0	0 / 0 / 0	90 / 143 / 25	0 / 0 / 29	0 / * / 0
<i>Yucca baccata</i> (Yuc bac)	1 / 0 / *	0 / 0 / 3	0 / 11 / 0	132 / 45 / 0	25 / 18 / 49	0 / * / 42
<i>Yucca brevifolia</i> (Yuc bre)	0 / 1 / *	1 / 0 / 0	2 / 3 / 1	38 / 1 / 10	6 / 0 / 15	2 / * / 11
<i>Yucca schidigera</i> (Yuc sch)	2 / 0 / *	3 / 1 / 1	3 / 12 / 12	0 / 1 / 21	0 / 1 / 0	0 / * / 0

## APPENDIX B. Nurse plant species: all canyons and all elevations.

	1000 m	1200 m	1400 m	1600 m	1800 m	2000 m
LEE						
Men spi	1	1		1		
Amb dum	2					
Cer lan			4	1		
Kra par		1				
Col ram			1	92	12	
Pru fas			1			
Gra spi				2		
Pin mon						2
Art tri						11
Open				2	5	
LUCKY STRIKE						
Amb dum	1					
Pso fre		1				
Col ram		2	26	23	2	
Eph nev				1		
Fal par					3	
Open			3	2	1	
CORN CREEK						
Amb dum		7				
Enc fru		2				
Lar tri		1				
Eri fas		1	3	7		
Kra par			4	3		
Enc vir			1			
Eph nev				2		
Pru fas				1		
Col ralm					13	11
Fal par					1	
Art tri						8
Open				4	1	2
TOTALS	4	17	43	141	38	34

VARIABILITY AMONG FIVE RIPARIAN COTTONWOOD  
(*POPULUS FREMONTII* WATS.) POPULATIONS: AN EXAMINATION  
OF SIZE, DENSITY, AND SPATIAL DISTRIBUTION

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**ABSTRACT.**—Various abiotic and biotic factors are known to affect tree size, including age, genetics, and environment. Knowledge of size variation within natural riparian tree populations has both ecological and restorative importance. We determined tree sizes, basal area densities, and spatial distributions of 5 *Populus fremontii* Wats. populations within the Rio Grande watershed in New Mexico. At each site 10 randomly spaced plots, perpendicular to the river and extending from the river to the end of the forest, were established. Diameter at breast height (DBH) and distance to the river were determined for 1803 trees within the 5 populations, and stand cover (measured as basal area [BA] per hectare) was determined for each population. Significant variation in tree size and basal area density existed among sites. Mean DBH per site ranged from 11.7 to 58.4 cm and differed significantly ( $P < 0.0001$ ) among sites. Mean BA per hectare also varied significantly ( $P < 0.0001$ ) among sites and ranged from 13.2 to 28.9 m<sup>2</sup> ha<sup>-1</sup>. Spatial distribution of trees in relation to the river also differed among sites. Mean distance from the river ranged from 50 to 353 m and differed significantly ( $P < 0.0001$ ) among sites. Tree size was both linearly and nonlinearly related to distance from the river, with models varying among sites. Patterns of distribution in these New Mexico *P. fremontii* populations may be influenced by differences in water availability across a site; trees farthest from water sources may experience greater water stress and, therefore, growth limitation. Increasing BA cover with increasing tree size indicated no real thinning of mature trees within a population. Recruitment and establishment of cottonwood seedlings and saplings was evident only at sites with newly formed floodplains. For these 5 populations tree size appeared to be affected by environmental factors.

*Key words:* *Populus fremontii*, *Rio Grande*, *riparian ecosystem*, *tree size variation*, *water stress*, *tree spatial distributions*, *basal area*.

Researchers from the disciplines of ecology and forestry focus on determining causes behind variation in growth and size among individual plants because such variation can indicate important differences in age, competition, genetics, and environment (Stoll et al. 1994). For a single tree, size can be determined by both biotic and abiotic factors and their interactions. Biotic factors include genetics, age, sex, herbivore impact, and inter- or intraspecific competition; abiotic factors include availability of nutrients, water, and light. Populations of riparian trees provide unique opportunities to study the factors that affect tree size, density, and distribution. During periodic flood events, trees often are established in even-aged cohorts or “isochrones” (Stromberg et al. 1991, Braatne et al. 1996) at various distances from the river channel. Thus, isochrones may be composed of even-size trees due to their common age. In addition, spatial distribution of isochrones is dependent upon

flood events that lead to seedling establishment. However, some environmental factors may affect tree growth and spatial distribution even more than age. For example, Roberts (1993) found that floodplain *Eucalyptus coolabah* growth and survival were more strongly affected by saline soils and dry conditions than by age. Other factors within riparian ecosystems can also affect tree growth, including distance to groundwater, nutrient status, stand density, reproductive mode (either sexual or asexual), and herbivore pressure (Stromberg 1993). Stand density and tree size are closely linked as well. Density-dependent effects on tree size are strong for many species (Condit et al. 1994, Stoll et al. 1994). However, despite this close relationship, riparian forest stand densities can be highly variable (Braatne et al. 1996).

One such riparian species with potential size and stand density variability among populations is *Populus fremontii* Wats. (Fremont

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cottonwood). This native riparian tree is the dominant forest species within the Rio Grande watershed in New Mexico and historically dominated other riparian zones of the south-western United States. *Populus fremontii* forests provide canopy and understory habitats that are preferred by many animal species including spiders (Jennings 1972), beavers (Irvine and West 1979, Crawford et al. 1993), and birds (Johnson et al. 1990, Crawford et al. 1993). Cottonwood forests are found in diverse areas along the Rio Grande basin; these areas vary in precipitation, temperature, elevation, and soil characteristics. Some riparian populations of *P. fremontii* are also isolated by geographic distance and by natural river constrictions that may serve as barriers to seed dispersal. Such environmental variation and possible genetic differentiation could lead to variability among populations in such stand characteristics as tree size, basal area, and spatial distribution.

Although riparian forests in New Mexico are of prime ecological importance, their fate is uncertain. Due to perturbations such as construction of dams and channelization, Rio Grande cottonwood forests are likely to disappear in the next 50 yr (Howe and Knopf 1991, Crawford et al. 1993). Factors contributing to this demise include increased competition from exotic tree species (e.g., *Tamarix ramosissima*; saltcedar), reduced water availability, and a lack of germination sites due to elimination of flood events. High use of groundwater from tree competitors, combined with restricted aboveground stream flow, may be causing water stress for cottonwood trees in New Mexico riparian zones (Crawford et al. 1993, Stromberg 1993). Aboveground stream flow is a significant water source for New Mexico riparian populations of *P. fremontii*; stream flow explains 68% of tree ring growth variation for these cottonwoods (J. Leffler personal communication). In addition, *Tamarix* trees in these riparian communities are known to increase soil salinity, possibly causing surface and leachate water to be unavailable to cottonwoods (Stromberg 1993, Busch and Smith 1995). Water stress, in turn, may limit the capacity of adult trees to grow and thrive. Several studies have concluded that these factors will lead to eventual elimination of cottonwood in the Southwest (Irvine and West 1979, Fenner et al. 1985, Asplund and Gooch 1988, Busch and Smith

1995). Deterioration of *Populus* populations due to strict river control measures is not uncommon in western North America (Rood and Heinze-Milne 1989, Rood and Mahoney 1990, Braatne et al. 1996).

Because of these threats to the survival of riparian cottonwood forests, documentation of forest stand parameters such as tree size, basal area, and spatial variation among natural riparian populations of *Populus fremontii* in New Mexico is of particular importance, both for ecological and conservation reasons. Knowledge about these characteristics gives a basis for further investigations into possible environmental factors (e.g., water availability) that affect these characteristics. If adverse environmental characteristics can be ameliorated, then such intervention may ensure the future survival of *P. fremontii* populations. If tree size and basal area variation is due to genetic differences, then future studies determining this genetic variability could identify genotypes that might be utilized in restoration efforts.

In 1994 we conducted a study to measure tree size, stand density, and spatial variation among 5 *P. fremontii* populations in central New Mexico. Howe and Knopf (1991) concluded that cottonwood populations in central New Mexico are even-aged. The apparent absence of extensive cottonwood regeneration along the Rio Grande since the introduction of upstream dams in the past half century supports this conclusion. However, for *P. fremontii*, an even-age distribution is not necessarily reflected in an even-size distribution. Differences among individuals in traits such as suckering, sex-specific growth, genotype, and environmental variability all contribute toward tree size differences in an even-aged stand.

We took forest stand measurements to explore population level differences in tree size, basal area, and spatial variation of *P. fremontii*. First we asked: Do tree sizes and basal area densities of cottonwoods differ among riparian populations? We hypothesized that if most cottonwood populations along the Rio Grande basin had been established during 1 or 2 common flood events prior to dam construction, then most populations would be composed of 1 or 2 even-aged isochrones. Furthermore, because of strict water control along the Rio Grande and its tributaries, these cohort populations may have similar water availability and therefore be of similar size.

Secondly, we asked: If size variation were observed, is this variability related to distance to a water source in the environment? We hypothesized that water stress would likely be more acute farther from the river, so that tree sizes would decrease as distance to the river increased. This is because aboveground stream flow can serve as an important water source for *P. fremontii*, and stream flow greatly impacts groundwater, the primary source of water for cottonwoods (Leffler and Evans 1999).

## METHODS

### Study Sites

We established 5 study sites to sample the *Populus fremontii* forest that spans 480 km along the Rio Grande and a major tributary, the Rio Chama (Fig. 1). The northernmost site is north of White Rock Canyon and includes a single site at Abiquiu (36°12'30"N, 106°19'06"W, 1807 m elev) along the Rio Chama. The following study sites were established south of White Rock Canyon: Corrales (35°14'16"N, 106°36'22"W, 1552 m elev), Los Lunas (34°48'22"N, 106°43'58"W, 1479 m elev), Bernardo (34°25'06"N, 106°50'06"W, 1444 m elev), and San Antonio (33°55'06"N, 106°52'06"W, 1380 m elev). These sites were chosen to sample the contiguous cottonwood forest within the Rio Grande basin in New Mexico; this forest runs just below Taos Gorge south to Elephant Butte Reservoir. Because of extensive channelization and levee construction, cottonwood populations south of Elephant Butte have been reduced to isolated patches (personal observation).

At each study site ten 10-m-wide randomly located plots were established within an approximate 0.5-km section of forest. Each plot was perpendicular to the associated river and extended from the riverbank to the outer edge of the riparian forest. Distances between plots ranged from 0 to 50 m. At the 4 Rio Grande sites, forest edge coincides with a levee road and water diversion channel, both parallel to the river. These diversion channels are common along the length of the western edge of the Rio Grande. At Abiquiu, the Rio Chama and an abandoned agricultural field border the forest. Within each plot all live cottonwood trees were tagged and mapped; over all plots a total of 1803 trees were catalogued.

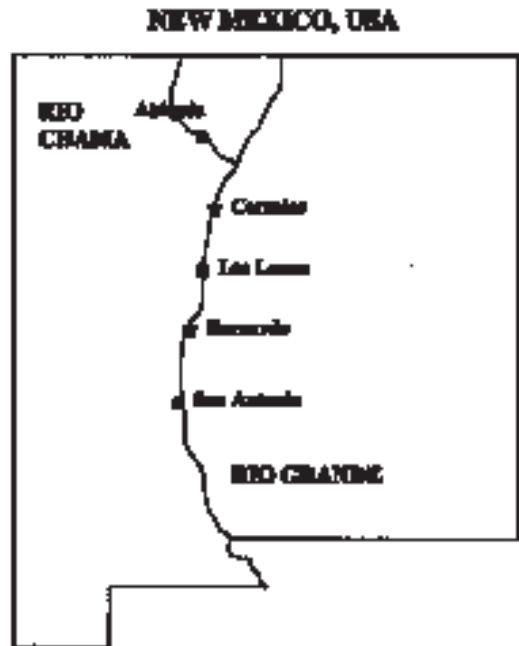


Fig. 1. Location of *Populus fremontii* study populations in New Mexico located at Abiquiu along the Rio Chama, and at Corrales, Los Lunas, Bernardo, and San Antonio along the Rio Grande.

In general, sampled cottonwood stands were mature and continuous throughout each study area; however, minor recruitment was observed at Corrales and San Antonio. At these sites the gallery forest ends abruptly with a 50-m (Corrales) or 200-m (San Antonio) stretch of newly established floodplain situated between the mature forest and the river. Young cottonwood trees inhabit these floodplains. At Corrales, the floodplain was sampled because most juvenile trees were large in size and many were of reproductive age. However, at San Antonio, the floodplain was not sampled because most trees were too small to tag (<4 cm DBH) without causing significant mortality.

### Measurements

For all plots and sites, tree diameter at breast height (DBH) (ca 1.45 m) was measured to the nearest centimeter for all live cottonwoods. We measured distance to the river to the nearest 0.1 m for each tagged tree. To determine the cross-sectional area of each tree, we calculated basal areas from DBH measurements using the general equation of Avery and Burkhart (1994) for any tree species, where:

$$\text{Basal Area (BA) (m}^2\text{)} = 0.00007854 (\text{DBH}^2).$$

Mean basal area per hectare, a measure of stand density, was calculated for each of 10 plots at all 5 sites using the area of each plot.

#### Analyses

For each site and over all sites, descriptive statistics were performed for tree size distributions. Differences among sites for mean tree size (DBH), distance to the river, and basal area per hectare were analyzed using fixed ANOVA and Bonferroni multiple range tests (SYSTAT 1996). Before analyses, DBH data were log-transformed to comply with normality assumptions of ANOVA. To investigate possible relationships between tree size and tree-spatial distributions, we performed least-squares regression analyses (both linear and nonlinear models) for each site separately, and for all sites pooled (SAS Institute 1989).

### RESULTS

#### Variation Among Sites in Tree Size, Spatial Distribution, and Basal Area

Contrary to our expectation of size uniformity, there was extensive variation among cottonwood populations in tree size within the Rio Grande watershed. Mean tree size (DBH)

was significantly different among sites and ranged from 11.7 cm at Corrales to 58.4 cm at Los Lunas (Table 1). The Los Lunas population contained extremely large trees compared to the other sites. Mean distance to the river for trees was significantly different among sites, ranging from 50.3 m at Los Lunas to 352.9 m at San Antonio (Table 1). Multiple range tests showed that all sites differed from one another for DBH and distance to the river. Basal area per hectare also differed significantly among sites (Table 1) and ranged from 28.9 m<sup>2</sup> ha<sup>-1</sup> at San Antonio to 13.2 m<sup>2</sup> ha<sup>-1</sup> at Corrales. Multiple range tests showed Los Lunas and San Antonio had similarly large basal area per hectare, while Abiquiu, Bernardo, and Corrales had comparable values.

#### Size and Distance to the River

The relationship between tree size and distance to the river was more complex than a simple linear function of distance from this possible water source. For data pooled over all 5 sites, the relationship was linear; in general, small trees were near the river and large ones farther away ( $F = 199.5$ ,  $P < 0.0001$ ,  $r^2 = 0.0993$ ; Fig. 2). However, this overall picture is somewhat misleading because spatial distribution of trees differed among individual sites and was often nonlinear. The least-squares line that best described tree distribution at

TABLE 1. ANOVA table for variation in tree size (DBH), distance to river, and basal area per hectare among 5 riparian *Populus fremontii* populations in New Mexico (AB = Abiquiu, CO = Corrales, LL = Los Lunas, BE = Bernardo, SA = San Antonio). Different letters denote significant differences among groups at  $P < 0.05$ .

Trait	Site	Trait mean ( $\pm s_{\bar{x}}$ )	df	F-value	P-value
DBH (cm)	AB	25.3 (0.5) a	4	480.5	0.0001
	CO	11.7 (0.9) b			
	LL	58.4 (2.7) c			
	BE	20.0 (0.6) d			
	SA	39.2 (0.8) e			
Distance to river (m)	AB	147.9 (2.8) a	4	2111.4	0.0001
	CO	65.5 (1.5) b			
	LL	50.3 (3.3) c			
	BE	95.2 (1.5) d			
	SA	352.9 (2.7) e			
Basal area per hectare (m <sup>2</sup> ha <sup>-1</sup> )	AB	14.3 (1.5) a	4	18.0	0.0001
	CO	13.2 (2.3) a			
	LL	28.0 (1.9) b			
	BE	14.0 (1.5) a			
	SA	28.9 (2.2) b			

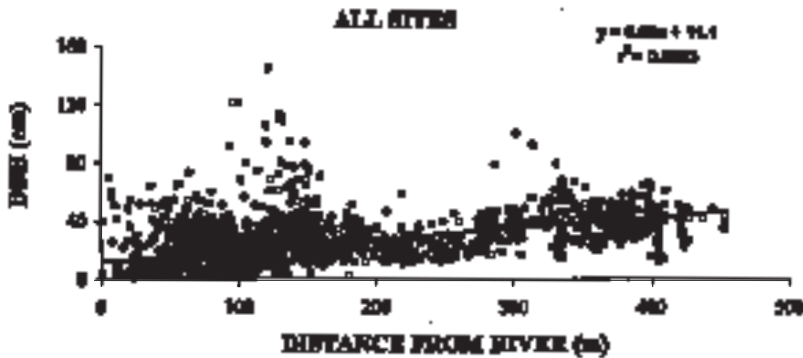


Fig. 2. Relationship between tree size (DBH) and distance to the river among 5 *Populus fremontii* populations in New Mexico. Data are pooled from all 5 sites (see Fig. 1).

Abiquiu was linear but negative; larger trees were near the river while smaller trees were close to the agricultural field (Fig. 3a). Tree distribution at Los Lunas also was linear but positive, with large trees clustered farther away from the river (Fig. 3b). However, tree distributions at both Corrales and Bernardo were nonlinear. At Bernardo large trees were found near the river and also near the diversion channel, whereas smaller trees were centered in the plots (Fig. 3c). Largest trees at Corrales were near the diversion channel, medium-small trees near the river, and smallest trees centered in the plots (Fig. 3d). No significant relationship was evident at San Antonio between DBH and distance to nearest water source (Fig. 3e).

#### DISCUSSION

##### Size, Distance, and Basal Area Variation Among Sites

In New Mexico we found significant variation in tree size among 5 riparian populations of *Populus fremontii* along the middle Rio Grande and one of its northern tributaries. This is contrary to what we expected because of the purported even-aged structure of these populations (Howe and Knopf, 1991) and because recruitment in these populations has virtually ceased with the construction of dams in the past 50 yr. Therefore, other factors besides age must be affecting growth rate. Tree size often is an indicator of physiological activity (Dickson 1991, Avery and Burkhardt 1994), and specifically for *P. fremontii* where size per se is not a good indicator of age (Howe and Knopf

1991). However, some size differences may be accounted for by age among *P. fremontii* populations. For example, at Corrales a portion of the population was established recently. Preliminary dendrochronological analysis shows that trees closest to the river at Corrales are approximately 15 yr old (Rowland et al. unpublished data), while the dominant forest at this site may be closer to 50 yr of age (C. Crawford personal communication).

Nonetheless, due to the purported even-aged structure of most middle Rio Grande *P. fremontii* populations, dramatic differences in tree size among populations in this study may not be age related. For example, large trees at Los Lunas recently have experienced overbank flooding, followed by establishment and luxuriant growth of herbaceous species in the understory. Such growth is indicative of a moist habitat. Sediment deposited by overbank flooding is a rich source of nutrients (Stromberg 1993). Such favorable moisture and nutrient conditions could have led to enhanced tree-growth rates at Los Lunas. Cottonwoods are known to require groundwater; however, surface soil moisture also is important to cottonwoods because they have extensive lateral root systems (Dickmann and Pregitzer 1992, Stromberg 1993). All 5 sites showed some within-site diversity of tree sizes. We suspect that such size ranges are due to within-site variability of nutrients, moisture, and sunlight. Intra- and interspecific competition for these favorable environmental conditions also may affect tree growth and size within a site.

Besides age, tree size diversity can be attributed to a number of biotic and abiotic

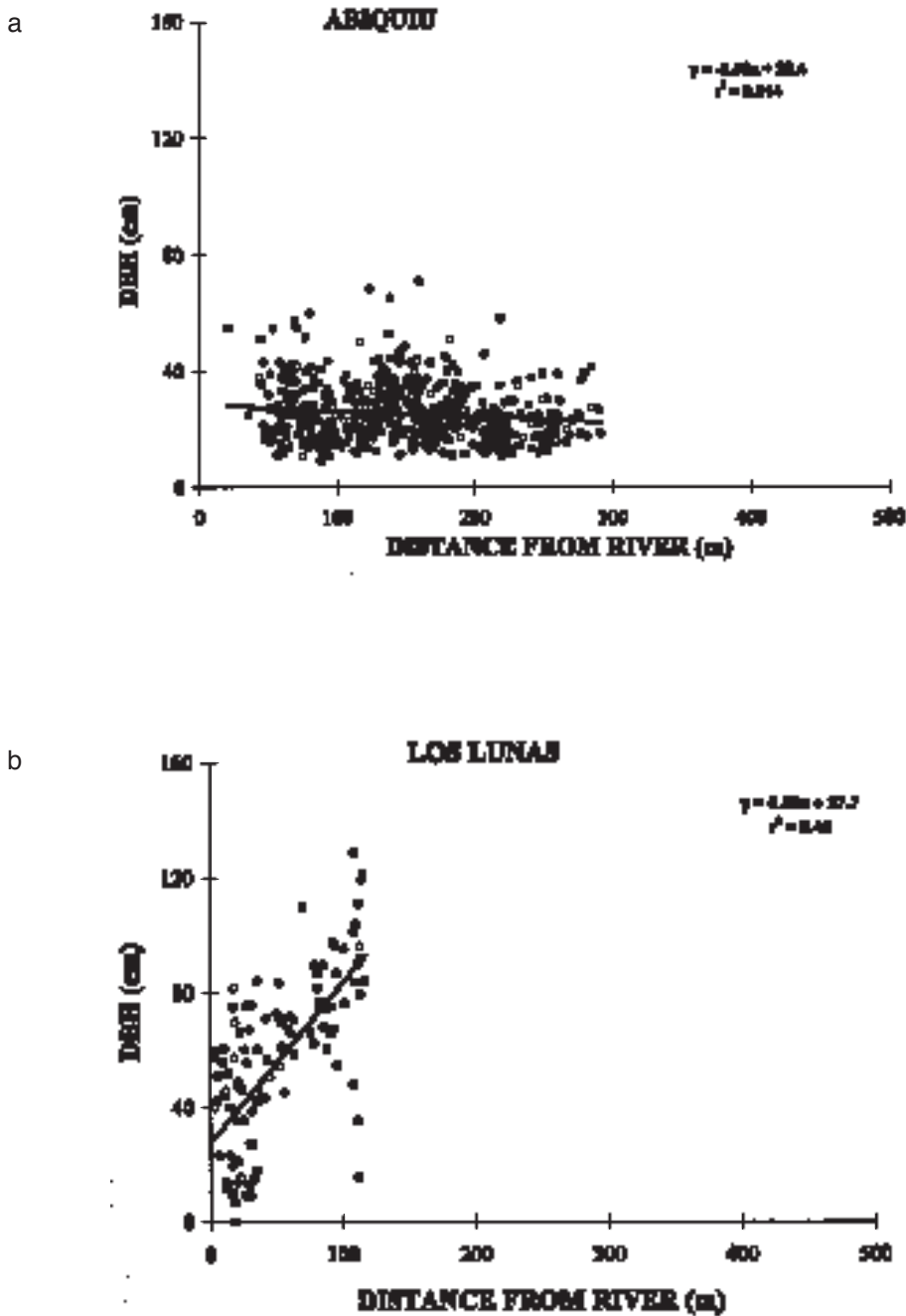
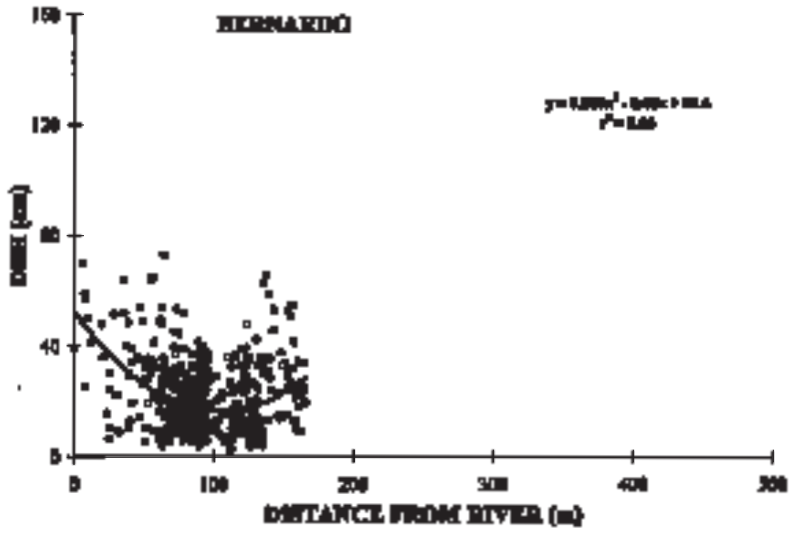


Fig. 3. Relationship between tree size (DBH) and distance to the river for 5 individual populations of *Populus fremontii* in central New Mexico. The data show a significant (3a) negative relationship at Abiquiu and (3b) positive linear relationship at Los Lunas.

c



d

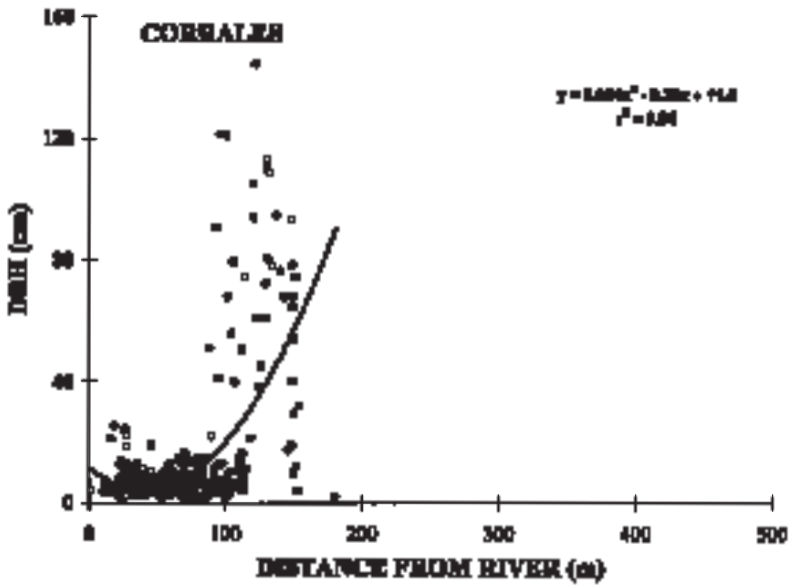


Fig. 3. Continued: (3c) nonlinear, quadratic relationship at Bernardo and (3d) nonlinear, quadratic relationship at Corrales.



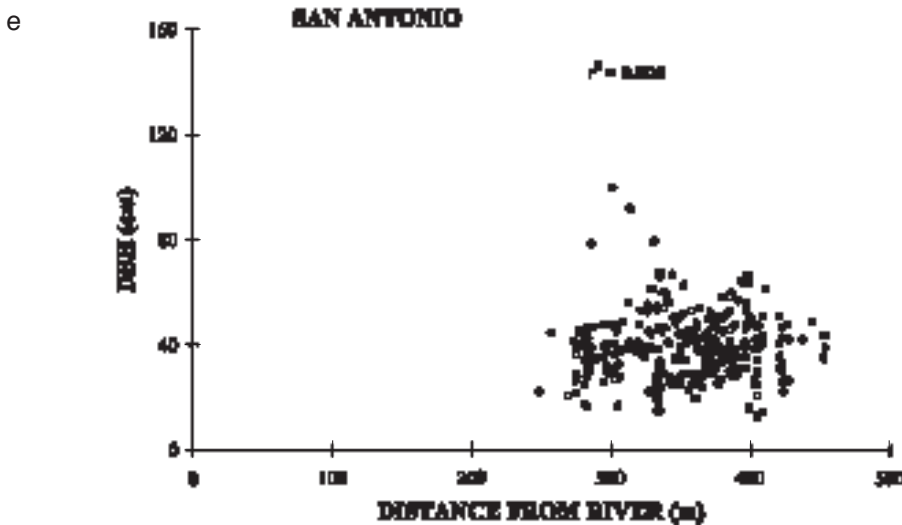


Fig. 3. Continued: (3e) no detectable relationship at San Antonio.

factors. Biotic factors affecting size variability in *P. fremontii* include suckering, sex-specific differences, genetic differences, and competition. Presence of abundant saplings only at Corrales and San Antonio indicates that recruitment of riparian cottonwoods in the recent past was limited to these sites. Asexual reproduction also may have contributed to some observed size variation. Howe and Knopf (1991) noted clonal reproduction for *P. fremontii* along various areas of the Rio Grande. Such asexual reproduction may explain the preponderance of smaller size classes (DBH = 10–20 cm) at Bernardo, where multiple-bole trees were common. However, to our knowledge quantitative assessments of asexual reproduction in riparian cottonwoods have not been made. To do so would require physical excavation of roots or, preferably, genetic identification of clones. Genetic variation also may have contributed to observed size differences among and within *P. fremontii* populations in New Mexico. For sugar maple (*Acer saccharum* Marsh.), recent studies (Perry and Knowles 1991, Young and Merriam 1994) have emphasized that, even at a small spatial scale, genetic variation can be substantial. Whether such genetically based small-scale spatial variation exists for *P. fremontii* remains to be seen. However, if present, it would be an invaluable source of genetic diversity that could be utilized in forest-stand restoration (Stromberg 1993).

The 5 cottonwood populations we observed in New Mexico were highly variable in stand density as well. Mean basal area per tree was significantly different among sites; this was not surprising because basal area is derived from DBH, which was significantly different among sites. As expected from DBH measurements, Los Lunas had the largest mean basal area per tree (0.33 m<sup>2</sup>). However, not as obvious were significant differences among sites in mean basal area per hectare (stand basal cover), with Los Lunas and San Antonio exhibiting higher basal area per hectare than the other 3 populations. These 2 sites had the largest trees as well. Based on these results, it appears that *P. fremontii* trees may not self-thin as they approach maturity; consequently, stand density increases with tree size. Intraspecific competition is likely to be great at these sites where both basal area per tree and stand density are high. Large variability in stand basal cover is a common result for many species of *Populus* (Braatne et al. 1996).

#### Size and Spatial Distribution

The observed diverse spatial distributions of cottonwood trees in New Mexico suggest that tree recruitment and growth might be affected by environmental conditions, possibly water availability, in these riparian communities. If size variability existed among these populations, we expected water availability might be driving much of this variation. We

hypothesized that large trees would be located near the river, a possible important water source for cottonwoods in these dry, southwest populations. However, the nonlinear distribution of trees at Bernardo and Corrales shows that large trees are found not only near the river, but also near the diversion channel, another likely aboveground water source.

Two sites, Abiquiu and Los Lunas, had a linear relationship between tree size and spatial distribution. The nonlinear distribution of trees associated with 2 possible aboveground water sources is absent at Abiquiu, where no 2nd source of water occurs. However, at Abiquiu, the linear relationship is as expected: large trees are located near the river, the only aboveground water source available. The linear relationship at Los Lunas is not as expected if tree size at this population is dependent upon proximity to an aboveground water source because the smallest trees are located near the river. However, this site is currently experiencing overbank flooding that could be influencing tree size by providing water uniformly across the population and by affecting groundwater levels. In addition, because of this overbank flooding, recruitment could have taken place in earlier high-flow years; the pattern of large trees being farther away from the streambed follows what would be expected if different age isochrones had previously been established.

At San Antonio the apparent absence of a significant tree-river spatial relationship may be due to the large stretch (>200 m) of dry floodplain that now separates the forest from the active river channel. The small-sized, abundant saplings in this area indicate this floodplain was established recently. The clustered distribution of more mature trees away from the river might eventually lead to greater dependence on precipitation and levee-channel water for tree water sources.

#### CONCLUSIONS

This study shows a large diversity of tree size, density, and spatial distribution of individuals among populations of *Populus fremontii* within the Rio Grande basin in New Mexico. Such large variation among these populations is surprising since they are found within a relatively small geographic area (480 km) compared to the species range of approximately

4500 km. In addition, the Rio Grande basin populations are contained within a contiguous stretch of forest, indicating they may be relatively connected via gene flow. Nonetheless, these populations differ significantly in many environmental parameters including precipitation, temperature, elevation, salinity, and moisture availability (Rowland et al. in press). If the observed size variability is genetically based, then these populations have the potential to evolve in diverse directions.

Fairly recent (within the past 10–15 yr) regeneration or recruitment of young *P. fremontii* saplings appears to be restricted to sites with newly established floodplains (San Antonio and Corrales). It is known that floodplain development and stabilization play significant roles in forest-stand regeneration of *P. fremontii* populations along the middle Rio Grande and its tributaries (Crawford et al. 1993). Extensive channelization and flood control have resulted in the virtual absence of regenerating forests along most of the Rio Grande basin. In this study it appears that, despite this purported cessation of recruitment, variation in size and density among populations of *P. fremontii* is extensive along much of the Rio Grande and one of its tributaries. This variability may be related to differing environmental conditions, either existing before flood control measures or, more likely, exacerbated by such perturbations. Further studies are needed to explore both the possible environmental and even genetic causes behind such variation in size, density, and spatial distribution.

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## BREEDING BEHAVIOR OF THE PLUMBEOUS VIREO IN NEW MEXICO

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**ABSTRACT.**—The Plumbeous Vireo (*Vireo plumbeus*) is a poorly studied songbird species that breeds within the interior western United States and Mexico. We studied the breeding behavior of Plumbeous Vireos within pinyon-juniper habitats in northeastern New Mexico in 1996 and 1997. Over both years we located and monitored 40 nests and conducted behavioral observations throughout the nesting cycle. From these observations we described and compared basic behavioral traits of male and female vireos during their nest-building, egg-laying, incubation, and nestling stages, and their response to potential predators near the nest. Male vireos displayed potential nest sites to females, but the females selected the site to be used and built most of the nest. Vireos often did not initiate egg-laying until 2–3 d after nest completion. The female tended to incubate eggs and brood nestlings more than the male, but both parents contributed equally in provisioning the young. Brown-headed Cowbirds (*Molothrus ater*) parasitized 77% of nests in 1996, 63% in 1997, and parasitism was the primary cause of nest failure in this population. The conspicuousness of vireos around the nest, particularly during the nest-building stage, may contribute to high parasitism levels. Vireo aggression near the nest may also act as a cue to help cowbirds locate nests.

*Key words:* Plumbeous Vireo, *Vireo plumbeus*, breeding behavior, brood parasitism, egg-laying, incubation, nesting cycle, nest-building, Solitary Vireo.

The Plumbeous Vireo (*Vireo plumbeus*) is a small (15–20 g), migratory songbird that breeds in the mountainous regions of the interior western United States and western Mexico and winters primarily in western Mexico (Curson and Goguen 1998). On its breeding grounds the Plumbeous Vireo resides mainly within conifer-dominated forests (Curson and Goguen 1998), and like many vireo species, it appears quite susceptible to brood parasitism by the Brown-headed Cowbird (*Molothrus ater*; Goguen and Mathews 1998, Ortega 1998, Chace et al. 2000). Although current population trends of the Plumbeous Vireo appear stable (Peterjohn et al. 1995), the prominence of cowbird parasitism in most populations that have been studied, and the large reductions in nesting success that result from it, have raised concern over whether this species may be at risk over large areas of its range (Marvil and Cruz 1989, Goguen and Mathews 1998).

Most aspects of Plumbeous Vireo ecology and behavior are relatively unknown. This is partly due to a paucity of research in the interior West. The prior subspecific status of the Plumbeous Vireo (formerly *Vireo solitarius plumbeus*) within the former Solitary Vireo

complex may also have limited research interest before its recent split and attainment of full species status (Johnson 1995, American Ornithologists' Union 1997). We studied Plumbeous Vireo breeding behavior in pinyon-juniper habitats of northeastern New Mexico in 1996 and 1997. At our study site this species breeds regularly within pinyon-juniper and mixed-conifer habitats and occasionally in riparian habitats (Goguen et al. 1998). It is also a common host of the Brown-headed Cowbird, experiencing parasitism in >85% of its nests in pinyon-juniper habitats in some years (Goguen and Mathews 1998). Our objective is to describe aspects of the breeding biology and behavior of this understudied species. Information gained from this research will provide basic life history data and insight into how vireo behavior influences rates of nest predation and brood parasitism.

### METHODS

#### Study Site

We conducted our research on the National Rifle Association Whittington Center (WC) and the adjacent V-7 Ranch (V7R) in Colfax

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County, northeastern New Mexico. The 13,350-ha WC, a National Rifle Association-affiliated shooting facility that remains mostly undeveloped, is ungrazed by livestock during the songbird breeding season. The 8090-ha V7R is an active cattle ranch that uses a seasonal grazing system at a moderate stocking rate (~45% annual forage use). Both sites lie along the eastern edge of the foothills of the Sangre de Cristo Mountains at the interface of shortgrass prairie and coniferous forest habitats.

We studied vireos on 8 previously established 35-ha plots within pinyon-juniper habitat (Goguen and Mathews 1998). Pinyon-juniper habitat lies in a narrow band on the lower slopes of the foothills (~1990–2130 m) between shortgrass prairie at lower elevations and mixed-conifer forests of ponderosa pine (*Pinus ponderosa*; plant names follow Stubbendieck et al. 1997) and Douglas-fir (*Pseudotsuga menziesii*) at higher elevations. Pinyon-juniper is an open woodland habitat dominated by pinyon pine (*Pinus edulis*), with one-seed juniper (*Juniperus monosperma*) scattered throughout. Woody understory consists of oaks (*Quercus* spp.), alder-leaf mountain mahogany (*Cercocarpus montanus*), and skunkbrush sumac (*Rhus aromatica*). Herbaceous understory is generally sparse, but intrusions of shortgrass prairie dominated by blue grama (*Bouteloua gracilis*) are common, particularly at the lower edge of the habitat.

Over 35 bird species regularly breed in the pinyon-juniper woodlands (Goguen and Mathews 1998). Among the most common breeding species are Spotted Towhee (*Pipilo maculatus*), Chipping Sparrow (*Spizella passerina*), Bush-tit (*Psaltriparus minimus*), Blue-gray Gnatcatcher (*Poliptila caerulea*), Western Wood-pewee (*Contopus sordidulus*), and Western Scrub-jay (*Aphelocoma californica*). The Brown-headed Cowbird is also common and heavily parasitizes several songbird species (Goguen and Mathews 1998). The Plumbeous Vireo, a regular breeder, is found in relatively low densities in this habitat (Goguen and Mathews 1998).

#### Research Methods and Analyses

We observed Plumbeous Vireo nests in pinyon-juniper habitats from May to July 1996 and 1997 as part of a study monitoring the nesting success of pinyon-juniper songbird communities. Each year nests were located

and monitored on, and in habitat surrounding, the study plots. We visited plots every other day to monitor nest fates and located nests by observing adult behavior. This allowed us to locate most nests (65%) in the nest-building or egg-laying stages. We checked all nests with extendable poles with mirrors to monitor nest contents and fate, and to determine parasitism status. Nests were considered successful if they fledged at least 1 vireo young. Nests were considered failed due to cowbird parasitism if they were abandoned within 3 d of the appearance of a cowbird egg or if the presence of a cowbird nestling led to the death of all vireo young.

By conducting intensive behavioral observations at a subset of vireo nests each year, we measured vireo behaviors throughout the nesting cycle. We divided the nesting cycle into 4 general periods: (1) Nest-building period began with the placement of the 1st piece of nesting material and continued until the 1st egg was laid; (2) egg-laying period started the morning the 1st egg was laid and continued until the last egg was laid; (3) incubation period started the morning of clutch completion and continued until the 1st egg hatched; and (4) nestling period ran from the day the 1st egg hatched to the day the last nestling fledged.

We observed vireo behavior from 10–15 m away from the nest in 60-min observations. All observations began after a 10-min buffer period to allow the birds to acclimate to our presence. Many nests were observed more than once in a stage (61% of nests) and/or in more than 1 stage (57% of nests), but never twice on the same day. We used the individual breeding pair as the unit in analyses. Behavioral measures obtained from repeat observations of the same nest during the same nesting interval were averaged, and only mean values were used.

During observations, we measured the following behaviors: (1) time spent on the nest by each sex; (2) total time nest was attended within 5 m, including on the nest, by at least 1 adult; (3) overall number of visits to the nest by the male and female (estimate of the amount of activity near the nest); (4) number of trips to the nest with nesting material or food; (5) number of “chatter” calls (a call consisting of a series of loud, harsh notes used by both sexes; Curson and Goguen 1998) by sex;

and (6) time spent singing by the male. Sexes were distinguished by song; only the male uses the primary song (Curson and Goguen 1998). We maintained additional notes on intraspecific behavior and recorded descriptions of encounters with predators or cowbirds. Upon completion of an observation, we checked nest contents and immediately departed from the nest site.

Using a modified Mayfield method (Heisey and Fuller 1985), we calculated nesting success and cause-specific failure rates of Plumbeous Vireo nests by year and nesting stage. Because of concerns of normality and large differences in variances, we made comparisons of behavioral variables within, and among, nesting stages using nonparametric tests (Sokal and Rohlf 1981). Differences were considered statistically significant if  $P < 0.05$ . Because of small sample sizes and low statistical power of tests, however, we also discuss trends in data when results approached significance ( $P = 0.10$  to  $0.05$ ).

## RESULTS AND DISCUSSION

We located and monitored 20 vireo nests in 1996 and 20 nests in 1997. Because of inaccessibility or late discovery, we were unable to determine parasitism status for 4 of these nests. We conducted behavioral observations at 14 nests for 72 h in 1996 and 9 nests for 17 h in 1997 for a total of 89 h of observation.

### Vireo Nesting Behavior

**VIREO ARRIVAL AND TERRITORY ESTABLISHMENT.**—Male Plumbeous Vireos arrived before females, generally in early May (Curson 1996). Males were often observed building “bachelor nests” prior to pairing. Bachelor nests are loosely constructed structures that resemble a shallow hammock. Often more than 1 bachelor nest was built and attended simultaneously. One male built at least 5 bachelor nests across the summer. Other closely related vireo species are also known to build bachelor nests (Blue-headed Vireo [*Vireo solitarius*], James 1978; White-eyed Vireo [*V. griseus*], Hopp et al. 1995; Gray Vireo [*V. vicinior*], J. Barlow personal communication). In the case of the formerly conspecific Blue-headed Vireo (Johnson 1995), bachelor nests appear to act as a place of display when the female arrives and may represent prospective nesting sites from which

the female selects (James 1978). In our research all bachelor nests were abandoned following pairing, and the significance of these nests remains unclear.

The interval between pair formation and nest initiation appeared to be short. In 1 case a male paired and started nest construction with a female during a 24-h period. In 2 other cases previously unpaired males were paired and nest-building when next observed approximately 48 h later. Nest-site selection involved both sexes. Males displayed prospective nest sites to females. In this display a singing male made repeated trips to a potential nest site, attaching materials such as insect or spider silk, while the female observed. Our brief observations did not allow us to determine the total number of sites displayed by each male, but in 2 cases we observed a male display at least 2 different sites to a female.

Although the male Plumbeous Vireo initially displays potential nest sites for the female, our observations suggest that ultimately the female selects the site to be used; males attach nest materials at  $>1$  prospective site, but the female joins in building at only one. In many other vireo species (e.g., Bell's [*Vireo bellii*], Black-capped [*V. atricapillus*], Blue-headed, Hutton's [*V. huttoni*], Philadelphia [*V. philadelphicus*], and Yellow-throated [*V. flavifrons*]), males and females appear to exhibit roles similar to those observed for the Plumbeous Vireo during nest-site selection; males display prospective sites while females choose the site to be used (James 1978, Brown 1993, Davis 1995, Grzybowski 1995, Moskoff and Robinson 1996). For example, male Blue-headed and Yellow-throated Vireos display 1 or more potential sites, but the female chooses among them or may even select a different site (James 1978). The process of nest-site selection in Plumbeous Vireos deserves a more complete examination.

**NEST-BUILDING STAGE.**—We observed 12 pairs building their nests for a total of 24 h. Plumbeous Vireos build an open, semipensile cup nest often placed near the end of a low branch or in the outer foliage near the top of a tree (Curson 1996). The main nest structure generally requires 4–5 d to complete. Lining of the nest extends the stage 2–3 additional days. The longest nest-building period we observed took 10 d.

First nesting attempts started during the 2nd week of May. The male initiated the nest

as part of the nest-site selection display and initially avidly assisted the female in the nest-building process (Fig. 1). The male's contribution became minimal after 1 or 2 d, however. In constructing the nest the female often sat in the nest and rotated her breast against the nest walls to form the cup shape after attaching new nesting materials. Although the male rarely contributed nesting material, he accompanied the female during 76% of her trips to the nest ( $n = 99$  trips). During these visits the male occasionally assisted in shaping the nest, but more often he simply perched close and sang. Only the female was observed constructing the nest's lining.

We often observed a hiatus between apparent completion of the nest and onset of egg-laying. Of 7 nests for which we have data, egg-laying was initiated with no pause in 2 cases, and with a 2- to 3-d pause in the other 5 cases. During the hiatus both adults visited the nest occasionally, but without new nesting materials. During the hiatus it was also common to observe either the male or female sitting quietly on an empty nest as if incubating. Of 6 observations conducted during the hiatus, females sat on the empty nest for at least 1 min during 2 observations, while males sat during 3 observations. In only the observations where adults were on the nest, females occupied the nest for an average of 11.5 min, while males averaged 20 min. During 1 observation, a male sat on an empty nest for 39 min. This male also sang from the nest for 2 min. Bent (1950) also reported an instance of a Plumbeous Vireo sitting on an empty nest.

Other vireo species are known to exhibit a brief (1–3 d) hiatus between nest completion and egg-laying (e.g., Bell's, Hutton's, and White-eyed Vireos; Brown 1973, Davis 1995, Hopp et al. 1995). The significance of this hiatus, and associated false incubation behavior for Plumbeous Vireos, is unclear. However, it may deceive cowbirds. Cowbirds generally parasitize nests during the host's egg-laying stage (Nolan 1978, Marvil and Cruz 1989) and may use the switch in host behavior from nest-building to longer bouts on the nest as a cue to assess when a host has begun laying its eggs. Plumbeous Vireo nests are parasitized prior to egg-laying more frequently than other hosts on our study site; 26% of 90 cowbird eggs were laid prior to vireo egg-laying, whereas other hosts examined received <10% of cow-

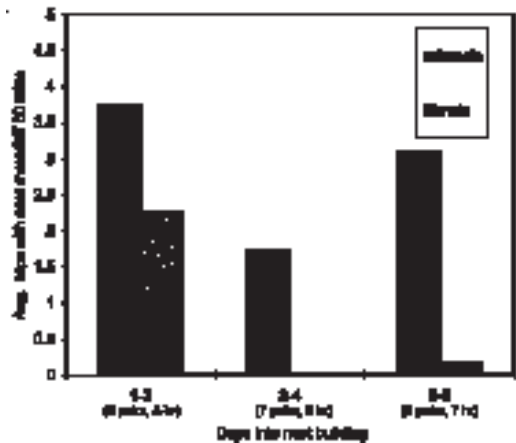


Fig. 1. Average number of trips with nesting material by Plumbeous Vireo pairs building nests in pinyon-juniper woodlands in New Mexico, 1996 and 1997. Delivery rate of nesting materials did not differ by sex during days 1–2 ( $U = 41.5$ ,  $P = 0.29$ ), but was higher for the female during days 3–4 ( $U = 38.5$ ,  $P = 0.02$ ) and days 5–9 ( $U = 31.0$ ,  $P = 0.03$ ).

bird eggs during this interval (Goguen 1999). Thus, this false incubation behavior may instigate early laying by cowbirds. Although Plumbeous Vireos typically accept cowbird eggs, of 23 cowbird eggs laid prior to vireo egg-laying, 30% were deserted with the nest and 9% were buried under the nest lining (Goguen 1999). These desertions are probably not a result of cowbird egg recognition by vireos, but rather they may represent a generalized response to an egg appearing in the nest at an inappropriate time (Rothstein 1975).

**EGG-LAYING STAGE.**—We observed 7 nests for a total of 11 h during the egg-laying stage. Females laid 1 egg per day. Among unparasitized vireo nests we observed 10 four-egg clutches and 1 three-egg clutch. Based on larger sample sizes, clutch sizes of Plumbeous Vireos are most commonly 4, occasionally 3, and rarely 5 (Chace et al. 2000). Thus, the egg-laying stage (i.e., the period from the morning of the 1st egg laid to the morning of the last egg) lasts from 2 to 4 d. The earliest vireo egg laid in 1996 was on 16 May, and the earliest in 1997 was 20 May. The peak of vireo clutch initiations in both years was in the last week of May to the 1st week of June.

Adult activity at the nest appeared to vary across the egg-laying stage (Table 1). Early in this stage adults tended to remain away from the nest for long periods. When an adult did

TABLE 1. Behavior during the egg-laying stage of Plumbeous Vireos nesting in pinyon-juniper woodlands in New Mexico, 1996 and 1997.

	Days into the egg-laying stage	
	1-2	3
Number of pairs observed	5	5
Number of 60-min observations	6	5
Minutes on nest by female <sup>a</sup>	19.6 (23.3)	29.3 (26.0)
Minutes on nest by male	11.2 (15.4)	18.7 (22.7)
Total minutes with an adult on nest	30.8 (20.7)	48.0 (21.7)
Visits to the nest by either adult	1.0 (1.7)	0.6 (0.55)
Total minutes nest unattended within 5 m by either adult	17.2 (18.8)	8.0 (17.9)

<sup>a</sup>All results reported as mean/60-min observation period (standard deviation). No means differed between days 1-2 and day 3 (Mann-Whitney U test,  $P > 0.05$ ).

visit the nest, it usually remained only briefly, as though checking on the nest. Time on the nest tended to increase for both sexes in the last day of egg-laying (i.e., the day before the final egg was laid; Table 1). On day 3 the female was present on the nest for >60 min for 2 of 5 observations. Based on pre-sunrise nest checks, females did not roost on the nest at either of 2 nests observed on the 2nd morning of egg-laying; but at 2 different nests observed on the 3rd morning, females were present roosting in both cases (Curson unpublished data). These results suggest that incubation may begin the day prior to the laying of the last egg.

**INCUBATION STAGE.**—We observed 11 nests for a total of 33 h during the incubation stage. This included 4 nests with only vireo eggs and 7 nests that contained vireo and at least 1 cowbird egg. Estimates of the length of the incubation stage range from 14 to 15 d (Marvil and Cruz 1989, Curson and Goguen 1998). In parasitized nests, however, incubation of the cowbird egg takes about 11 d.

Both sexes took turns incubating the clutch, although the female tended to spend more time incubating than the male ( $n = 11$  pairs, mean minutes on nest per hour  $\pm s$ ; female =  $34.7 \pm 15.3$  min  $h^{-1}$ , male =  $21.1 \pm 12.1$  min  $h^{-1}$ ; Mann-Whitney U test,  $U = 86.0$ ,  $P = 0.09$ ). Female Plumbeous Vireos possess a full, vascularized ventral brood patch while males possess only a partial, nonvascularized patch (Curson and Goguen 1998). Adults generally replaced each other on the nest as incubation bouts were completed. Because of nearly constant incubating, the nest was attended almost continuously during this stage (Table 2). While incubating, females were silent and still, moving only rarely to rotate the eggs or shift position, and only vocalizing with chatter or con-

tact calls near the end of an incubation bout. Males were also usually silent but sang from the nest in 14 of 36 incubation bouts (38%). While 1 adult incubated, the non-incubating adult rarely remained close to the nest. In most cases the non-incubating adult disappeared from the nest vicinity. Although Willard (1908) reported a non-incubating adult frequently feeding an incubating adult on the nest, we did not observe males feeding incubating females, or vice versa.

We were able to observe many incubation switches between the male and female. The process generally involved fairly predictable patterns: Males moved about the territory while singing, occasionally approaching the vicinity of the nest. Near the time of a switch, the female uttered "chatter" or soft contact calls, presumably to signal the male. The male then slowly moved from branch to branch approaching the nest. When the male arrived, the female left either quietly or with soft contact calls, while the male quickly replaced her on the nest. Males did not always replace the female. On 4 occasions the male, rather than incubating, perched near the nest and sang. In 1 of these cases the male sang close to the nest for 32 min until the female returned and resumed incubating.

**NESTLING STAGE.**—We observed 12 nests for a total of 21 h during the nestling stage. Three of these nests had only cowbird nestlings, 8 had only vireos, and 1 had both cowbird and vireo nestlings. Most of our observations (20 h) took place at nests with nestlings that were <10 d old. The nestling stage lasts 13-16 d in unparasitized nests (Marvil and Cruz 1989, Curson and Goguen 1998). In parasitized nests in which the cowbird hatches first, the later-hatching vireo eggs rarely survive beyond a few days (Marvil and Cruz 1989), while the



TABLE 2. General behavioral characteristics based on nesting stage of Plumbeous Vireos nesting in pinyon-juniper woodlands in New Mexico, 1996 and 1997.

	Nesting stage			
	Nest-building	Egg-laying	Incubation	Nestling
Number of pairs observed	12	7	11	12
Number of 60-min observations	24	11	33	21
Total minutes nest attended (Adult on or within 5 m) <sup>a</sup>	19.0 (15.9)a	44.7 (20.2)b	58.7 (3.2)b	42.8 (17.2)b
Minutes adult on nest <sup>a</sup>	6.4 (7.0)a	38.2 (21.4)bc	55.8 (5.7)c	33.3 (20.6)b
Visits to the nest by female <sup>a</sup>	4.0 (3.6)a	0.5 (0.5)b	0.5 (0.5)b	1.6 (1.3)b
Visits to the nest by male	0.8 (1.6)	0.1 (0.4)	0.7 (0.8)	1.1 (1.2)
Chatter call, male (min)	0.3 (0.3)	0.3 (0.3)	0.9 (0.9)	2.1 (3.6)
Chatter call, female (min)	0.2 (0.3)	0.1 (0.1)	0.2 (0.4)	0.9 (2.3)
Singing (min)	14.1 (7.9)	10.6 (9.5)	21.6 (12.2)	13.4 (11.6)

<sup>a</sup>All results reported as mean/60-min (standard deviation). Based on Kruskal-Wallis tests, means were significantly different among nesting stages for total time nest attended ( $H = 23.04$ , 3 df,  $P < 0.001$ ), total time adult on nest ( $H = 23.60$ , 3 df,  $P < 0.001$ ), and visits to the nest by the female ( $H = 13.80$ , 3 df,  $P = 0.003$ ). For these variables, values followed by differing letters are significantly different. For all other variables, means are not significantly different ( $P > 0.05$ ).

TABLE 3. Adult brooding and food delivery rates during the nestling stage of Plumbeous Vireos nesting in pinyon-juniper woodlands in New Mexico, 1996 and 1997.

Age of young	Age of nestlings <sup>a</sup>		
	1-3 ( $n = 8$ h)	4-6 ( $n = 4$ h)	7-9 ( $n = 8$ h)
Brooding (mean min on nest h <sup>-1</sup> [s])			
Female	31.4 (25.3)	18.5 (21.1)	13.3 (21.0)
Male	13.5 (18.1)	15.4 (29.8)	4.1 (9.89)
Total <sup>b</sup>	44.9 (26.8)	33.9 (24.4)	17.4 (21.0)
Food delivery rate (mean feeding trips h <sup>-1</sup> ([s])			
Female	0.6 (0.7)	1.0 (0.80)	1.6 (1.4)
Male	0.8 (1.0)	0.5 (0.6)	1.9 (2.1)
Total <sup>b</sup>	1.4 (1.5)	1.5 (1.3)	3.6 (2.3)

<sup>a</sup>Number of different pairs observed equals number of hours in all cases.

<sup>b</sup>Mean total brooding time and mean total feeding trips did not differ based on age groupings of nestlings (Kruskal-Wallis test,  $P > 0.05$ ).

cowbird can fledge in only 10 or 11 d (Scott 1979).

During the nestling stage adults spent most time either brooding or searching for food for the nestlings. Both adults brooded the nestlings, but the female tended to brood more than the male (Table 3). Time spent brooding tended to decrease for both sexes as the nestlings matured (Table 3). During the initial 1-2 d, adults generally replaced each other on the nest as they delivered food, maintaining nearly constant brooding. During this period brooding bouts by the female sometimes exceeded 1 h. As the chicks matured, brooding became less frequent and by day 9 generally ceased during the daytime. This suggests that nestlings were capable of thermoregulation by this age.

Both adults contributed to feeding the young, but we found no evidence that either sex provided more food than the other (Table 3). Feeding rates increased as the chicks grew

older (Table 3). We did not have an adequate sample to evaluate the influence of nestling number on feeding rates, or to compare feeding rates at nests containing only a cowbird versus only vireo nestlings. Although a cowbird nestling probably receives more food than a similar-aged, but smaller, vireo nestling, a lone cowbird in a nest probably requires fewer food deliveries than a brood of vireo nestlings (e.g., Davison 1998).

Early in the nestling stage, nest switches by brooding adults took place in a manner similar to incubation switches described previously. Males sang from the nest during about half of observed brooding bouts (5 of 9 bouts), but usually only briefly (overall, males sang during 6.7% of 141.5 min on the nest). Both adults often foraged for food for nestlings within 10 m of the nest. When both adults were off the nest simultaneously, they often foraged together. Early in the nestling stage (before day 7), all

fecal sacs observed ( $n = 4$ ) were consumed by adults. Later in this stage some fecal sacs ( $n = 6$ ) were eaten (33.3%), but most were simply removed (66.7%). We obtained little information during the final days of the nestling stage and fledging.

#### Summary of Behaviors Through All Nesting Stages

Several general patterns existed across the nesting stages (Table 2). Visits to the nests were highest during nest-building and nestling stages as a result of regular delivery of nesting materials and food. Time on the nest was highest during incubation. Total time that an adult was present near the nest was also highest during incubation, but was consistently high during all stages in which eggs or young were present. Across all stages the female tended to spend more time on the nest than the male (Wilcoxin signed-ranks test,  $z = -1.83$ ,  $P = 0.07$ ). Singing rate did not differ among nesting stages. Chatter calling was observed rarely through most of the nesting cycle but appeared to be performed more commonly during the nestling stage. Chatter calls are believed to be used in longer-distance communication between males and females (Curson and Goguen 1998). Chatter calls may have been used most frequently in the nestling stage because of frequent approaches to the nest by feeding adults. Adults often called when approaching the nest with food, apparently to alert the other brooding adult. When adults were not brooding, chatter calls may also have been used to alert nestlings of an upcoming food delivery.

#### Vireo Nesting Success

Seventy-six percent of nests ( $n = 17$ ) were parasitized in 1996 and 63% ( $n = 19$ ) in 1997. These are among the highest recorded parasitism rates for this species, but they are lower than rates observed in previous years of research on this study site (1992–1995; mean = 86% parasitized; Goguen and Mathews 1998). Nests frequently contained more than 1 cowbird egg, averaging 2.15 cowbird eggs/parasitized nest in 1996, and 1.58 in 1997. Overall, of 25 parasitized nests across both years, 44% contained 1 cowbird egg, 36% contained 2, 12% contained 3, and 8% contained 4.

Parasitism during the nest-building stage led to the desertion of 3 nests prior to completion. Among nests that reached egg-laying,

nesting success was similar among years, and cowbird parasitism was the primary cause of nest failure (Table 4). Plumbeous Vireos rarely fledge their own young from nests that are parasitized during their egg-laying stage (Marvil and Cruz 1989, Goguen 1999). Cowbird eggs have a shorter incubation period and usually hatch about 3 d earlier than vireo eggs. The early hatching of the cowbird reduces vireo hatching success, and even if eggs hatch, the larger cowbird is able to outcompete the smaller young for food (Marvil and Cruz 1989). In this study parasitism led to nest failures during the egg-laying stage by causing desertions, probably due to clutch reduction by cowbirds, and, in 1 case, by removing all vireo eggs so that only 3 cowbird eggs remained. Most nest losses to parasitism resulted from starvation of vireo young during the nestling stage (Table 4). Across both years vireos averaged 2.36 vireo fledglings per unparasitized nest ( $n = 11$ ) and 0.24 vireo and 0.44 cowbird fledglings per parasitized nest ( $n = 25$ ). In 3 cases, 2 cowbirds were fledged from the same nest, but no mixed broods containing both vireo and cowbird young were fledged.

Nest predation was also a regular cause of failure (20.0% of parasitized and 18.2% of unparasitized nests were depredated), but probably had little overall impact on this heavily parasitized population. Plumbeous Vireos appear to be single-brooded in this population, but pairs that lost a nest to predation typically re-nested. These re-nesting attempts, however, were just as susceptible to parasitism as initial attempts because parasitism probabilities did not differ across the breeding season (Goguen 1999). Pairs that fledged a cowbird did not re-nest. Thus, pairs that raised cowbirds suffered total loss of reproductive potential for that year.

#### Response to Cowbirds and Predators

During our observations we witnessed several encounters between vireos and potential nest predators or cowbirds. Plumbeous Vireos exhibited different responses to a potential predator, depending on the specific circumstances of the encounter. When away from their nest, vireos joined other songbirds in mobbing potential threats. For example, we observed a pair of vireos join Western Wood-pewees in mobbing a cowbird. Close to their nest the

TABLE 4. Nesting success and cause-specific nest failure rates<sup>a</sup>, by nesting stage, for Plumbeous Vireos nesting in pinyon-juniper woodlands in New Mexico, 1996 and 1997.

Year	Nesting stage			All stages
	Egg-laying	Incubation	Nestling	
1996 ( <i>n</i> = 20)				
Successful (%)	72.3	74.6	54.0	29.1 <sup>b</sup>
Failed due to predation (%)	0.0	17.0	9.2	
Failed due to parasitism (%)	27.7	8.5	36.8	
1997 <sup>c</sup> ( <i>n</i> = 20)				
Successful (%)	93.0	74.0	47.5	32.7
Failed due to predation (%)	0.0	13.0	17.5	
Failed due to parasitism (%)	7.0	6.5	35.0	

<sup>a</sup>Rates calculated using a modified Mayfield method described by Heisey and Fuller (1985).

<sup>b</sup>Success rate across all stages calculated by multiplying proportion successful across the 3 nesting stages.

<sup>c</sup>Nest failures due to causes other than predation and parasitism accounted for an additional 6.5% during incubation stage in 1997.

response varied depending on whether an adult was on or off the nest. Usually if an adult was on the nest, and a potential predator approached, its initial response was to sink low into the nest until only its beak and tail protruded. We observed this behavior by vireos in response to a female cowbird, a Northern Mockingbird (*Mimus polyglottos*), and humans near the nest. The vireo usually remained on the nest in these encounters, unless the intruder approached closely, in which case the vireo flushed and attacked the intruder with swoops, strikes, and loud scolding calls, typically attracting its mate in the process.

Often when we approached the nest to check contents, both adults were off the nest. In these cases vireos initially flew near, chatter calling occasionally and changing perches frequently. As we neared the nest, the vireos became more agitated, using scolding calls and making closer flights. Once we were at the nest, vireos generally became extremely agitated, scolding constantly, and sometimes swooping. Responses to cowbirds or other small birds near the nest may be intense. We observed a vireo drive away a female cowbird that was apparently attacking its nestlings. A freeze-dried model of a female cowbird placed close to a vireo nest was usually viciously attacked with close swoops and bill strikes (Curson 1996). Often the vireos even perched on the model's back, repeatedly biting it on the head and neck.

For an avian brood parasite, the quality of a given host depends upon both the costs associated with locating and parasitizing its nests and benefits received in terms of parasite recruitment (Payne 1977). Cowbirds use host

behavior to locate nests (Norman and Robertson 1975, Thompson and Gottfried 1976), and Plumbeous Vireos were extremely conspicuous around the nest. Males often sang near or at the nest during nest-building and while on the nest in other stages. Both sexes frequently made long, direct flights to the nest when delivering nesting materials. Further, aggressive actions of this species may act as a cue for cowbirds to locate a nest (Smith 1981), while presenting little threat to the cowbird when laying (Curson 1996). Plumbeous Vireos accepted and often fledged cowbird eggs in our study (see also Marvel and Cruz 1989). Thus, our observations suggest that Plumbeous Vireos represent a high-quality host for cowbirds: nests are readily located and parasitized with little risk, and cowbird eggs are fledged at a high rate.

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## BREEDING ECOLOGY OF WHITE-FACED IBIS (*PLEGADIS CHIHI*) IN THE UPPER KLAMATH BASIN, CALIFORNIA

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**ABSTRACT.**—The White-faced Ibis (*Plegadis chihi*) is a California state and U.S. Fish and Wildlife Service species of special management concern. We studied White-faced Ibis breeding ecology from May through July 1995 on Lower Klamath National Wildlife Refuge (NWR) in the upper Klamath Basin of California. A total of 2029 pairs nested in 3 colonies exclusively in early-successional hardstem bulrush (*Scirpus acutus*). Nest initiation dates ranged from 10 May to 12 June, and mean clutch size was 3.16. Reproductive success averaged 87% apparent nest success ( $n = 115$ ), 82% hatchability, 97% whole and partial brood survival, and 2.39 fledglings per successful nest. Mayfield estimates of nest survival were 79.1% during the laying and incubation period and 95% during the nestling period. Overall nest success as estimated by the Mayfield method was 75.4%. Our estimates of nest success are some of the highest reported anywhere in the literature for White-faced Ibis. Therefore, Lower Klamath NWR may maintain preferred White-faced Ibis breeding habitats in years of otherwise poor habitat conditions across the Intermountain West.

*Key words:* White-faced Ibis, *Plegadis chihi*, breeding ecology, wetlands, Klamath Basin, California, nest success.

During the 1960s and 1970s, White-faced Ibis (*Plegadis chihi*; AOU 1998) populations declined sharply in North America from negative effects of organochlorine pesticides and extensive wetland losses from drought and drainage (Ryder 1967, King et al. 1980). White-faced Ibis have a limited number of consistent breeding sites (Sharp 1985), and the Great Basin White-faced Ibis population (Earnst et al. 1998) is recognized by the California Department of Fish and Game (CDFG) and the U.S. Fish and Wildlife Service (USFWS) as a species of special concern and a species of management concern, respectively (Remsen 1978, USFWS 1995, L. Comrack, CDFG, personal communication).

Within North America, marshes of the Great Basin are considered a stronghold of White-faced Ibis reproduction (Ryder 1967, Ryder and Manry 1994), and the Great Basin White-faced Ibis population's nesting biology in this region has been well studied (Kotter 1970, Kaneko 1972, Capen 1977, Alford 1978, Steele 1980, Henny and Herron 1989, Kelchlin 1994, 1996, 1997, Henny 1997). In contrast, from 1914 to 1986, only small numbers (maximum 12 pairs) nested sporadically in the Klamath Basin of southern Oregon and northeastern California (Grinnell and Miller 1944, Ryder

1967, Booser and Sprunt 1980, Follansbee and Mauser 1994). However, by 1994 on Lower Klamath National Wildlife Refuge (NWR), the White-faced Ibis population had increased dramatically to 3900 pairs (Follansbee and Mauser 1994).

Conservation and management of White-faced Ibis habitat requires comprehensive knowledge of their nesting biology. In 1994, Follansbee and Mauser (1994) monitored 30 White-faced Ibis nests on Lower Klamath NWR and observed 96.6% apparent nest success. The purpose of our study was to verify this remarkably high estimated nesting success of White-faced Ibis on Lower Klamath NWR and investigate reproductive ecology in greater detail. Specifically, our objectives were to (1) estimate the breeding population size of each colony at Lower Klamath NWR, (2) describe characteristics of habitat used by nesting colonies, and (3) collect reproductive ecology data for a larger and more representative sample of White-faced Ibis nests.

### STUDY AREA

We studied White-faced Ibis from 26 May to 28 July 1995 on Lower Klamath NWR (42°N,

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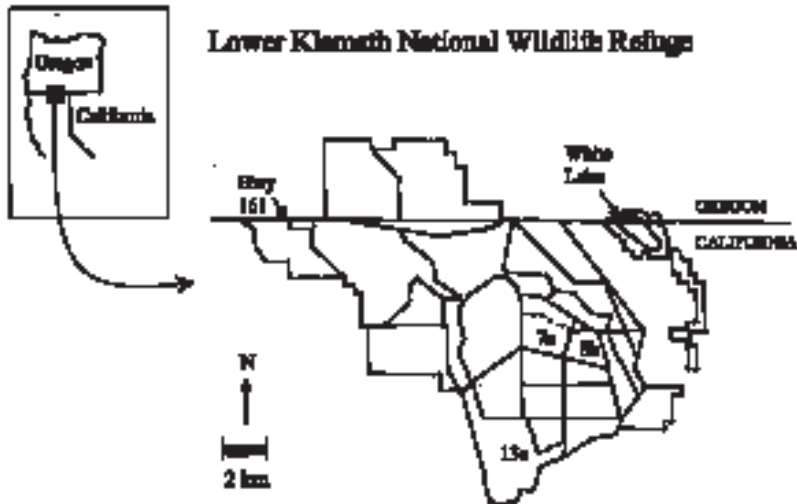


Fig. 1. Location of White-faced Ibis colonies (7a, 8b, and 13a) within Lower Klamath National Wildlife Refuge, Siskiyou County, California.

121°45'W), Siskiyou County, California (Fig. 1). Lower Klamath NWR is 1220 m in elevation and contains 19,500 ha of managed permanent and seasonal wetlands, uplands, and barley fields (Mauser et al. 1994).

## METHODS

### Breeding Population

We located White-faced Ibis colonies by searching for early morning and late evening foraging flights. To estimate the total number of breeding pairs on Lower Klamath NWR, we conducted a single sunrise flyout count at each colony during incubation and early nestling periods. We assumed that during these periods 1 member of the pair would remain on the nest and the other would leave the nesting area to forage (Belknap 1957, Kotter 1970). Therefore, our counts would result in an estimate of breeding pairs. We began each count as soon as we observed birds leaving the colony and terminated it when the 1st birds returned. Because sunrise flyout counts were ineffective at 1 colony (13a), on 20 June 2 observers estimated population size from an aerial overflight.

### Nesting Ecology

Within each of the 3 colonies, we randomly selected a sample of 40–45 active nests (containing at least 1 egg) by systematically choosing every 10th nest along a modified zigzag belt transect (Krebs 1989) that included nests

from both the center and edge of the colony. White-faced Ibis nests tended to be clustered in patches of emergent vegetation surrounded by water. Thus, to avoid sampling the majority of nests from a small area, we interspersed nest selection by choosing a maximum of 4 nests per patch. We marked nests by attaching colored flagging tape or clothes pins to nearby vegetation.

To decrease the possibility of nest abandonment during the egg-laying period, we delayed our 1st colony visit until the majority of nests were being incubated. To avoid thermal stress to eggs and/or chicks (Tyler 1933, Belknap 1957, Kotter 1970, Ryder and Manry 1994), we visited colonies during the morning (0700–1000) or evening (1700–1830) hours unless temperatures were less than 7°C. We made an average of 5 visits per colony from 31 May to 17 July, with an average interval of 6 d between successive visits (range 3–14 d). During each visit we recorded the number and age of eggs and/or nestlings. Incubation stage was estimated by egg flotation (Westerskov 1950), assuming a 22-d incubation period (Bent 1926, Belknap 1957, reviewed in Ryder and Manry 1994), and nestling age was estimated from known hatching dates or from growth and development of feather tracts (Belknap 1957, Kotter 1970, E. Kelchlin, Stillwater NWR, Fallon, NV, personal communication).

We determined the fate of eggs (e.g., missing, hatched, unhatched, or destroyed) by revisiting

nests 1–5 d after their projected hatching dates. Nestling fate was determined by monitoring nests until they failed or until chicks reached 6–10 d old, in which case we considered them as having “fledged” (i.e., capable of leaving the nest to escape a predator). Nestlings older than 7–10 d are mobile and frequently leave the nest during investigator approach, making it difficult to count them accurately (Frederick et al. 1993, Ryder and Manry 1994). If nests had missing eggs or young, we searched the nest site area thoroughly for remains of eggs or chicks.

For all nests we calculated mean clutch size and nest initiation date (Julian) for each colony. Nest initiation dates were estimated by back-dating from our egg flotation data, assuming a 2-d laying interval (Kotter 1970, reviewed in Ryder and Manry 1994).

#### Reproductive Success

APPARENT NEST SUCCESS.—We calculated 4 measures of reproductive success for each colony: (1) apparent nest success was the proportion of all nests that hatched at least 1 egg, (2) hatchability was the proportion of eggs that hatched from successful nests (those hatching at least 1 egg), (3) whole brood survival was the proportion of successful nests that fledged at least 1 chick (6–10 d old), (4) partial brood survival was the proportion of chicks reaching 6–10 d of age from nests that fledged at least 1 chick, and (5) fledging success was the mean number of chicks (6–10 d old) fledged per successful nest.

MAYFIELD NEST SUCCESS.—We used the Mayfield (1961, 1975) method to calculate nest success and daily nest survival rates for each colony, with standard errors calculated according to Johnson (1979). We compared daily survival rates among colonies using Z tests (Johnson 1979).

UNSUCCESSFUL NESTS.—For failed nests we distinguished between destroyed nests (at least 1 egg/nestling destroyed by a predator) and 3 categories of abandoned nests: (1) eggs intact but no longer attended by parents, (2) cracked or flattened eggs in the water near the nest, and (3) cracked or flattened eggs in the nest.

#### Statistical Analyses

Using simple linear regression, we determined whether clutch size varied with nest

initiation date. Clutch sizes among colonies were compared using 1-way ANOVA. Because nest initiation data did not meet assumptions of normality and homogeneity of variances (Dowdy and Wearden 1991), we compared nest initiation dates among colonies using nonparametric 1-way ANOVA (Kruskal-Wallis Test; Hintze 1995). Statistical analyses were performed using NCSS (Hintze 1995).

## RESULTS

### Breeding Population

We located 3 White-faced Ibis colonies on Lower Klamath NWR in 1995 (Fig. 1) with an estimated 2029 breeding pairs (Table 1). Colony 7a was in a 242-ha permanent marsh dominated by early-successional hardstem bulrush (*Scirpus acutus*; Hickman 1993), colony 8b in a 302-ha permanent marsh characterized by early-successional hardstem bulrush interspersed with common cattail (*Typha latifolia*; Hickman 1993), and colony 13a in a 1334-ha unit with approximately 800 ha of seasonal marsh habitat dominated by early-successional hardstem bulrush. White-faced Ibis nested exclusively in patches of hardstem bulrush with relatively low stem densities (i.e., water was visible under nests). All 3 colonies included Franklin's Gulls (*Larus pipixcan*; AOU 1998) and Forster's Terns (*Sterna forsteri*; AOU 1998); colonies 7a and 13a also included Black-crowned Night Herons (*Nycticorax nycticorax*; AOU 1998), Snowy Egrets (*Egretta thula*; AOU 1998), and Great Egrets (*Casmerodius albus*; AOU 1998).

### Nesting Ecology

Clutch size averaged 3.16 and did not vary among colonies ( $F_2 = 2.79$ ,  $P = 0.07$ ; 1-way ANOVA), but mean nest initiation dates varied from 14 (colony 7a) to 31 May (colony 8b; Kruskal-Wallis ANOVA,  $\chi^2 = 87.5$ ,  $P < 0.0001$ ; Table 1). For all colonies combined, clutch size was negatively correlated with Julian nest initiation date ( $y = 7.09 - 0.03x$ ,  $r = -0.30$ ,  $n = 124$ ,  $P = 0.001$ ).

### Reproductive Success

APPARENT NEST SUCCESS.—Reproductive success in all colonies averaged 87% apparent nest success, 82% hatchability, 97% whole brood survival, 97% partial brood survival, and 2.39 fledglings per successful nest (Table 2).

TABLE 1. Number of breeding pairs, mean nest initiation date, and average clutch size for White-faced Ibis nesting at Lower Klamath National Wildlife Refuge, California, 1995.

Colony	Number of breeding pairs <sup>a</sup>	Mean $\pm$ <i>s</i> (range)		Number of nests <sup>b</sup>
		Nest initiation date	Clutch size	
7a	1149	14 May $\pm$ 2 (10–20 May)	3.23 $\pm$ 0.58 (2–4)	40
8b	305	31 May $\pm$ 4 (26 May–10 June)	2.93 $\pm$ 0.93 (1–5)	41
13a	575	25 May $\pm$ 7 (14 May–12 June)	3.30 $\pm$ 0.79 (1–5)	45
Overall	2029	24 May $\pm$ 9 (10 May–12 June)	3.16 $\pm$ 0.79 (1–5)	126

<sup>a</sup>Estimated by sunrise flyout counts (colonies 7a, 8b) and aerial census (colony 13a).

<sup>b</sup>Sample size of monitored nests used for nest initiation date and clutch size analyses.

MAYFIELD NEST SUCCESS.—Daily nest survival was 0.9850 and did not vary among colonies during the incubation ( $Z \leq 0.89$ ,  $P \geq 0.38$ ) or nestling periods ( $Z \leq 1.57$ ,  $P \geq 0.12$ ). Although daily survival rates did not differ between the incubation (DSR = 0.9910  $\pm$  0.0025) and nestling periods (DSR = 0.9940  $\pm$  0.0030;  $Z = -0.71$ ,  $P = 0.48$ ), we kept these periods separate for calculating overall Mayfield nest success, which averaged 75% (Table 3).

UNSUCCESSFUL NESTS.—Of 17 nests that failed, 13 were lost during the incubation period (6 destroyed by predators, 7 abandoned), and 4 were lost during the nestling period (3 destroyed by predators, 1 abandoned). Of 8 abandoned nests, 1 was abandoned with eggs intact, 2 had cracked and/or flattened eggs in the water near the nest, 4 had cracked and/or flattened eggs still in the nest, and 1 had a dead flattened chick still in the nest.

#### DISCUSSION

The reliance of White-faced Ibis at Lower Klamath NWR on hardstem bulrush for nesting was similar to that of White-faced Ibis breeding in the Great Basin (Kaneko 1972, Sharp 1985, Schreur 1987, Henny and Herron 1989, Cornely et al. 1994). Before the 1980s Lower Klamath NWR contained relatively few early-successional emergent marshes because most marsh units were managed as long-term permanent wetlands or seasonal wetlands. In the early 1980s refuge staff began to remove water from seasonal marshes during late spring and early summer to stimulate seed production of moist-soil plants (Fredrickson and Taylor 1982). This resulted in expansion of early-successional emergent plants, particularly thin stands of hardstem bulrush favored by White-faced Ibis.

White-faced Ibis nesting on Lower Klamath NWR in 1995 experienced higher apparent nesting success (87%) than had been reported previously (i.e.,  $\leq 69\%$ ; Kotter 1970, Kaneko 1972, Capen 1977, Alford 1978, Kelchlin 1994). Follansbee and Mauser (1994) also reported very high apparent nest success (96.6%) for a single White-faced Ibis colony on Lower Klamath NWR during 1994. Although our estimate of hatchability (82%) was lower than that reported for other colonial nesting species (88.6%; Koenig 1982), it was nonetheless higher than that documented in other White-faced Ibis studies (i.e.,  $\leq 66\%$ ; Kotter 1970, Kaneko 1972, Capen 1977, Alford 1978, Kelchlin 1994). Our overall estimate of 2.39 fledglings (i.e., 6–10 d old) produced per nest was similar to other White-faced Ibis studies. Over a 2-yr period the number of 10-d-old fledglings produced per successful nest ranged from 1.47 to 3.04 in the Carson River Basin, Nevada, and 2.00 to 3.10 in Colorado (Schreur 1987, Kelchlin 1994, 1996). In Utah the minimum number of fledglings (i.e., 7 d old) produced per nest was 0.10 and the maximum was 2.67 (Kotter 1970, Kaneko 1972, Steele 1980). In Nevada an average of 2.54 fledglings (i.e., 7–10 d old) was produced per successful nest (Henny and Herron 1989).

Our estimate of fledgling production may be positively biased because we monitored chick survival from hatching to 8 d of age. In a study of radio-marked nestlings, Kelchlin (1996) reported that White-faced Ibis nestlings younger than 11 d old experience higher survival than older nestlings. Frederick et al. (1993) found a similar pattern of differential survival in Tricolored Herons.

Our Mayfield (1961, 1975) estimate of nest success during the laying and incubation period was 79%, which was lower than our



TABLE 2. Apparent nest success for 3 White-faced Ibis colonies on Lower Klamath National Wildlife Refuge, California, 1995.

Colony	Percent nest success <sup>a</sup> ( <i>n</i> <sup>b</sup> )	Percent hatch <sup>c</sup> ( <i>n</i> <sup>d</sup> )	Percent whole brood survival ( <i>n</i> <sup>b</sup> )	Percent partial brood survival ( <i>n</i> <sup>e</sup> )	Fledging success <sup>f</sup> (mean ± <i>s</i> ) ( <i>n</i> <sup>b</sup> )
7a	91 (35)	86 (104)	92 (13)	97 (33)	2.46 ± 0.97 (13)
8b	88 (40)	84 (107)	100 (30)	96 (74)	2.37 ± 0.89 (30)
13a	83 (40)	77 (110)	96 (23)	98 (56)	2.39 ± 1.23 (23)
Overall	87 (115)	82 (321)	97 (66)	97 (163)	2.39 ± 1.02 (66)

<sup>a</sup>Nest success was the proportion of all nests that hatched at least 1 egg.

<sup>b</sup>Total number of nests on which calculations were based.

<sup>c</sup>Percent hatchability, defined as the proportion of eggs that hatched from successful nests.

<sup>d</sup>Total number of eggs on which calculations were based.

<sup>e</sup>Total number of chicks on which calculations were based.

<sup>f</sup>Fledging success was the mean number of chicks (6–10 d old) fledged per successful nest.

TABLE 3. Mayfield (1961, 1975) estimates of White-faced Ibis nest success during the laying/incubation and nestling periods on Lower Klamath National Wildlife Refuge, California, 1995.

Colony	Laying/incubation period <sup>a</sup>					Nestling period					
	Exposure days	Nests	Losses	Daily survival	Percent nest survival <sup>c</sup>	Exposure days	Nests	Losses	Daily survival	Percent nestling survival <sup>d</sup>	Overall nest success <sup>e</sup>
7a	445.5	40	3	0.9933	0.0039	84.0	37	1	0.9942	0.0058	80.1
8b	349.5	41	5	0.9857	0.0064	68.8	36	0	1.0000	0.0000	68.8
13a	652.0	45	5	0.9923	0.0034	81.8	40	3	0.9885	0.0066	74.6
TOTAL	1447.0	126	13	0.9910	0.0025	79.1	113	4	0.9940	0.0030	75.4

<sup>a</sup>Laying/incubation period included laying period of 4 d and incubation period of 22 d.

<sup>b</sup>Standard error (*s*) calculated following Johnson (1979).

<sup>c</sup>Percent nest survival for the laying/incubation period calculated as (daily survival rate for laying + incubation)<sup>26</sup> \* 100 (Johnson 1979).

<sup>d</sup>Percent nestling survival for the nestling period calculated as (daily survival rate)<sup>8</sup> \* 100 (Johnson 1979).

<sup>e</sup>The product of percent nest survival \* percent nestling survival.

estimate of 87% apparent nest success. The Mayfield method accounts for nests that were destroyed before they were found and is usually a less biased estimator of nest success (Johnson 1979, Hensler and Nichols 1981). Our Mayfield estimates of nest success during the laying and incubation period (79.1%) and the nestling period (95.3%) are similar to those reported by Kelchlin (1996; 79.9% and 95.0%, respectively) and higher than those documented by Kelchlin (1997; incubation = 63.2%, nestling = 89.3%). Our Mayfield estimate of overall nest success (75.4%) is almost identical to the 75.9% Mayfield estimate of overall nest success documented by Kelchlin (1996) but higher than the 56.4% overall Mayfield nest success reported in 1996 by Kelchlin (1997).

Clutch size declined later in the breeding season, a pattern well documented in other White-faced Ibis studies (Alford 1978, Steele 1980, Henny and Herron 1989) and among birds in general (Lack 1968).

We suspect the high nest success and fledgling rate for White-faced Ibis on Lower Klamath NWR can be attributed to a combination of (1) sturdy and favorable nesting habitat (hardstem bulrush), (2) accessible foraging habitats within the refuge and adjacent private cattle pastures that contained abundant resources (primarily earthworms) throughout the nesting season, (3) colonies that remained flooded throughout the nesting period, reducing accessibility by mammalian predators, (4) low densities of Franklin's Gulls and other potential avian predators, and (5) a relatively favorable climate during the nesting season.

One explanation for the rapid increase in White-faced Ibis breeding populations on Lower Klamath NWR is the expansion of favorable nesting and foraging habitat brought about by previously described changes in habitat management. In addition, the increase may be due in part to immigration of White-faced Ibis from the Great Salt Lake marshes, which were drastically affected by flooding from 1982 through 1985 when traditional colonies were reduced by 80% (Ivey et al. 1988). Finally, the increased breeding populations on Lower Klamath NWR may have included White-faced Ibis dispersing from main breeding colonies in northwestern Nevada (1985–1994 breeding pair average = 2373) during drought conditions in 1991 and 1992 when, respectively, 0 and 315 breeding White-faced Ibis were reported

(W. Henry, Stillwater NWR, Fallon, NV, personal communication).

Within the Intermountain West, White-faced Ibis nesting locations can vary considerably among years, with certain sites being used repeatedly while others are used only intermittently (Ryder 1967). Ryder (1967) suggested that this nomadic nesting pattern may be associated with annual fluctuations in hydrology of wetlands where White-faced Ibis nest. Indeed, in years of hydrologic extremes (i.e., drought or flooding), limitation of high-quality breeding habitats would increase the importance of areas with suitable wetlands. Historically, Lower Klamath NWR has received a relatively stable water supply, and so some wetlands can be managed for early-successional hardstem bulrush while others are managed traditionally for breeding and migrating waterfowl. Therefore, Lower Klamath NWR may maintain preferred White-faced Ibis breeding habitats in years of otherwise poor habitat conditions across the Intermountain West.

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## ALGAE OF DEVILS HOLE, NEVADA, DEATH VALLEY NATIONAL PARK

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**ABSTRACT.**—We examined algal flora in the aquatic system of Devils Hole, Nevada. The water is seasonally warm, near neutral in pH, and rich in dissolved carbonate, indicative of deeply circulating groundwater flowing through carbonate rock. Most algae were benthic, with only a few planktonic representatives. Eighty-four terminal identifications in 44 genera were recorded, with diatoms and blue-green algae the most speciose groups. Diatoms were major contributors to the grazing food web. Large, mat-forming filamentous algae have an important influence on the physicochemical and general structure of the benthic substrates in Devils Hole.

*Key words:* Death Valley, Devils Hole, algae, Cyanobacteria, Bacillariophyta, Chlorophyta, thermal springs, desert.

Devils Hole is the collapsed top of a stretch fault leading to a flooded cave system. Carr (1988) and Riggs et al. (1994) discuss the geological development of Devils Hole. The water surface, which is about 15 m below the immediate land surface, is the hydrologic head of the regional Ash Meadows groundwater flow system. In many ways Devils Hole is quite similar to the spring ecosystem of Montezuma Well, Arizona (Boucher et al. 1984, Blinn et al. 1994). Over the last 25 yr, Devils Hole aquatic ecosystem has been studied primarily as it relates to the Devils Hole pupfish (*Cyprinodon diabolis* Wales), which is federally listed as endangered, while other facets of the ecosystem have received limited attention. The National Park Service and the United States Fish and Wildlife Service are now supporting broader studies of the Devils Hole aquatic ecosystem. A logical first step is to summarize what is known about the algal community, hence this paper. Then more in-depth work can build upon this base.

### DESCRIPTION OF DEVILS HOLE

Devils Hole, part of the Great Basin Desert, lies in a disjunct portion of Death Valley National Park in southwestern Nevada (36°25'31"N, 116°17'28"E; 2400 ft elevation). The surface configuration of Devils Hole is that of an elongate rectangle with the long axis oriented northeast-southwest (Fig. 1). At the water's

surface its dimensions are approximately 22.0 × 3.5 m (Gustafson and Deacon 1998). Distance to the water, its vertical walls, and orientation of the walls restrict direct insolation to 0–4 h per day (United States Fish and Wildlife Service 1980), depending on the season. The south end of the near-surface water overlies a shallow shelf. This “upper shelf” (Fig. 2) is actually a large breakdown boulder wedged between walls of the fault. The shelf is usually at least partially covered with gravel and cobble, especially along its west side where it meets the west wall of the fault. Dimensions of the upper shelf are approximately 3.0 × 6.3 m, with water depth ranging from 0.0 m at the south end to 0.8 m at the north end. Along the west, north, and east sides of Devils Hole, walls are essentially vertical and extend down to approximately 9 m below the water's surface. The walls have a microtopography of grooves and pits which greatly increases their surface area and facilitates algal colonization (Burkholder 1996). Below the upper shelf is the “lower shelf” (Fig. 2) that slopes downward into the cave. Water depths over this shelf are 5.0–9.0 m (Gustafson and Deacon 1998). From the north end of the lower shelf, the cave system drops to unknown depths; the deepest recorded penetration (using SCUBA, 15 August 1991) was to 133 m without reaching the bottom. In the explored portion of the cave system are several branches of the cave that allow deeply circulating groundwater (Fig. 3). One

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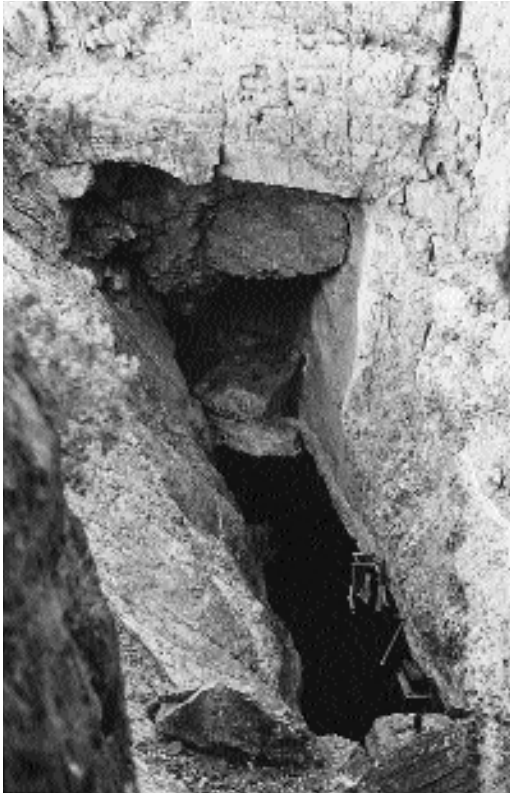


Fig. 1. Looking into Devils Hole, Nevada. Northeast is to the top of the photo.

branch extends above the water level to ground surface (Devils Hole No. 2), but at a distance that precludes light reaching the water. There is no conclusive evidence that water ever flowed out of Devils Hole. There is visual evidence that, in prehistoric times, the water level possibly was at least 1 m below the current level (Hoffman unpublished data).

Physicochemical characteristics of the water in Devils Hole are remarkably stable because the water source has been a huge regional aquifer for thousands of years (Winograd et al. 1997). The physicochemistry has been reported by many authors (Walker and Eakin 1963, Brown and Feldmeth 1971, Bateman et al. 1974, Garside and Schilling 1979, Deacon and Baugh 1985, Hershler and Sada 1987, Gustafson and Deacon 1998). Following is a summary of their measurements: temperature = 32–33°C; pH = 7.1–7.5; dissolved oxygen = 2.0–8.1 mg L<sup>-1</sup>; total dissolved solids = 410–870 mg L<sup>-1</sup>; conductivity = 820 μS cm<sup>-1</sup>; SiO<sub>2</sub> = 21–23.5 mg L<sup>-1</sup>; NO<sub>3</sub> = below detection to



Fig. 2. Longitudinal cross section of the upper 10 m of Devils Hole viewed from the east. The horizontal line is the current water level. US = upper shelf; LS = lower shelf (redrawn with permission from Gustafson and Deacon 1998).



Fig. 3. Longitudinal cross section of the upper 60 m of Devils Hole, viewed from the east, showing conduits that allow for deeply circulating groundwater. The horizontal line is the current water level (redrawn with permission from Gustafson and Deacon 1998).

0.5 mg L<sup>-1</sup>; P = below detection to 0.024 mg L<sup>-1</sup>; Ca = 46–51 mg L<sup>-1</sup>; HCO<sub>3</sub> = 300–311 mg L<sup>-1</sup>. Deep waters are uniform annually and dielily, while shallow waters over the upper shelf have greater variability (Gustafson and Deacon 1998). This variation is due to the high surface area-to-volume ratio, which favors gas and heat flux, and to the greater photosynthesis that occurs on the upper shelf. Variability is greater at the south end (shallowest water) and along the west wall (greatest insolation) of the shelf. The principal source of chemical constituents of Devils Hole water is probably largely from parent rock through which groundwater courses. However, external sources of chemicals, particularly inorganic and organic nutrients, include inputs from rainwater runoff and owl pellet deposits (Deacon and Baugh

1985) as well as from wind- and insect-transported material, dead animals (owls, mice, bees, and ants), and bat guano.

The single paper on the algae of Death Valley (Durrell 1962) does not include any samples from Devils Hole.

The indigenous fauna of Devils Hole is relatively limited, although little examined. Animals reported from Devils Hole include a pupfish (*Cyprinodon diabolis* Wales), riffle beetle (*Stenelmis calida* Chandler), amphipod (*Hyaella azteca* [Saussure]), snail (*Tryonia variegata* Hershler and Sada), planarian (*Dugesia* sp.), and unidentified copepods, ostracods, and protozoans. Recent collections have disclosed other previously unidentified animals including 3 insects, oligochaete worms, gastrotrichs, nematodes, and ciliated protozoans. These additional animals are important because many are from groups known to feed on microalgae (Bott 1996).

#### METHODS AND MATERIALS

Ten algal collections were made over a period of 14 yr (1984–1998). Mat-forming filamentous macroalgae were collected by SCUBA divers, whereas benthic algae were collected by scraping from rock surfaces and by incubating microscope slides in the water. Sets of 10 slides each were left for 6 months on the upper and lower shelves and suspended on the west wall. In addition to field collections, algae were identified from gut contents of the riffle beetle. Two water samples were collected for phytoplankton analysis, 1 from 3 m deep in the deep-water area, and the other from the water overlying the center of the upper shelf. Each was collected in a 2.2-L Beta Plus horizontal bottle. The sample was divided into 250-mL bottles and preserved in Lugol's solution.

Identifications were made to the lowest level possible. Some genera were not taken further due to the lack of appropriate keys or to the need for culturing to make identifications. In the results section we use the term *terminal identifications* for whatever identification level is the lowest possible with available keys. Most often this can be considered synonymous with species. However, with a few algae, forms and varieties could be identified. We acknowledge that there will eventually be more terminal identifications in the

future due, in part, to better identification aids and, in part, to more intensive surveys.

In 1986 we collected two 2.2-L water samples to be tested for algal growth potential (Table 3). One was collected at the water's surface and the 2nd at 30.5 m using SCUBA gear. Both samples were filtered through a 0.2- $\mu$ m pore-size filter and kept chilled in the dark. Each sample was tested using the following solutions: original sample (= control); sample plus 0.05 mg L<sup>-1</sup> phosphorus; sample plus 1.0 mg L<sup>-1</sup> nitrogen; sample plus 0.05 mg L<sup>-1</sup> phosphorus and 1.0 mg L<sup>-1</sup> nitrogen. The test was conducted using the alga *Selenastrum* sp., a species not found in Devils Hole but a common test organism.

#### RESULTS AND DISCUSSION

Algae represent a diverse component of the biota in Devils Hole, although algal diversity is low compared with other aquatic ecosystems. Studies spanning more than 14 yr have identified 44 genera and 77 terminal identifications in the system (Table 1). In contrast, Kidd and Wade (1963) and Czarnecki and Blinn (1979) reported over 123 algal taxa, some of which are endemic, in the near thermally constant spring system of Montezuma Well, Arizona. Perhaps the low diversity in Devils Hole results from limited substrates and from the limited solar insolation that reaches submerged substrates in the system.

Three different algal groups were found in Devils Hole: Cyanobacteria (blue-green algae), Bacillariophyta (diatoms), and Chlorophyta (green algae). Diatoms constituted the most diverse algal group, with 54 terminal identifications in 18 genera. Mattson et al. (1995) found a similar dominance of diatoms over cyanobacteria and green algae in karst, spring-fed streams in north central Florida. Green algae were represented by the fewest species. Most algal species were present in low numbers. Only 12 species were considered dominant on any particular sample date (Table 2). This observation suggests that animal grazing may control algal diversity. Physicochemical conditions may restrict occurrence of other taxa. Of the recorded dominants, *Lyngbya limnetica* Lemm. was always dominant and *Spirogyra* sp. was dominant in spring. Most algal species were microscopic and benthic. While this physiognomy is associated with habitats

having abundant physical scouring (Peterson 1996), scouring occurs only rarely in Devils Hole. A small group of species was found to be planktonic, but the majority of these were also represented in the benthos. The phytoplankton of Montezuma Well was also predominantly derived from taxa that inhabit substrates (Boucher et al. 1984).

All these algal groups, and many genera and species, found in Devils Hole have been collected in other Great Basin waters and soils (Durrell 1962, Shields and Drouet 1962, Johansen et al. 1981, Ashley et al. 1985). Soils near Devils Hole may serve as a source of periodic algal introductions into Devils Hole.

In Devils Hole algae seem to be the main source of organic carbon (presence and influence of bacteria has not been examined). While this is typical of desert streams (Lamberti 1996), it is not typical of nearby spring pools which have abundant macrophytes.

#### Cyanobacteria

Cyanobacteria comprised the 2nd most diverse algal group in Devils Hole, represented by 20 genera and 24 terminal identifications. No species were planktonic that were not also present in the benthic community. The lower species diversity of cyanobacteria compared with diatoms is somewhat surprising given the ambient temperature of 32–33°C. DeNicola (1996) cites several examples of cyanobacteria replacing diatoms at elevated temperatures even below 30°C. It may be that overall algal diversity is not evenly spread throughout the photic zone. Also, the circumneutral pH may restrict occurrence of some cyanobacteria.

There is probably only 1 dominant mat-forming filamentous macroalga present. The taxon identified as *Plectonema* sp. (Minckley and Deacon 1975) is undoubtedly *Lyngbya* sp. The 2 genera are very similar morphologically and difficult to separate. *Lyngbya* sp. occurs sporadically on the upper shelf, but a dense carpet of this taxon occurs on the lower shelf. In Devils Hole there are 2 species of *Lyngbya*, *L. limnetica* Lemm., and *L. maiuscula* (Dillw.) Harvey. There is little chance of confusing the 2 species since *L. limnetica* has quite narrow cells (1–2  $\mu\text{m}$ ) compared to *L. maiuscula* (20–40  $\mu\text{m}$ ). Only scant evidence exists that *Lyngbya* sp. is used for food by either the riffle beetle

or the pupfish (Minckley and Deacon 1975). Dense mats of *Lyngbya* sp. on the lower shelf cover much of the substrate. Baugh and Deacon (1983) estimated substrate coverage to be about 80%. This large biomass may be important in locking up available nutrients and releasing them more evenly across time.

Cyanobacteria have been found only rarely in the diet of pupfish and more commonly in the diet of the riffle beetle. These algae may be ingested incidental to feeding on other organisms (Minckley and Deacon 1975). In our April samples of riffle beetles, a large percentage had ingested "unidentified cyanobacterial filaments." These were probably *Oscillatoria* sp., but they may have been ingested incidentally because the food-collecting structures of riffle beetles scrape up benthic algae of a particular size rather than being taxon selective. Even so, the main food of the riffle beetles was a diatom (see below).

The importance of cyanobacteria in Devils Hole is in stark contrast to their absence in the plankton of Montezuma Well (Boucher et al. 1984); Kidd and Wade (1963) reported 11 cyanobacteria at Montezuma Well, with no mention of relative abundance. Perhaps the difference is associated with relatively higher pH in Devils Hole (7.1–7.5) compared to Montezuma Well (6.5).

#### Bacillariophyta

Bacillariophyta (diatoms) was the most diverse algal group in Devils Hole, with 18 genera and 54 terminal identifications (Table 1). Thirteen genera were monospecific in occurrence. *Nitzschia* sp. and *Achnanthes* sp. were the taxonomically dominant genera, with 11 and 10 species, respectively. These diatom genera were also the dominant algae in the collapsed travertine springmound of Montezuma Well (Czarnecki 1979, Blinn et al. 1994) and in springs and spring-fed streams in Florida (Whitford 1956, Mattson et al. 1995). *Denticula elegans* Kütz, numerically dominant in Devils Hole, is a known Great Basin thermophil found in water and soil (Ashley et al. 1985). Burkholder (1996) reports that *Denticula* sp. is endosymbiotic with *Synechococcus* sp. in nitrogen-poor lakes. Perhaps a similar relationship allows *D. elegans* to dominate in Devils Hole. Diatom dominance at 32–33°C is surprising as they are usually replaced by

TABLE 1. Algal species identified from Devils Hole, Nevada, Death Valley National Park.

Taxa	Benthos	Phytoplankton	Diets
CYANOBACTERIA (cyanobacteria)			
(20 genera, 24 terminal identifications)			
<i>Anabaena</i> sp.	X	X	
<i>Anacystis gelatinosa</i> (Henn.) Lemm.	X		
<i>Aphanocapsa</i> sp.	X		
<i>Calothrix thermalis</i> (Schwae) Hansg.	X		
<i>Chaemosiphon</i> sp.	X		
<i>Chroococcus turgidus</i> (Kütz) Nag.	X		
<i>Chroococcus</i> sp.		X	
<i>Gloeocapsa</i> sp.	X	X	
<i>Heterohormogonium schizodichotmum</i> Copeland	X		
<i>Lyngbya maiuscula</i> (Dillw.) Harvey	X		
<i>Lyngbya limnetica</i> Lemm.	X	X	
<i>Lyngbya</i> sp.	X		X <sup>b</sup>
<i>Microcoleus vaginatus</i> (Vauch.) Gomont	X		
<i>Microcystis</i> sp.	X		
* <i>Myxosarcina amethystine</i> Copeland	X		
* <i>Oscillatoria amphibia</i> Ag.	X		
<i>Oscillatoria amphigranulata</i> van Goor	X		
<i>Oscillatoria princeps</i> Vauch.	X		
<i>Oscillatoria</i> sp.	X		
<i>Phormidium purpurascens</i> (Kütz.) Gom.	X		
<i>Plectonema</i> sp.	X		X <sup>a</sup>
<i>Raphidiopsis</i> sp.	X		
<i>Scytonema</i> sp.	X		
* <i>Synechococcus lividus</i> Copeland	X		
* <i>Synechococcus minervae</i> Copeland	X		
<i>Synechococcus</i> sp.	X	X	
<i>Synechocystis</i> sp.	X	X	
* <i>Thalophila imperialis</i> Copeland	X		
Unidentified cyanobacterial filaments			X <sup>b</sup>
BACILLARIOPHYTA (diatoms)			
(18 genera, 54 terminal identifications)			
<i>Achnanthes affinis</i> Grun.	X		
* <i>Achnanthes exigua</i> Grun.	X	X	
<i>Achnanthes exigua</i> Grun. var. <i>heterovalva</i> Krasske	X		
* <i>Achnanthes gibberula</i> Grun.	X		
* <i>Achnanthes grimmer</i> Krasske	X		
<i>Achnanthes hungarica</i> (Grun.) Grun.	X		
* <i>Achnanthes lanceolata</i> (Bréb.) Grun.	X		
<i>Achnanthes linearis</i> (W. Sm.) Grun.	X		
<i>Achnanthes minutissima</i> Kütz	X		
<i>Achnanthes submarina</i> Hust.	X		
<i>Achnanthes suchlandtii</i> Hust.	X		
<i>Achnanthes</i> sp. 1	X		
<i>Achnanthes</i> sp. 2	X		
<i>Anomoeoneis serians</i> (Bréb.) Cl. var. <i>brachysira</i> (Bréb.) Cl.	X		
<i>Brachysira aponina</i> Kutz.	X		
<i>Caloneis ventricosa</i> Ehr.	X		
<i>Caloneis</i> sp.	X		
<i>Cocconeis</i> sp.			X <sup>b</sup>
<i>Coscinodiscus</i> sp.	X		
<i>Cymbella angustata</i> (W. Sm.) Cl.	X		
<i>Cymbella cesatii</i> (Rabh.) Grun.	X	X	
<i>Cymbella delicatula</i> Kütz	X		
<i>Cymbella fonticola</i> Hust.		X	
<i>Cymbella microcephala</i> Grun.	X		
* <i>Cymbella minuta</i> Hilse	X		



TABLE I. Continued.

Taxa	Benthos	Phytoplankton	Diets
<i>Cymbella minuta</i> f. <i>latens</i> (Krasske) Reim.	X		
<i>Cymbella norvegica</i> Grun.	X		
<i>Cymbella</i> sp.			X <sup>b</sup>
* <i>Denticula elegans</i> Kütz	X	X	X <sup>b</sup>
<i>Eunotia arcus</i> Ehr.	X		
* <i>Eunotia pectinalis</i> (Dillw.) Rabh.	X		
<i>Eunotia praeruptia</i> Ehr.	X		
<i>Eunotia</i> sp.			X <sup>b</sup>
<i>Fragilaria arcus</i> (Ehr.) Cl.	X		
<i>Fragilaria vaucheriae</i> (Kütz) Peterson	X		
<i>Fragilaria</i> sp.	X		X <sup>b</sup>
<i>Gomphonema angustatum</i> (Kütz) Rabh.	X		
<i>Gomphonema intricatum</i> Kütz	X		
<i>Gomphonema</i> sp.	X		
<i>Mastogloia smithi</i> Thw. var. <i>lacustris</i> Grun.	X		
<i>Navicula frustulum</i> Hust	X		
* <i>Navicula minima</i> Grun.	X		
<i>Navicula parva</i> (Menegh.) Cl.-Euler	X	X	
<i>Navicula tripunctata</i> (O. F. Müll.) Bory		X	
<i>Navicula</i> sp.			X <sup>b</sup>
<i>Nitzschia amphibia</i> Grun.	X		
<i>Nitzschia denticula</i> Grun.	X		
<i>Nitzschia dissipata</i> (Kütz) Grun.	X		
<i>Nitzschia fonticola</i> Grun.	X		
* <i>Nitzschia frustulum</i> (Kütz) Grun.	X		
<i>Nitzschia hantzschiana</i> Rabh.		X	
<i>Nitzschia kutzingiana</i> Hilse	X		
<i>Nitzschia pales</i> (Kütz) W. Sm.	X		
<i>Nitzschia paleacea</i> Grun.		X	
<i>Nitzschia romana</i> Grun.	X		
<i>Nitzschia vitrea</i> Norman	X		
<i>Nitzschia</i> sp.	X		X <sup>b</sup>
<i>Pinnularia</i> sp.	X		
<i>Stephanodiscus astraea</i> (Ehr.) Grun.			
<i>minutula</i> (Kütz) Grun.	X		
<i>Synedra rumpens</i> Kütz	X		
<i>Tabellaria flocculosa</i> (Roth) Kütz	X		
Unidentified diatoms			X <sup>a</sup>
CHLOROPHYTA (green algae)			
(6 genera, 6 terminal identifications)			
<i>Chlorococcum</i> sp.		X	
<i>Elakatothrix viridis</i> Wille	X		
<i>Gloeocystis</i> sp.		X	
* <i>Oedogonium</i> sp.	X		X <sup>b</sup>
<i>Protococcus</i> sp.	X		
<i>Spirogyra</i> sp.	X		X <sup>b</sup>

\*Previously reported from warm springs

<sup>a</sup>Pupfish diet (Minckley and Deacon 1975)<sup>b</sup>Riffle beetle diet

cyanobacteria above 20°C (DeNicola 1996). Perhaps most diatom diversity is on the upper shelf where temperatures are less stable (Gustafson and Deacon 1998), thereby maintaining thermal refugia.

The majority of diatoms were members of the benthos, many of which are indicative of circumneutral waters with notably high car-

bonates and waters with elevated temperatures (Patrick and Reimer 1966, 1975). Some have also been found to be epiphytic on *Lyngbya limnetica*. Only 4 taxa were found in the phytoplankton that were not in the benthic community.

Both the pupfish (Wales 1930, Minckley and Deacon 1975) and riffle beetle depend

TABLE 2. Dominant algal taxa in Devils Hole, Nevada, on selected dates.

Taxon	Microhabitat	Date
CYANOBACTERIA		
<i>Chroococcus turgidus</i> (Kütz) Nag.	Benthos	April 1998
<i>Lyngbya limnetica</i> Lemm.	Benthos	All sample dates
<i>Oscillatoria princeps</i> Vauch.	Benthos	April 1998
<i>Synechocystis</i> sp.	Phytoplankton	June 1984
BACILLARIOPHYTA		
<i>Cymbella norvegica</i> Grun.	Phytoplankton	November 1986
<i>Denticula elegans</i> Kütz.	Benthos	December 1983 April 1998
<i>Navicula minima</i> Grun.	Benthos	November 1986
<i>Nitzschia amphibia</i> Grun.	Benthos	April 1998
CHLOROPHYTA		
<i>Gloeocystis</i> sp.	Benthos	June 1984
<i>Protococcus</i> sp.	Benthos	June 1984
<i>Spirogyra</i> sp.	Benthos	Every spring

Table 3. Algal growth potential for water from Devils Hole, Nevada, using the test alga *Selenastrum* sp.

Site	Control	+0.05 mg LP <sup>-1</sup>	+1.0 mg LN <sup>-1</sup>	+0.05mg LP <sup>-1</sup> +1.0 mg LN <sup>-1</sup>
Maximum specific growth rate - day <sup>-1</sup>				
Surface water	0.77	1.22	0.70	0.90
30.5-m water	0.56	1.12	0.87	1.16
Maximum standing crop - cells mL <sup>-1</sup>				
Surface water	1.54 × 10 <sup>4</sup>	3.48 × 10 <sup>4</sup>	1.39 × 10 <sup>4</sup>	3.80 × 10 <sup>4</sup>
30.5-m water	1.02 × 10 <sup>4</sup>	3.80 × 10 <sup>4</sup>	1.15 × 10 <sup>4</sup>	3.55 × 10 <sup>4</sup>
Dry weight - mg L <sup>-1</sup>				
Surface water	0.31	1.04	0.28	1.01
30.5-m water	0.20	1.14	0.23	0.94

heavily upon diatoms as a food throughout the year. The riffle beetle consumed predominantly *Denticula elegans* and only a few other taxa (Table 1). It is likely that the snails also depend heavily on diatoms as a food.

#### Chlorophyta

Green algae are relatively minor contributors to algal diversity in Devils Hole. This observation might have been expected since green algae are more sensitive to high temperatures than cyanobacteria (Brues 1929) and require more light. However, DeNicola (1996) suggests that Chlorophyta may dominate at temperatures of 15–30°C. In Devils Hole only 6 genera and 6 terminal identifications of Chlorophyta were found. Four species were benthic and 2 were planktonic.

Two filamentous green algae occur in Devils Hole, *Spirogyra* sp. and *Oedogonium* sp.

The latter is found only sporadically and is present in the riffle beetle diet. *Spirogyra* sp. is seasonally common, mainly on the upper shelf. This alga has been found in gut contents of both the riffle beetle and pupfish (Minckley and Deacon 1975), but at low levels. *Spirogyra* sp. may be incidentally ingested by the pupfish while it catches invertebrate prey (Minckley and Deacon 1975). Beds of *Spirogyra* sp. are, however, important in their influence on the physical environment of the upper shelf. *Spirogyra* sp. beds can become dense in spring and summer. James (1969) gives an annual chronology of the build-up of the beds, and Gustafson and Deacon (1998) illustrate some monthly and annual differences in percent coverage. *Spirogyra* sp. beds can occupy much of the water column over the upper shelf and cover much of the gravel-cobble substrate. In doing so the beds cover substrate

interstices and contribute to increased water temperatures by reducing mixing of shelf water with deeper water. Both conditions are detrimental to the survival of the larval pupfish (Gustafson and Deacon 1998).

The 2 chlorophyte taxa found in the phytoplankton, *Chlorococcum* sp. and *Gloeocystis* sp., have not been found associated with substrates in Devils Hole. Neither genus has been identified in dietary studies. The riffle beetle diet occasionally did include a considerable amount of unidentified algal cells, however, some of which resembled *Protococcus* sp.

#### Algae and Water Chemistry

Results from algal growth potential experiments indicate that phosphorus was the most limiting nutrient in Devils Hole. Groundwater typically is low in both nitrogen and phosphorus (van der Kamp 1995). Addition of phosphorus to Devils Hole water increased both algal growth and maximum standing crop (Table 3). Deacon and Baugh (1983) noted that owl pellets dropped into the water increased both O-PO<sub>4</sub> and N-NO<sub>3</sub> and suggested these nutrients would stimulate algal growth.

Deacon and Baugh (1985) provide information on the monthly and annual variability of primary productivity on the inner and outer portions of the upper shelf. They suggested the variability is due to light intensity and duration and the quantity of nutrients available. In the 1970s, when declining water levels (due to excessive groundwater pumping) began exposing the surface of the upper shelf, artificial lighting was used to stimulate primary productivity in Devils Hole (Osborn 1983, Deacon 1985).

Production of oxygen through photosynthesis is important to the survival of pupfish eggs and larvae (Deacon et al. 1995, Gustafson and Deacon 1998). Particularly important is the diel fluctuation in dissolved oxygen. Oxygen production is mostly due to microscopic benthic algae rather than the large, filamentous algae or phytoplankton. Bubbles rapidly appear on the encrusting benthic algae as soon as direct sunlight strikes them.

#### Threats to the Devils Hole System

A drop in water level beyond the upper shelf will likely impact the algal community by reducing the surface suitable for diatom colo-

nization. This will have effects on both biomass and diversity throughout the ecosystem. On the west wall diatoms may be able to follow dropping water levels down the wall. But there is a limit to their movement because direct insolation occurs only a few meters down this wall due to the geometry of the fault. Beyond that point diatoms may not survive in high densities. A positive effect of dewatering the 1st shelf may be reducing the negative influence of *Spirogyra* sp. upon larval pupfish survival. However, this may never become important because larval pupfish depend so greatly upon substrate interstices to avoid adult cannibalism (Gustafson and Deacon 1998).

#### Future Research

Desert springs often have stability in most physicochemical characteristics, with only solar input varying (Boucher et al. 1984). They seem to offer a link between the artificiality of laboratory environments and the more variable natural environments. Such springs provide invaluable settings that could be studied more. Boucher et al. (1984) have also shown how these springs are useful in comparing temperate and tropical aquatic ecosystems.

The comparison of ecosystems in Devils Hole and Montezuma Well should be fruitful. They are alike in many ways, but they vary in the amount of solar input due to the smaller opening at Devils Hole. Additionally, the Montezuma Well ecosystem can be compared to that in Crystal Pool, a large spring near Devils Hole with water coming from the same aquifer, but which has marginal macrophyte beds and a water outflow.

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work done in disparate fields. The senior author also thanks Eric Gustafson for his collaborative fieldwork, especially while SCUBA diving, and for his insightful discussions of the Devils Hole aquatic system. Many thanks go to Sam Rushforth and Jeff Johansen for their very helpful reviews of this paper.

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## RESPONSE OF WINTERING BUTEOS TO PLAGUE EPIZOOTICS IN PRAIRIE DOGS

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**Abstract.**—Several species of raptors winter at Rocky Mountain Arsenal National Wildlife Refuge (Refuge) including the Bald Eagle (*Haliaeetus leucocephalus*), Ferruginous Hawk (*Buteo regalis*), Red-tailed Hawk (*Buteo jamaicensis*), and Rough-legged Hawk (*Buteo lagopus*). Raptors were monitored each winter from 1988–89 to 1996–97 using a standardized road survey. Black-tailed prairie dogs (*Cynomys ludovicianus*) form a major component of the prey base for wintering raptors on the Refuge, with 1850 ha of active prairie dog towns mapped in 1988. Prairie dog town areas and population density were determined by mapping active towns and conducting visual counts on study plots to determine population density on an annual basis from 1988 to 1996. Large-scale plague epizootics were documented on the Refuge in 1988–89 and 1994–95, reducing prairie dog towns by 95% and 99%, respectively. A significant relationship was found in the numeric response of Ferruginous Hawks to changes in prairie dog town area ( $r^2 = 0.96$ ,  $P < 0.001$ ) and minimum estimated population ( $r^2 = 0.97$ ,  $P < 0.001$ ), but not to estimated prairie dog density ( $r^2 = 0.07$ ,  $P = 0.486$ ). This contrasted sharply with the responses to prairie dog town area found for Red-tailed ( $r^2 = 0.11$ ,  $P = 0.377$ ) and Rough-legged Hawks ( $r^2 = 0.04$ ,  $P = 0.612$ ).

*Key words:* *buteos, raptors, prairie dogs, plague, predator/prey response.*

Several species of raptors winter on the Rocky Mountain Arsenal National Wildlife Refuge (Refuge), including the Bald Eagle (*Haliaeetus leucocephalus*), Ferruginous Hawk (*Buteo regalis*), Red-tailed Hawk (*Buteo jamaicensis*), and Rough-legged Hawk (*Buteo lagopus*). More than 70 Bald Eagles have been observed simultaneously using a communal roost site on the Refuge, and large numbers of buteos were counted on road transects during 1988 (U.S. Fish and Wildlife Service 1989). This makes the Refuge an opportune area for evaluating the relationship between wintering buteos and prairie dogs. Black-tailed prairie dogs (*Cynomys ludovicianus*) create, through their burrowing and grazing activities, a dynamic component of the short- and mid-grass prairies, the “prairie dog ecosystem.” This ecosystem provides habitat for a wide variety of wildlife species, from black-footed ferrets (*Mustela nigripes*) and Burrowing Owls (*Athene cunicularia*) to swift fox (*Vulpes velox*) and Mountain Plovers (*Charadrius montanus*). Prairie dogs may therefore be considered a *keystone species* to the shortgrass prairie (Miller et al. 1994). Clark et al. (1989) found more than 100 vertebrate species associated with prairie dog colonies, and Kotliar et al.

(1997) found at least 10 species to be dependent on prairie dogs for their survival. Prairie dogs form a major component of the prairie ecosystem on the Refuge, occupying 1850 of 6900 ha (27%) in October 1988 (Stollar et al. 1992).

Plague (*Yersinia pestis* infection) epizootics have periodically affected prairie dog towns on the Refuge from 1988 to 1995 (Ebasco Services, Inc. 1989, U.S. Fish and Wildlife Service 1996). To maintain crucial habitat for wintering raptors, especially the Bald Eagle, the U.S. Fish and Wildlife Service (Service) began working to reestablish prairie dogs to their former levels. The focal point of this effort was prairie dog relocations into areas previously occupied, based largely on the 1988 (pre-plague) distribution (Ebasco Services, Inc. 1989). From 1989 to 1993 the Service relocated 5800 prairie dogs to the Refuge from off-Refuge sources (U.S. Fish and Wildlife Service 1994). A monitoring program to gauge effectiveness of the relocation program was initiated and included mapping active prairie dog towns and determining prairie dog abundance.

Other researchers have documented changes in populations of breeding (Woffinden and Murphy 1977, Smith et al. 1981) and migratory

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(Cully 1991) raptors during prey declines. Data presented herein examine fluctuations in prairie dogs caused by plague epizootics and concurrent changes in the number of wintering raptors.

Data we present were collected to establish baseline population levels for a wide variety of wildlife species found on the Refuge prior to and during cleanup operations. Therefore, we did not establish a priori a rigorous study design specifically for analyzing prairie dog and raptor population data.

#### DESCRIPTION OF STUDY AREA

The Refuge, located approximately 16 km northeast of downtown Denver, was established in 1942 by the U.S. Army to manufacture chemical and incendiary weapons. After World War II private companies leased the arsenal's industrial sites for the manufacture of pesticides and herbicides. Designated a Superfund site in 1986, the arsenal is currently undergoing environmental remediation. Congress passed legislation in 1992 that establishes the arsenal as a national wildlife refuge upon completion of environmental cleanup. The Refuge Act also states the arsenal will be managed "as if it were a national wildlife refuge" during the cleanup. Data collected and analyzed here are part of a larger-scale effort to characterize populations of wildlife at the Refuge. The Refuge currently covers over 6900 ha in a mosaic of habitat types including wetland, riparian, and various types and successional stages of grasslands.

#### METHODS

##### Raptor Surveys

Road surveys were used to monitor raptor abundance and distribution on the study area and to provide an index of raptor habitat use and availability. Road censusing is a cost-efficient method of surveying widely distributed raptors. This method has been used extensively by a number of researchers to monitor raptor population trends (Johnson and Enderson 1972, Bauer 1982) and habitat/perch use (Marion and Ryder 1975, Fischer et al. 1984).

We surveyed raptors weekly or biweekly from November 1988 through March 1997. Surveys were conducted along a 38.6-km route, 2 h after sunrise on calm days with no

precipitation, by a single observer from an automobile traveling at 24–32 km h<sup>-1</sup>. Only birds observed with an unaided eye were recorded. However, if birds were not readily identifiable to species, the vehicle was stopped and the observer used binoculars or a spotting scope to make an identification. Species, age class when possible, activity, perching substrate, segment (km) of transect, and a specific location were recorded for each raptor observed.

Simple linear regression was used to analyze prairie dog and raptor data, with significance for the regression model determined at  $P < 0.05$ .

##### Prairie Dog Distribution

Prairie dog distribution was determined using aerial photo interpretation and field verification in all surveys conducted from 1988 to 1993 (Ebasco Services Inc. 1989, U.S. Fish and Wildlife Service 1994). We used frosted mylar placed over black-and-white section photographs as a field reference guide. Boundaries of prairie dog towns were then marked with a pencil in the field. Boundaries of black-tailed prairie dog towns are generally easy to identify by the marked change in vegetation height. Mapping was usually conducted in the spring after emergence of prairie dog litters. Upon completion of field mapping, we determined the area of each town using a Radian's Contour Plotting System-1 (CPS-1) for the 1988–1990 surveys and an electronic planimeter for the 1991–1993 surveys.

Prairie dog town distribution was mapped in 1994–1996 using a Global Positioning System (GPS) and software (Pathfinder™) from Trimble Navigation Limited (Sunnyvale, CA). We collected data in the field using a TDC1 GPS datalogger. GPS positions were collected by walking the perimeters of active prairie dog towns and recording positions at 10- to 15-sec intervals. GPS data files collected and stored in the rover unit were then downloaded to a computer with Pathfinder™ software for subsequent differential analysis. Differential correction (to increase accuracy to 2–5 ms) was completed using community base station files downloaded from the U.S. Forest Service in Fort Collins, Colorado. We then read area features (i.e., prairie dogs towns) and determined the size of each area using Pathfinder™ software. Final maps were developed with ArcView™ software (Esri Inc., Redlands, CA).

### Prairie Dog Abundance

Visual counts have been used to estimate populations of white-tailed prairie dogs (*Cynomys leucurus*) and Richardson's ground squirrels (*Spermophilus richardsonii*) and have been shown to correlate well with estimates obtained from mark-recapture data from the same sites (Fagerstone 1983, Fagerstone and Biggins 1986, Menkins et al. 1990). We chose visual counts, developed to evaluate black-footed ferret habitat (Biggins et al. 1993), as a method of estimating population density of black-tailed prairie dogs on the Refuge. Study plots were not selected on a random basis, due to certain site characteristics needed to conduct visual counts. Site characteristics included visibility of the entire study plot from a single location, vegetation height, size of prairie dog town, and topographic relief. The number of study plots varied from year to year and was based on the number and size of prairie dog towns available. Plot size varied from 2 ha in the 1988–1990 surveys to 4–9 ha in the 1991–1994 surveys. Severe reductions in prairie dog town sizes from the 1994–95 plague epizootic limited the choice of plot sizes. Plot sizes for the 1995 surveys ranged from 0.68 to 2.16 ha and for the 1996 surveys from 0.78 to 2.25 ha. Using a surveyor's transit and geodimeter, we established plots, marking corners with 1.83-m lengths of polyvinyl chloride (PVC) tubing. Pin flags were set out at approximately 10-m intervals along plot sides to further assist in determining whether prairie dogs were in or out of the plot during counts. Visual counts were performed using a window-mounted spotting scope from a vehicle parked adjacent

to the plot. Counts were conducted for 3 consecutive days on each plot, starting approximately .5 h after sunrise and continuing (with 15 min between counts) until prairie dog numbers began to decrease, usually mid-morning. The highest individual count of prairie dogs recorded during the 3 d of visual counts was then used to determine density of each plot (highest count/area). Densities were then summed and divided by the number of plots to determine mean density for each year.

## RESULTS

### Prairie Dog Distribution and Abundance

The distribution of prairie dog towns changed dramatically after plague events. Reductions of 95% and 99% were caused by plague epizootics in 1988–89 and 1994–95, respectively (Table 1).

Prairie dog town areas and population estimates represent peak (summer) population levels and were adjusted for the years 1992–1994 due to plague epizootics occurring before arrival of wintering raptors. Area affected by plague was subtracted from total area determined earlier in the year. Therefore, the population estimate data used in regression analyses are 10,822 (1992), 16,430 (1993), and 3,619 (1994). The area data were adjusted as well for the same time period with 608 ha (1992), 727 ha (1993), and 154 ha (1994) used in the regression analysis. These values represent a more accurate depiction of the prairie dog population available to raptors as they arrive on their wintering grounds. The 1st epizootic occurred from November 1988 to September

TABLE 1. Prairie dog population fluctuations pre- and post-plague at Rocky Mountain Arsenal NWR, 1988–1997.

Year	Mean density <sup>a</sup>	Study plots (n)	Area (ha)	Population estimate
1988 <sup>b</sup>	20.2 ± 8.00	24	1850.8	37,406
1989 <sup>b</sup>	20.2 <sup>c</sup>	—	99.8	2017
1990 <sup>b</sup>	12.2 ± 4.80	6	232.9	2842
1991	14.6 ± 3.57	9	555.6	8134
1992	17.8 ± 6.20	12	608.0	10,822
1993	22.6 ± 6.10	12	727.0	16,430
1994	23.5 ± 4.13	10	154.0	3619
1995a	50.9 ± 28.46	9	72.9	3708
1995b	50.9 <sup>c</sup>	—	9.0	458
1996	41.1 ± 15.88	8	35.9	1478
1997	54.8 ± 26.60	6	139.8	7640

<sup>a</sup>Mean density ± 1 s

<sup>b</sup>1988–1990 data from Stollar et al. (1992)

<sup>c</sup>No density data for this year; density estimated



TABLE 2. Numbers of buteos observed during road surveys from November through March at the Rocky Mountain Arsenal NWR, 1988–1997.

Year	Number of surveys	RTHA <sup>a</sup>	RLHA	FEHA
1988–89	17	6.6 (6.0) <sup>b</sup>	4.0 (2.5)	34.1 (20.8)
1989–90	12	3.0 (4.6)	4.9 (2.1)	3.8 (2.2)
1990–91	19	4.8 (2.2)	2.7 (1.8)	2.6 (1.6)
1991–92	16	4.0 (2.8)	4.6 (2.6)	6.7 (4.1)
1992–93	16	4.2 (2.5)	3.7 (2.4)	8.7 (4.7)
1993–94	16	6.4 (2.8)	4.1 (1.6)	10.3 (3.6)
1994–95	13	2.8 (1.3)	1.9 (1.4)	3.8 (2.2)
1995–96	15	6.1 (6.9)	1.1 (1.0)	1.6 (1.5)
1996–97	16	7.0 (3.4)	5.6 (4.0)	2.7 (1.9)

<sup>a</sup>Standardized AOU notation

<sup>b</sup>Mean value (s)

1989, reducing the town area by 95%, and the 2nd from June 1994 to July 1995, reducing the town area by 99%. Recovery of prairie dog populations following these epizootics was facilitated by relocations from off-Refuge sources.

#### Raptor Surveys

Mean values of Ferruginous and Red-tailed Hawks declined after the first prairie dog plague epizootic, while Rough-legged Hawks increased following the die-off (Table 2). Rough-legged Hawks fluctuated throughout the study period. Red-tailed Hawks showed an initial rise in mean values in 1990–91, before dropping again in 1991–92. Red-tailed Hawks also showed a rapid rise near the end of the study period. Ferruginous Hawks increased steadily after the large drop in 1989 through 1991 ( $\bar{x} = 34.1 \pm 20.8$  in 1988–89;  $\bar{x} = 2.6 \pm 1.6$  in 1990–91), until 1994–95, when the prairie dog population again experienced a massive plague epizootic. The drop in numbers of Ferruginous Hawks in 1994–95 was almost identical to the drop in 1989–90 and then hit an all-time low in 1995–96 ( $\bar{x} = 1.6$ ), before rebounding in 1996–97.

There was no significant correlation between counts of Red-tailed or Rough-legged Hawks and prairie dog area ( $r^2 = 0.11$ ,  $P = 0.377$  and  $r^2 = 0.04$ ,  $P = 0.612$ , respectively), density ( $r^2 = 0.25$ ,  $P = 0.171$  and  $r^2 = 0.07$ ,  $P = 0.501$ , respectively), and minimum estimated prairie dog population ( $r^2 = 0.15$ ,  $P = 0.305$ , and  $r^2 = 0.03$ ,  $P = 0.623$ , respectively). Ferruginous hawk/minimum estimated prairie dog population ( $r^2 = 0.97$ ,  $P < 0.001$ ) and Ferruginous Hawk/prairie dog area ( $r^2 = 0.96$ ,  $P < 0.001$ )

are the only portions of the model showing significance (Fig. 1).

#### DISCUSSION

Ferruginous Hawks are known to specialize on ground squirrels and lagomorphs (Wakeley 1974, 1978, Blair and Schitoskey 1982, Gilmer and Stewart 1983, Johnsgard 1990). Cully (1991) found that numbers of Ferruginous Hawks are closely associated with local distribution of prairie dogs during fall migration. A similar spatial relationship was found in the 1988–89 plague epizootic on the Refuge. As plague eliminated large colonies on the eastern side of the Refuge, higher numbers of Ferruginous Hawks were found on the remaining healthy prairie dog colonies in the northwestern portion of the Refuge.

These data indicate that distribution of Ferruginous Hawks on the Refuge is based on areal distribution of prairie dogs rather than prairie dog density. Minimum estimated population was also significant, but it is calculated as a product of areal distribution and density, implicating areal distribution as the major factor in determining significance. Dramatic changes in prairie dog density failed to elicit a significant response by Ferruginous Hawks. There may be some lower threshold density for black-tailed prairie dogs that would elicit a negative response (or lack of response) by Ferruginous Hawks, but it does not show up in these data. One would expect predators to respond to variations in density of prey, but in this case prairie dogs, even at relatively low densities (1990–91, 12.2–14.6 ha<sup>-1</sup>), may be more available to these raptors than other

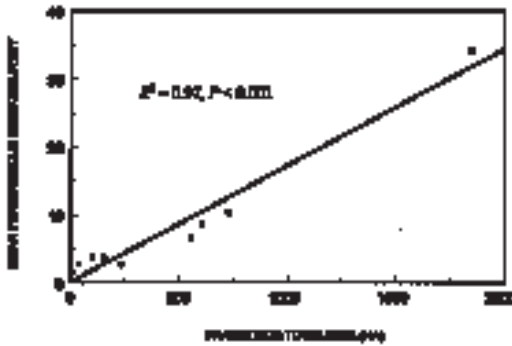


Fig. 1. Linear regression of mean Ferruginous Hawks per survey versus prairie dog town area (ha) from 1988–89 through 1996–97 at Rocky Mountain Arsenal NWR.

prey resources. The other factor that may contribute to poor performance of density in the model is that density was estimated, rather than actually measured, for 2 of the sample periods (1989 and 1995b). However, it is believed that these are reasonable estimates of actual densities and are therefore included in the analysis.

Density on prairie dog towns increased significantly in 1995–96, from  $\bar{x} = 23.47$  ( $s = 4.13$ ) in 1994 to  $\bar{x} = 50.86$  ( $s = 28.46$ ) in 1995, and  $\bar{x} = 41.16$  ( $s = 15.88$ ) in 1996. This resulted mainly from large reductions in prairie dog area due to plague and a concurrent wet year in 1995. These 2 factors acted together to force the reduced number of prairie dogs onto smaller areas where they could keep vegetation clipped short to facilitate predator detection. This hypothesis is supported by studies in which deferred grazing (increasing the height of vegetation) by cattle reduced the size and extent of prairie dog towns, with a concurrent rise in density (Knowles 1982, Uresk et al 1982, Uresk and Bjugstad 1983, Cable and Timm 1988). One would expect to see a lower threshold value (very low numbers of prairie dogs) that would fail to elicit a response by Ferruginous Hawks. The low prairie dog town area observed in September 1995 (9.0 ha), with a mean of 1.6 ( $s = 1.5$ ) Ferruginous Hawks, was probably very close to this threshold value. Therefore, it would appear that prairie dog area is the most significant part of the model explaining the response of Ferruginous Hawks. This response was observed through 2 separate cycles of plague epizootics in prairie dogs, further increasing the validity of the model. The power of this model may allow some pre-

dictive exercises to be made. Based on the data, an extrapolation to predict a lower size limit of a prairie dog town that would elicit a response from a single Ferruginous Hawk is 5.6 ha/Ferruginous Hawk (based on 1995–96 Ferruginous Hawks,  $\bar{x} = 1.6$ ,  $s = 1.5$ ; and prairie dogs, 9.0 ha). This model is further supported by data collected in the Denver metropolitan area (Plumpton 1996), which show Ferruginous Hawks using small, isolated prairie dog towns.

Red-tailed and Rough-legged Hawks are more diverse in their prey selection, and changes in prairie dog distribution and abundance on the Refuge did not result in a substantial response by these species. Changes in the relative abundance of these species on the Refuge are probably tied more to variations in abundance and availability of small mammals on wintering areas.

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## STATUS OF *DESCURAINIA TORULOSA* (BRASSICACEAE)

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**ABSTRACT.**—*Descurainia torulosa* was established in 1983 based on material collected in northwestern Wyoming. The species is now known from 2 disjunct populations in southwestern Wyoming, and recent collections have expanded the known distribution within the northern portion of its range. The north-south disjunct distribution and apparent habitat differences have stimulated questions concerning the degree of relatedness between the disjunct elements to the point that the southern populations have been suggested to be a distinct taxon. Recognition of *D. torulosa* as a distinct species has also been questioned. This paper is based on field examination of *D. torulosa* populations, study of all known *D. torulosa* herbarium specimens, and analysis of nucleotide sequence from the internal transcribed spacer regions 1 and 2 of nuclear ribosomal DNA (ITS-1 & 2) from population exemplars. Cladistic analysis of the sequence data support our conclusion, based on morphological analysis. Northern and southern populations of *D. torulosa* are conspecific. Western North American *Descurainia* is in need of modern, critical taxonomic revision.

*Key words:* Brassicaceae, *Descurainia*, taxonomic status, DNA, ITS-1 & 2, rare plant.

*Descurainia torulosa* was described by Reed Rollins (1983) from material collected near Brooks Lake, Fremont County, northwestern Wyoming. Rollins (1983) considered *D. torulosa* distinctive because of the branching habit, short stature, closely appressed but flaring torulose siliques, and extremely short pedicels. The taxon is endemic to Wyoming, with a disjunct distribution (Fig. 1), and had been designated a category 1 (threatened) candidate for federal listing as threatened or endangered (U.S. Fish and Wildlife Service 1990). A re-evaluation of the situation (Marriott 1991) resulted in the recommendation that *D. torulosa* be reassigned to category 2 (additional information needed) status.

In 1988 several specimens of *Descurainia* collected in Wyoming were sent by the Rocky Mountain Herbarium (RM) to Brassicaceae expert Reed Rollins (Harvard University) for his determination. Three collections, 2 from Park County in northwestern Wyoming (R. Kirkpatrick 5191a; E. Evert 10062) and 1 from Pine Butte in Sweetwater County approximately 240 km to the south (Dueholm 10779), were given provisional determinations as "*D. torulosa* (?)" (Rollins 1988). Rollins indicated that more material was needed to clarify the situation for *D. torulosa*.

The apparent rarity of *Descurainia torulosa*, as well as the curious disjunct distribution (Fig. 1) and differing ecological settings for the northern and southern populations, stimulated field research by pertinent federal land management agencies. These studies (Dorn 1989, Marriott 1991, 1992) produced much new information on the distribution, ecology, and morphological aspects of *D. torulosa*. They also drew attention to 2 taxonomic questions. Does *D. torulosa* merit recognition as a distinct species? If so, do the northern and southern population systems represent the same taxon? Dorn (1989) first suggested that *D. torulosa* might be just a variant form of *D. incana* (= *D. richardsonii*), a common, widespread species in the Rocky Mountain region.

The objective of this study was to evaluate the taxonomic status of *Descurainia torulosa* Rollins and, using morphological and DNA sequence data, to assess the degree of divergence between the northern and southern population systems.

### MATERIALS AND METHODS

Between 18 and 20 July 1997, we surveyed documented (Marriott 1992) *Descurainia torulosa* populations in Fremont, Park, Sweetwater,

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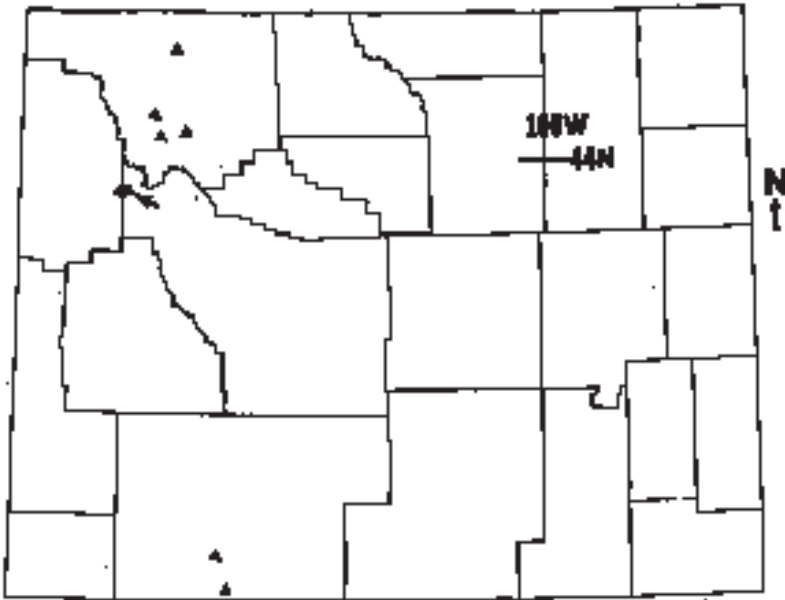


Fig. 1. Map of the state of Wyoming showing the distribution of *Descurainia torulosa* populations. County lines are shown, and the arrow indicates the location for the type collection.

and Teton counties of western Wyoming. At each site 4–10 individuals were collected for DNA extraction, and a like number selected as herbarium voucher specimens. We recorded observations of plant habit, reproductive status, and habitat for each specimen. Latitude and longitude were determined using the Global Positioning System. For comparison purposes, DNA samples and voucher specimens were also secured for *D. incana* var. *viscosa* and *D. sophia* from locations in and around Laramie, Wyoming (Table 1). Additional specimens of varieties of *D. incana* and *D. pinnata* (see Table 1) were obtained from dry herbarium specimens on file at the Rocky Mountain Herbarium (RM). All vouchers have been filed at RM.

Young leaf tissues of mature *Descurainia torulosa* plants were excised, immediately frozen in liquid nitrogen, and stored on dry ice for transport to the laboratory (Millan et al. 1996). Upon return to the lab, DNA was extracted following the protocol of Torres et al. (1993). We extracted DNA from dry herbarium leaf material using the same protocol and determined DNA concentrations by UV spectroscopy.

Symmetric polymerase chain reaction (PCR) amplification of ITS-1 and ITS-2 regions was conducted using the forward and reverse strand primers, ITS5 and ITS4 respectively,

from White et al. (1990). Each 50- $\mu$ l PCR mixture included 50 ng of DNA extract, 0.5  $\mu$ M of each primer, 100  $\mu$ M each of 4 dNTPs, 5  $\mu$ l of PCR buffer (100 mM Tris-Cl [pH 8.3], 500 mM KCL, 15 mM MgCl<sub>2</sub>, and 0.1% [w/v] gelatin), and 1 unit of *Taq* polymerase (Stratagene, La Jolla, CA). The reaction mixture was overlain with 60  $\mu$ l of sterile mineral oil. Thermal cycling was performed using an MJ Programmable Thermal Cycler (MJ Research, Inc.) programmed for 2 min initial denaturation at 94°C, 25 PCR cycles of 1 min denaturation at 94°C, 2 min of annealing at 54°C, and 2 min of extension at 72°C. The final extension time of the last cycle was increased to 4 min. Reactions lacking template DNA were included as negative controls.

PCR product yield and quality were initially evaluated via electrophoresis of a 10- $\mu$ l aliquot in 1.0% agarose using a TAE buffer (40 mM Tris-acetate, 1 mM EDTA, pH 8.0). Successful amplifications were then purified using Centricon 100 columns (Amicon, Inc.) following the manufacturer's directions, and then lyophilized. The lyophilized double-stranded products were sent to Macromolecular Resources, Colorado State University, for automated sequencing.

The ITS-1 & 2 region DNA sequences (5' to 3') obtained from the automated sequencer

TABLE 1. DNA sources<sup>a</sup>.

Taxon	Locality	Collection	GenBank Number
<i>Descurainia incana</i>			
var. <i>incana</i>	WY, Carbon Co., Coal Creek Canyon	Redder 56	AF205582
var. <i>incana</i>	WY, Natrona Co., Pathfinder Dam	Roderick 4822	AF205583
var. <i>viscosa</i>	WY, Albany Co., Eagle Rock	Bricker 531	AF118859
<i>D. pinnata</i>			
var. <i>brachycarpa</i>	WY, Carbon Co., Third Sand Creek	Roderick 1124	AF205584
var. <i>filipes</i>	WY, Carbon Co., Rawlins	Roderick 697	AF205585
var. <i>nelsonii</i>	WY, Carbon Co., N. Shirley Basin	Roderick 6116	AF205586
<i>D. sophia</i>	WY, Albany Co., Laramie	Bricker 548	AF118860
	WY, Carbon Co., Medicine Bow River	Roderick 3565	AF205587
<i>D. torulosa</i>	WY, Sweetwater Co., Pine Butte	Bricker 550	AF118861
	WY, Sweetwater Co., Lion Bluffs	Bricker 551	AF118862
	WY, Teton Co., Breccia Cliffs	Bricker 552	AF118863
	WY, Fremont Co., Brooks Lake	Fertig 16913	AF118865

<sup>a</sup>All vouchers are on file, Rocky Mountain Herbarium (RM), University of Wyoming.

output were double-checked against their respective chromatograms and then manually aligned. Position number 1 in the aligned sequence corresponded to the 1st position where sequence was available for all samples. Sequence alignment on the 3' end was terminated at position 624 because alignments beyond that position became dubious. Ambiguous base determinations within the 624 base pair span were coded in the matrix as "N." The complete data matrix of aligned sequence was subjected to parsimony analysis using the program PAUP 3.1.1 (Swofford 1991).

There is no known explicit phylogenetic hypothesis for the member species of *Descurainia*. As a consequence, relationships amongst the taxa included in this study (Table 1) are unknown. *Descurainia sophia* was originally selected as the potential outgroup since it is not native to North America and is presumably distinct from the *Descurainia* species native to the Rocky Mountain region. We conducted a preliminary cladistic analysis to explore the relationship between *D. sophia* and the remaining taxa included in this study. This preliminary analysis utilized the HEURISTIC search option with the TREE BISECTION-RECONNECTION (TBR) branch swapping option, and the MULPARS, COLLAPSE, and ACCTRAN optimization options, with sequence from *Sinapis alba* (Rathgeber and Capesius 1989) designated as the outgroup. A more intensive phylogenetic analysis for those taxa listed in Table 1 was executed using the EXHAUSTIVE search option, with *D. sophia* designated as the outgroup, saving

all most parsimonious trees. To evaluate relative branch support, we conducted 500 replicates of bootstrap analysis and decay analysis.

DNA sequences generated in this study have been submitted to GenBank (Table 1). The matrix of aligned ITS-1 & 2 sequences is available from the authors.

## RESULTS

The preliminary analysis, rooted with *Sinapis alba*, resulted in 3 equally most parsimonious trees of 164 steps (not shown). The strict consensus of these 164 step trees had a topology exactly like that illustrated in Figure 2, with the addition of *Sinapis alba* as the rooting outgroup. This analysis confirmed an outgroup position for *Descurainia sophia* relative to the *torulosa-incana-pinnata* ingroup, at least until a more appropriate outgroup is identified.

The exhaustive search, rooted with *Descurainia sophia*, resulted in 3 equally most parsimonious trees of 86 steps with the consistency index of 0.826 and retention index of 0.795. The g1 value for this analysis was -1.7068, indicating significant phylogenetic signal within the sequence data. Sixty-eight of 624 characters are phylogenetically informative, while 459 are invariant. Pairwise mean and absolute distances are provided in Table 2.

Taxa in the *torulosa-incana-pinnata* ingroup occupy 2 clades (Figure 2). Population exemplars for *Descurainia torulosa* are all located in the same clade, along with 1 variety each from *D. pinnata* and *D. incana*.



Fig. 2. Strict consensus of the 3 equally most parsimonious trees (86 steps) obtained in an exhaustive search rooted with *Descurainia sophia*. Bootstrap values >50% and decay values (in parentheses) are located above the branches. Numbers below each branch indicate the number of base substitutions.

#### DISCUSSION

Cladistic analysis of the molecular data suggests that *Descurainia torulosa* is part of a complex that includes both *D. incana* and *D. pinnata*, and that each of these taxa is paraphyletic. Furthermore, the present sample set reveals 2 clades within this complex, with the population exemplars for *D. torulosa* comprising the terminal cluster in 1 of these clades. Finally, the 2 known southern populations (Pine Butte and Lion Bluffs) are more similar to each other than either is to the sampled northern populations (Breccia Cliffs and Brooks Lake). However, the sampled northern populations do not form a similar clade.

A thorough examination of all known *Descurainia torulosa* specimens demonstrates that the diagnostic morphological characters used by Rollins (1983) to distinguish this species are variable and unreliable in terms of species determination. Rollins (1983) noted that the procumbent, probably perennial, habit of *D. torulosa* was unique for *Descurainia* in North America. Some details concerning the growth habit remain unresolved. Plants from the Sweetwater County populations appear to be annuals (also see Marriott 1992), although vegetative rosettes, suggesting a biennial or perennial habit, were encountered as well. Plants from northern populations appear to be bien-

nial, although some flowering/fruitlet individuals appeared to be in the 1st season of growth. The long-lived perennial habit does not appear to exist within *D. torulosa*. Contrary to the type description, the growth form for all small, flowering individuals examined ranges from erect to decumbent, but definitely not procumbent. Larger, presumably older, flowering specimens tend to be more decumbent in form.

Rollins (1983) placed diagnostic significance in a suite of fruit characters, namely the closely appressed but flaring (curving outwards) torulose siliques and the extremely short pedicels ( $\leq 2.5$  mm). In Dorn's (1992) treatment of *Descurainia*, no mention of growth habit or form is made in the diagnostic key for species. Fruit characters, however, are relied upon heavily, and Dorn (1992) adds fruit pubescence as the primary character to distinguish *D. torulosa* (hairy) from *D. incana* (usually glabrous). In comparing the spectrum of fruit characters putatively diagnostic for *D. torulosa* against those from scores of *Descurainia* specimens from throughout the Rocky Mountain region on file at RM (e.g., *D. californica* [Gray] Schulz, *D. incana* [Bernh. ex Fisch. & Meyer] Dorn, *D. pinnata* [Walt.] Britt.), we have concluded that there is no unequivocal character, nor suite of characters, that can be used to distinguish *D. torulosa* with absolute reliance. Plants determined as *D. torulosa* have siliques ranging from appressed to weakly divergent, and the degree to which siliques are torulose ranges from mild to obvious, but is not qualitatively different from torulose fruits seen in a wide range of *D. incana* specimens. Fruit pubescence, which Rollins (1983) did not specify, but which Dorn (1992) emphasized as diagnostic for *D. torulosa*, is also polymorphic. Except for plants from the Pine Butte population in Sweetwater County, all other known populations of *D. torulosa* have plants with conspicuously pubescent ovary walls and fruits. Furthermore, plants from the Lion Bluff population, also Sweetwater County and ca 55 km northwest of the Pine Butte site, are otherwise indistinguishable from plants in the Pine Butte population, except for having hairy ovary and fruit walls. Although Dorn was aware of these southern populations (Dorn 1989), it appears that he did not include them within his circumscription of *D. torulosa*, as he listed the *D. torulosa* distribution ("nw" and "c") to include only the northern populations. Finally,

TABLE 2. Matrix of pairwise distances between taxa/populations included in this analysis. Values above the diagonal are mean distances. Values below the diagonal are absolute distances measured in number of character-state changes.

Sample <sup>a</sup>	1	2	3	4	5	6	7	8	9	10	11	12
1	531	-	0.020	0.013	0.015	0.013	0.020	0.025	0.017	0.010	0.023	0.056
2	548	24	0.051	0.053	0.050	0.048	0.043	0.049	0.043	0.045	0.045	0.015
3	550	12	31	0.015	0.023	0.026	0.036	0.041	0.033	0.022	0.038	0.066
4	551	8	32	9	0.015	0.013	0.028	0.028	0.022	0.012	0.030	0.064
5	552	9	30	14	14	0.018	0.026	0.031	0.023	0.017	0.030	0.060
6	fer	8	29	16	11	-	0.023	0.028	0.022	0.013	0.026	0.064
7	697	12	26	17	16	14	-	0.012	0.007	0.022	0.008	0.055
8	1124	15	30	17	19	17	7	-	0.005	0.023	0.010	0.061
9	4822	10	26	13	14	13	4	3	-	0.020	0.008	0.057
10	6116	6	27	7	10	8	13	14	12	-	0.023	0.055
11	Desc	14	27	18	18	16	5	6	5	14	-	0.051
12	3565	34	40	39	36	39	33	37	34	33	31	-

<sup>a</sup>531 = *Descurainia incana* var. *viscosa*; 548 = *D. sophia*; 550 = Pine Butte population of *D. torulosa*; 551 = Lion Bluffs population of *D. torulosa*; 552 = Breccia Cliffs population of *D. torulosa*; fer = Brooks Lake population of *D. torulosa*; 696 = *D. pinnata* var. *filipes*; 1124 = *D. pinnata* var. *brachycarpa*; 4822 = *D. incana* var. *incana*; 6116 = *D. pinnata* var. *nelsonii*; Desc = *D. incana* var. *incana*.



the short pedicel is very nearly diagnostic for *D. torulosa*. However, individual specimens of *D. incana* have been encountered that have pedicels as short as 3 mm.

*Descurainia torulosa* exhibits an interesting disjunct distribution. The north and south populations appear to occupy distinctly different habitats. The southern populations are located in the Green Basin, the northern populations associated with the Absaroka Mountains (Knight 1994), and the major vegetation types in these regions are quite different. If, however, the physical aspects of populational microhabitats are considered, these disjunct populations are not so different. The north-south disjuncts occupy a similar elevational range, but more specifically, the microhabitats are very similar. These populations are found at the base of cliffs in a narrow zone where the cliff face above provides a somewhat sheltering alcove. The rooting substrates for these populations, consisting of exfoliated, coarsely textured rock materials from the cliff, are also physically similar. Overall, the observable microhabitat similarities for the north and south disjunct populations of *D. torulosa* are striking.

In conclusion, morphological evidence does not support recognizing *D. torulosa* as a species distinct from *D. incana*. There is no single unequivocal diagnostic character or suite of characters that serve to distinguish *D. torulosa* from *D. incana*. Furthermore, molecular data presented here indicate that *D. torulosa* is part of a complex that includes morphological entities currently placed in both *D. incana* and *D. pinnata*. The taxonomic status of *D. torulosa* is not resolved, and modern revisionary study of the North American elements of *Descurainia* is needed before resolution of the issue can be clarified. The increased morphological sample evaluated in this study, in concert with molecular data, suggest that *D. torulosa* is more appropriately treated at the infraspecific level. However, until species concepts and relationships within *Descurainia* are better clarified, the question of how to best treat *D. torulosa* (e.g., place in synonymy, treat as an infraspecific taxon, or as distinct species) must wait.

#### SPECIMENS EXAMINED

**Fremont Co.:** Wind River Range, near Brooks Lake, 2 mi NW of lake, 10,000 ft, 8

July 1966, *R.W. Scott 761*, (Holotype: GH, Iso-type: RM); southern Absaroka Mts, Continental Divide ridge ca 1.3–2 mi NW of Brooks Lake and 0.4 mi W of Upper Jade Lake, ca 2–2.5 air mi NE of Togwotee Pass, 10,080–10,280 ft, 23 July 1990, *H. Marriott 11282* (RM); southern Absaroka Range, E side of Continental Divide ridge, ca 0.4 mi W of Upper Jade Lake, ca 1.3 air mi NW of Brooks Lake, ca 2 air mi NE of Togwotee Pass, 26 July 1996, *Fertig 16913* (RM).

**Park Co.:** Absaroka Range, North Fork Shoshone River drainage, ridge E of Sweetwater Creek, ca 4–5 mi N of US Hwy 14, 16, & 20, 7500–8000 ft, 16 June 1986, *Evert 10062* (RM); Absaroka Range, North Fork Shoshone River drainage, many pinnacled ridges E of Clearwater Creek, ca 3–4 miles N of US Hwy 14, 16, & 20, 7200–8000 ft, 19 June 1986, *Evert 10143* (RM); Absaroka Mt, along Hunter Creek Trail, ca 3 mi E of South Fork Ranger Station, ca 43 mi SW of Cody, ca 8800 ft, 29 July 1989, *Evert 18092* (RM); Absaroka Mts, ca 22 air mi SW of Meeteetse in the vicinity and W of the jet of Middle Fork of Wood River and Beaver Creek, 7500–8300 ft, 26 July 1984, *Kirkpatrick 5049* (RM); Absaroka Range, ca 21 air mi W of Meeteetse, along ridge between the North Fork Pickett Creek and Little Rose Creek up to “peak” 11448, 10,000–11,400 ft, 29 July 1984, *Kirkpatrick 5191a* (RM); Absaroka Range, E of Wapiti Ridge, on ridge between Houlihan and Bobcat Creeks ca 2 air mi SE of Citadel Mt, 8000–9000 ft, 12 July 1996, *R. Hartman 55177* (RM).

**Sweetwater Co.:** N side of Pine Butte, below top of rim, ca 8300 ft, 20 July 1980, *K. Dueholm 10779* (RM); Washakie Basin, N and NW side of Pine Butte, ca 33 air miles SE of Rock Springs, 8500 ft, 21 July 1987, *H. Marriott 10635* (RM); Lion Bluffs at NE end of summit of Quaking Asp Mt, ca 12 air mi SE of Rock Springs, 8300–8400 ft, 22 July 1991, *A. Flinck & H. Marriott 1* (RM); Pine Butte, W exposure along base of cliffs, 7600 ft, 18 July 1997, *J.S. Bricker 549 & G.K. Brown* (RM); Pine Butte, W exposure along base of cliffs, 7600 ft, 18 July 1997, *J.S. Bricker 550 & G.K. Brown* (RM); E terminus of Asp Mt at Lion Bluffs, 18 July 1997, *J.S. Bricker 551 & G.K. Brown* (RM).

**Teton Co.:** Southern Absaroka Mts, base of cliffs at E end of Breccia Cliffs, ca 1.9 air mi NNW of Togwotee Pass, 10,100 ft, 23 July

1990, *H. Marriott 11293*, (RM); southern Absaroka Mts, base of cliffs near W end of Breccia Cliffs, ca 3.6 air mi NNW of Togwotee Pass (N of Lost Lake), 10,500 ft, 27 July 1990, *A. Flinck #1* (RM); southern Absaroka Mts, base of cliffs at W end of Sublette Ridge, ca 0.6 mi W of Togwotee Pass, 20 July 1997, *J.S. Bricker 552 & G.K. Brown* (RM); southern Absaroka Mts, base of cliffs at W end of Sublette Ridge, ca 0.6 mi W of Togwotee Pass, 20 July 1997, *J.S. Bricker 553 & G.K. Brown* (RM).

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## INTERSPECIFIC DIFFERENCES IN GRASS SEED IMBIBITION

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**ABSTRACT.**—Seeds from 12 grass species were studied relative to mode of wetting and time of exposure to water to document interspecific differences in imbibition characteristics. Imbibition causes seeds to become wet, and wet seeds are more detectable to consumers than dry seeds. Thus, germination potential and ability to remain undetected by consumers may represent an important trade-off. Seeds wetted for 0–192 h in vials imbibed water at rates equivalent to seeds wetted by contact with wet paper towels pressing against their seed coat, except for seeds of *Avena sativa*, which weighed more after wetting in 2-mL vials with free water (0.471 g vs. 0.432 g). Seeds from different species imbibed water at different rates. These data show that interspecific variation in imbibition for seeds is high and support an expectation that imbibition potential can interact with detectability to consumers in an evolutionary trade-off.

*Key words:* consumers, depredation, detectability, grass seed, imbibition, olfaction, volatile compounds.

Seeds are an important resource in ecosystems of the Intermountain western United States, serving as plant reproductive units and food resources for consumers. Rodents are adept at locating seeds in soil by olfaction (Howard and Cole 1967, Howard et al. 1968, Lockard and Lockard 1971, Reichman 1981, Vander Wall 1998). In their dual role as reproductive units and food sources, seeds are potentially excellent subjects for studying evolutionary trade-offs and interactions between biota.

The distribution of seeds in the environment is spatially and temporally variable (Nelson and Chew 1977, Reichman 1984, Jorgensen 1996). Therefore, the ability of seeds to survive and germinate is dependent upon spatial and temporal foraging characteristics of consumers (Price and Reichman 1987), particularly in arid lands. However, detectability and subsequent survivorship of seeds is more than a function of their distribution and the foraging characteristics of consumers. Vander Wall (1995, 1998) observed that rodents more easily found wet-seed caches than dry-seed caches, locating 449 of 450 wet-seed caches but only 60 of 450 dry-seed caches. Seeds release volatile compounds (Fielding and Goldsworthy 1982, Zhang et al. 1993) that are apparently detectable to rodents (Simon and Raja Harun 1972). Therefore, it may be expected that plant species with hydrophobic

seeds would be able to avoid detection by consumers, thereby increasing their survivorship. However, even hydrophobic seeds need to imbibe water to germinate.

Germination depends, in part, on exposure to water in the substrate. Imbibition (the adsorption of water by nonliving or senescent materials and subsequent swelling caused by adhesion of the water to internal surfaces of materials) is the initial step in germination (Bradford 1995). Vertucci and Leopold (1984) found that soybean (*Glycine max*) seeds fully dried from initial water contents of <24% were severely damaged, whereas soybean seeds fully dried from initial water contents of >24% were only slightly affected. Thus, seeds that imbibe water slowly, or to a low level of seed moisture, may be damaged and display reduced germination ability compared with seeds that imbibe water quickly or to saturation. Therefore, it may be expected that seeds would either easily imbibe water and thereby be detectable to consumers, or strongly resist imbibition and thereby suffer possible tissue damage and reduced ability to germinate.

Seeds must imbibe water to germinate, but imbibition may also make seeds detectable to consumers and susceptible to depredation. There may be a trade-off between imbibition characteristics and the ability to remain hidden from consumers. Hart et al. (1959) and Christian and Lederle (1984) demonstrated

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that seeds from different species contain different amounts of water at the same relative humidity. Additionally, we hypothesize that seeds will exhibit interspecific variation in their relative ability to imbibe or resist water. In part, such a response may be based upon competition between seed adaptations to germinate and adaptations to resist detection by consumers. A 1st step toward investigating this question is documentation of seed imbibition response under different wetting conditions, particularly comparing how repeatable laboratory methods (seeds wetted en mass in 2-mL vials) may compare to conditions that better approximate those experienced by seeds in soil (seeds wetted by paper towels pressing against their seed coat). Finally, we measured the imbibition characteristics of seeds from 12 grass species from the Intermountain western United States relative to time of exposure to water in an effort to detect and measure interspecific differences.

#### METHODS

We investigated imbibition characteristics of seeds from 12 species of grass common to the Intermountain western United States (states where seeds were actually collected are identified in Table 1) relative to mode of wetting and imbibition rate during June and July 1997. Seeds were supplied by Granite Seed Company, Lehi, Utah, and were dried appropriately for storage. Experiments were con-

ducted on seed samples weighed to the nearest 0.001 g with a digital balance, with each sample comprising 10 individual seeds. Wetting experiments were conducted using water purified by reverse osmosis. All analyses were conducted with SPSS for Windows (Norusis 1993), and multiple comparisons were conducted with the LSD test.

To investigate imbibition in an ecologically relevant way (i.e., seeds wetted by moist soil pressing against their seed coat), we mimicked the soil environment by wrapping seeds in paper towels and placing them in the bottom of tubs with sufficient free water to ensure saturation; seeds in tubs were pressed against the paper towel with sponges placed under a 2nd tub that was partially filled with water. We compared mass between 10 dry-seed samples, 10 samples wetted in 2-mL vials, and 10 samples wrapped in paper towels. Wetting was conducted overnight for times ranging between 16 and 20 h. Wetted samples were pat-dried with paper towels to remove free water immediately before weighing. One-way analysis of variance was used to compare dry, vial-wetted, and paper-towel-wetted seed mass. The assumption of normality was assessed using the Shapiro-Wilk test, and heteroscedasticity was assessed using Levene's test.

To measure the effect of time of exposure, we used only samples in vials. Percent mass gain was compared for 5 samples each, from the same 12 grass species used in the 1st experiment, wetted for times ranging from 0 (weighed

TABLE 1. Mean mass (g) of 10 samples of 10 seeds each from 12 grass species from the western United States (State) under 3 conditions of exposure to water (unwetted [Dry], wetted in a vial [Vial], wetted in contact with wet paper towels [Towel] for 16–20 h), and probability of equality ( $P$ ). Values accompanied by the same superscript in the same row are not different.

Species	State	Exposure			$s_{\bar{x}}$	$P$
		Dry	Vial	Towel		
<i>Achnatherum hymenoides</i>	CO	0.048 <sup>b</sup>	0.059 <sup>a</sup>	0.058 <sup>a</sup>	0.001	0.000
<i>Agropyron dasystachyum</i>	WA	0.039 <sup>b</sup>	0.056 <sup>a</sup>	0.051 <sup>a</sup>	0.002	0.000
<i>Andropogon gerardii</i>	TX	0.019 <sup>b</sup>	0.038 <sup>a</sup>	0.038 <sup>a</sup>	0.002	0.000
<i>Agropyron intermedium</i>	WA	0.063 <sup>b</sup>	0.110 <sup>a</sup>	0.109 <sup>a</sup>	0.005	0.000
<i>Agropyron spicatum</i>	WA	0.053 <sup>b</sup>	0.087 <sup>a</sup>	0.085 <sup>a</sup>	0.003	0.000
<i>Avena sativa</i>	UT	0.308 <sup>c</sup>	0.471 <sup>a</sup>	0.432 <sup>b</sup>	0.014	0.000
<i>Bromus biebersteinii</i>	WA	0.069 <sup>b</sup>	0.092 <sup>a</sup>	0.091 <sup>a</sup>	0.001	0.000
<i>Hordeum brachyantherum</i>	CA	0.068 <sup>b</sup>	0.129 <sup>a</sup>	0.129 <sup>a</sup>	0.006	0.000
<i>Hordeum vulgare</i>	UT	0.386 <sup>b</sup>	0.568 <sup>a</sup>	0.570 <sup>a</sup>	0.017	0.000
<i>Secale cereale</i>	SD	0.240 <sup>b</sup>	0.354 <sup>a</sup>	0.347 <sup>a</sup>	0.011	0.000
<i>Stipa neomexicana</i>	AZ	0.187 <sup>b</sup>	0.221 <sup>a</sup>	0.218 <sup>a</sup>	0.003	0.000
<i>Triticum arvense</i>	UT	0.496 <sup>b</sup>	0.708 <sup>a</sup>	0.727 <sup>a</sup>	0.020	0.000

immediately after wetting) to 192 h (8 d). Seeds were pat-dried to remove free water immediately before weighing. The effects of species and wetting time were analyzed with a 2-way factorial analysis of variance. Data were square-root transformed to near normality (Johnson and Wichern 1992), and the homoscedasticity assumption was assessed using Levene's test.

## RESULTS

For all species, exposure to water for 16–20 h resulted in seeds that weighed more than dry seeds (Table 1). However, only for *Avena sativa* did mass differ between vial-wetted and paper-towel-wetted seeds (0.471 g vs. 0.432 g; *F*-test,  $P < 0.00$ ; LSD test,  $P = 0.019$ ; Table 1). *Agropyron dasystachyum* (*F*-test,  $P < 0.000$ ; LSD test,  $P = 0.070$ ) and *Triticum arvense* (*F*-test,  $P < 0.000$ ; LSD test,  $P = 0.096$ ) vial-wetted and towel-wetted seeds were marginally different (Table 1).

Species imbibed water at different rates ( $P < 0.000$ ; Figs. 1, 2, 3) when wetted for times ranging between 1 and 192 h (1, 2, 3, 4, 5, 6, 7, 8, 9, 24, 48, 72, 96, 120, 144, 168, 192 h;  $P < 0.000$ ). Imbibition varied widely between species, resulting in maximum mass gains ranging from 23% for *Stipa neomexicana* to 305% for *Agropyron dasystachyum* after 8 d.

## DISCUSSION

We began this study by documenting that seeds wetted in vials imbibed water at rates equivalent to seeds wetted by contact with wet paper towels. The inclusion of dry seeds in this experiment increases the statistical power of the analysis, thereby increasing the chance of detecting a difference between vial-wetted and paper-towel-wetted seeds. Even with this bias, we detected no tendency for seeds to increase in mass to a greater extent when wetted pressing against paper towels. A difference was observed only for *Avena sativa*, and its seeds were actually wetted more efficiently in vials (Table 1). We regard this experiment as an important piece of methodological documentation. Therefore, by showing that vial-wetted seeds achieved equivalent mass compared to paper-towel-wetted seeds, we offer a measure of confidence that the succeeding experiments are good models of naturally occurring phenomena.

Seeds displayed wide interspecific variation in their ability to imbibe water (Figs. 1, 2, 3). We believe this is attributable to structural adaptations that regulate imbibition (Boesewinkel and Bouman 1995). Immediately upon wetting, seeds gain some mass. Observations ranged from 1.7% mass gain for *Achnatherum hymenoides* to 24.8% mass gain for *Andropogon gerardii*. This immediate mass gain is probably caused by adhesion to the surface of the seeds. The point of this is that not all mass gain is due to imbibition. Some mass gain is simply due to water adhering to the seed surface, and the amount apparently varies by species. Mass gain attributable to adhesion was subtracted from our samples prior to analysis.

*Andropogon gerardii* mass increased immediately (due to adhesion) but then plateaued through 9 h of imbibition (Fig. 1). *Stipa neomexicana* (Fig. 2) imbibed the least amount of water, followed by *Achnatherum hymenoides* (Fig. 1) and the 4 grain species (Fig. 3). Finally, the 4 grain species appeared to display substantially less sample-to-sample variation in their imbibition characteristics than the other species (Figs. 1, 2, 3).

At the beginning of this experiment, we hypothesized that seeds from various plant species would display interspecific differences in imbibition characteristics because of a trade-off between ability to remain undetected by consumers (Vander Wall 1995; i.e., remain dry) and ability to germinate, driven in part by a need to imbibe water. These data provide ample support for this hypothesis.

Somewhat unexpectedly, there was wide sample-to-sample variation in percent mass gain for some species. For instance, after 8 d of exposure *Agropyron dasystachyum* displayed mass gains ranging between 115% and 305% (Fig. 1). Similar variation is clearly evident for other species (Figs. 1, 2). However, it is also apparent that sample-to-sample variation for the 4 grain species (Fig. 3) appears to be less than for the other species. It is possible that this sample-to-sample variation may be caused by genotypic or phenotypic differences between individual seeds (McGinley et al. 1987, Roach and Wulff 1987). Also, seed mass is highly variable within some species (Kranntz 1997), and this may affect imbibition. The relative lack of variation observed for grain species may be attributable to a lack of genotypic or phenotypic variation caused by selective breeding. If

## Small Seeds

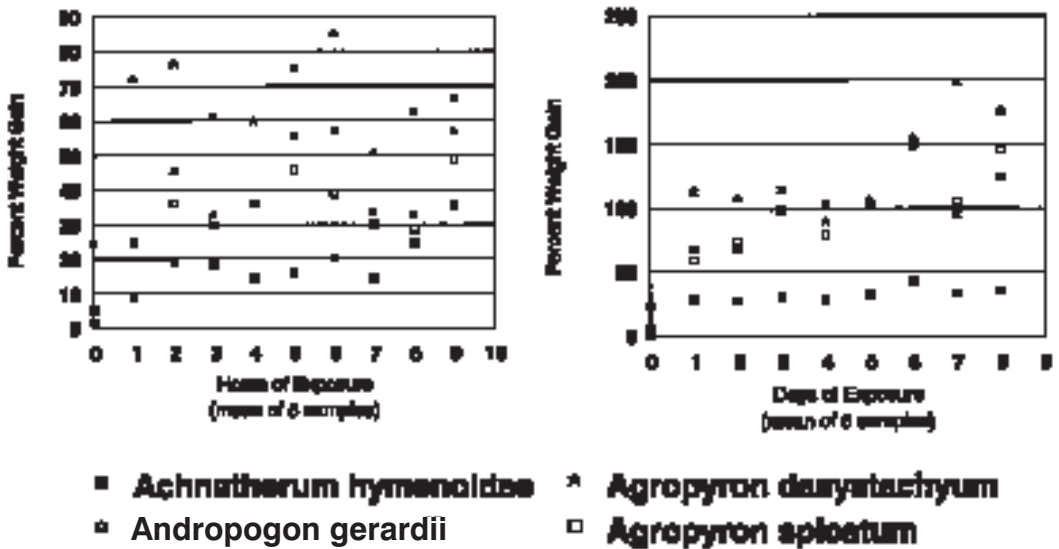


Fig. 1. Percent mass gain as a function of hours of exposure (left) and days (right) to water for seeds from 4 grass species with small-sized seeds. Data points from the hours of exposure experiment are mean mass gain from 5 samples of 10 seeds each; data points from the days of exposure experiment are mass gain of individual 10-seed samples. Note different ordinate scales.

## Medium Seeds

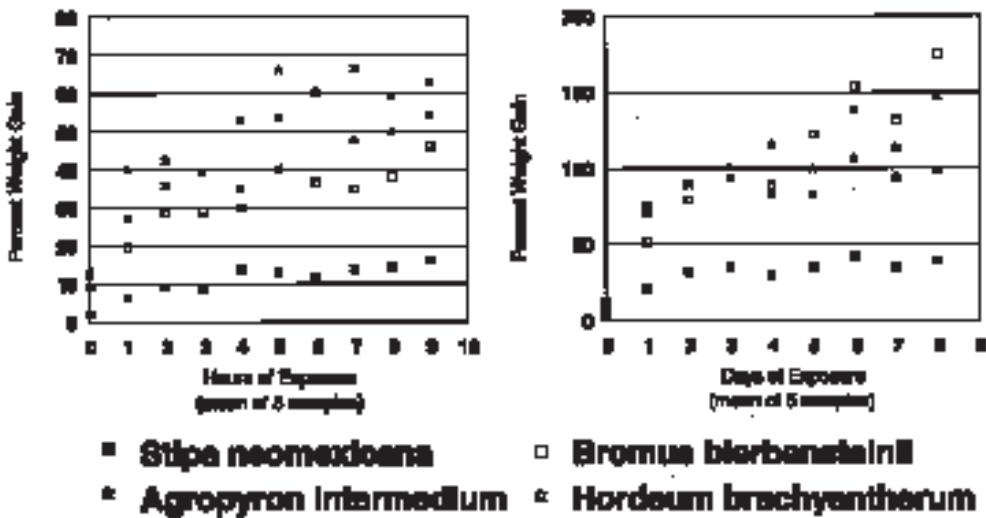


Fig. 2. Percent mass gain as a function of time of exposure to water for seeds from 4 grass species with medium-sized seeds. Data point descriptions are as in Figure 1. Note different ordinate scales.

## Grain Crop - Large Seeds

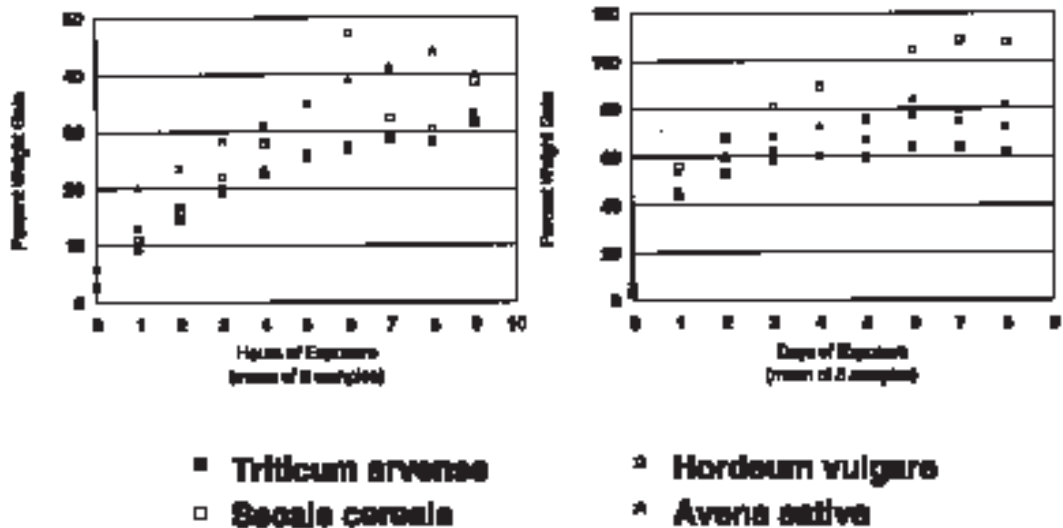


Fig. 3. Percent mass gain as a function of time of exposure to water for seeds from 4 grain crops (grasses) with large-sized seeds. Data point descriptions are as in Figure 1. Note different ordinate scales.

the observed differences are attributable to genotypic or phenotypic differences, then these data suggest that individual seeds are important, and their survival is very much under the influence of natural selection.

Because small mammals are important consumers of seeds (Chew and Chew 1970, Sohlt 1973, Price and Joyner 1997), the interaction between them and seed resources is an important concern in ecology, particularly in arid lands. The dual role of seeds as plant reproductive units and food for primary consumers justifies the interest. It is clear that seeds are unevenly distributed in the ecosystem (Reichman 1984, Jorgensen 1996). This may influence small mammal foraging (Reichman 1981, Price and Reichman 1987) and may influence microhabitat use (e.g., Price 1978). However, Vander Wall's (1995, 1998) results illustrate that seeds interact with the ability of rodents to find them in the soil. Our results demonstrate that imbibition of seeds varies between species. These differences could result from our hypothesized trade-off between the ability to remain undetected to consumers and the ability to germinate. Other factors, such as dispersal ability (Donohue 1997, Lord et al. 1997), may

also be involved by interacting with imbibition characteristics to affect seed survival.

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## ECOLOGICAL IMPACTS OF SEED HARVESTER ANTS ON SOIL ATTRIBUTES IN A *LARREA*-DOMINATED SHRUBLAND

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**ABSTRACT.**—The influence of seed harvester ant (*Pogonomyrmex rugosus*) colonies on soil properties and soil surface and moisture characteristics was investigated through comparison of adjacent, nonnest (reference, 4 m beyond ant colony) areas in Las Vegas, Nevada. Effects of ant colonies on both terrace and slope sites were investigated. Soil moisture content and soil bulk density in a creosote bush (*Larrea tridentata*)–dominated shrubland were significantly lower, while soil temperature, soil organic matter, and percent pore space were significantly higher in soils with ant nests relative to adjacent reference soils. Soil pH and texture did not differ significantly between nest and reference soils. Among soil surface characteristics, percent bare soil and rock (gravel, cobble, and boulder) cover were not significantly different between nest and reference soils. In evaluating soil moisture characteristics, soils with ant nests had a significantly higher water infiltrability and greater depth of water penetration, but a significantly lower area of water spread (surface-water runoff) at both terrace and slope sites. Between the 2 geomorphic surfaces, water infiltrability and depth of water penetration were significantly greater at the terrace than at the slope. Water-borne soil movement (fluvial erosion) was significantly greater at the slope than terrace but did not differ significantly between nest and reference soils. The presence of active *P. rugosus* colonies in the *L. tridentata*–dominated shrubland altered certain soil properties and appeared to have a protective influence on the soil by fostering more infiltration and less runoff of surface water in southern Nevada.

*Key words:* *Pogonomyrmex rugosus*, nests, colonies, soil properties, soil surface, soil moisture, geomorphic surfaces, terrace, slope, *Larrea tridentata*, Las Vegas, southern Nevada.

The seed harvester ant (*Pogonomyrmex rugosus* Emery) occurs in arid and semiarid plant communities throughout much of the southwestern United States (Carlson and Whitford 1991). *Pogonomyrmex rugosus* nests are often surrounded by conspicuous clearings from which the ants have removed vegetation. Soils of subterranean *Pogonomyrmex rugosus* have lower bulk density, higher water infiltrability, and higher organic matter content than surrounding soils in New Mexico (Whitford 1988). The western harvester ant (*P. occidentalis*), a closely related species, also affects soil properties in New Mexico by reducing soil pH, bulk density, and moisture content and by increasing soil salinity and organic matter (Carlson and Whitford 1991). Subterranean ants may also alter soil texture, affect soil pore size, and cause localized accumulations of organic and inorganic nutrients in ponderosa pine (*Pinus ponderosa*) and pinyon pine–Utah juniper (*Pinus monophylla*–*Juniperus osteosperma*) woodlands in New Mexico (Carlson and Whitford 1991).

The xerophytic creosote bush–white bursage (*Larrea tridentata*–*Ambrosia dumosa*) shrub-

land is a common vegetation type in southern Nevada, and yet the extent of ant nest influence on soil properties, as well as on soil surface and moisture characteristics, remains poorly understood. The presence of 217 ant colonies located in a 10-ha site appears to have localized influences on soil surface variables and soil moisture status in southern Nevada. The objectives of this study were to determine if subterranean *P. rugosus* activity significantly alters soil attributes in a *Larrea tridentata*–dominated shrubland in southern Nevada. Two questions were addressed: (1) Do various properties and surface (bare soil and rock) characteristics of nest soils differ from adjacent reference (nonnest) soils? (2) Do ant activities alter the moisture status of nest soils compared to adjacent reference soils on 2 distinct geomorphic surfaces (terrace and slope)?

### METHODS

#### Study Site

The study site is in Henderson, Clark County, Nevada (roughly 36°00'N, 115°00'W; elevation 750 m). This site is dominated by

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xerophytic *L. tridentata* shrubs. Other woody taxa are sparsely distributed, including white bursage (*Ambrosia dumosa*), ratany (*Krameria parvifolia*), winterfat (*Eurotia lanata*), golden-head (*Acamptopappus shockleyi*), Mojave yucca (*Yucca schidigera*), indigo bush (*Psoralea argemone*), and brittle bush (*Encelia virginensis*). Several species of cacti (*Opuntia* spp.) are also present in low abundance in this vegetation zone. Soils are sandy in texture and calcareous with abundant loose rocks on the surface. Soils are derived from nearby limestone-dolomite mountains and hills (Rowlands et al. 1977).

Although the Las Vegas valley is an area of primarily winter and summer rainfalls, total amount of annual precipitation varies considerably from year to year. Rainfall can last from several hours to several days (Rowlands et al. 1977). Mean annual precipitation ranges from 118 to 183 mm in the *L. tridentata*-*Ambrosia dumosa* shrublands (Beatley 1974). Summer monsoonal rainfalls and storms can sometimes be locally intense. Spring 1997 was extremely arid, with total precipitation of <10.0 mm, falling well below the annual average of 25.4 mm (Climatological Data, Las Vegas). Maximum summer and minimum winter air temperatures range from above 40°C to below 0°C, respectively (Lei and Walker 1997a, 1997b). Relative humidity of 20% or less is common due to a combination of low precipitation, low cloud cover, high evaporation rate, and high air temperature during summer seasons (Lei and Walker 1997a).

#### Field Surveys and Soil Collections

Field surveys were conducted during spring 1997 in southern Nevada. At the time of soil collection, the weather was hot and the soil appeared extremely dry. All 217 *P. rugosus* nests at a 10-ha site were identified. Each ant colony had multiple nest entrances, subterranean chambers (cavities), and tunnels (runways). Diameters of the exposed soil surface (disc) at each ant colony were measured to the nearest centimeter by computing average length and width of the nest. A reference (adjacent, nonnest areas) was established 4 m from the edge in a random direction from each nest.

Soil samples from the 217 nest discs of *P. rugosus* and from adjacent reference points

were excavated approximately 10 cm in diameter to depths of 15 cm. Soil samples were sieved through a 2-mm mesh to remove plant roots and rocks >2 mm in diameter. Soil was defined as <2 mm in diameter, while large particles were not considered soil. Nest soils were collected approximately midway between the disc edge and center of each ant nest. All tests were performed on sieved soils dried at 105°C for 72 h. Soil samples were measured for pH, percent moisture, bulk density, compaction, percent pore space, organic matter, and texture.

#### Laboratory and Statistical Analyses

Soil moisture was determined gravimetrically by calculating the difference between fresh and oven-dried mass. Soil temperature readings were taken in the field at the soil surface (0 cm) and at 15 cm below the soil surface on ant colonies and reference points. To measure bulk density, a core of soil of known volume was carefully removed from the field. Fresh soil cores were oven-dried at 105°C until they reached a constant mass. Soil cores were then weighed, dividing dry mass by volume to determine soil bulk density. Soil compaction was estimated using a penetrometer inserted into the soil. Average pore space was determined using the equation:

$$\text{pore space (\%)} = 100 - (D_b/D_p * 100),$$

where  $D_b$  is bulk density of the soil and  $D_p$  is average particle density, usually about 2.65 g cc<sup>-1</sup> (Hausenbuiller 1972, Davidson and Fox 1974). Soil organic matter was obtained by mass loss on ignition at 550°C for 4 h. Soil pH was measured by preparing a paste consisting of a ratio of 1:1 soil:distilled water mixture and by measuring with an electrode pH meter. Soil salinity (total soluble salts) was determined by a Beckman electrical conductivity bridge. A slurry consisting of equal parts of soil and distilled water paste was used to determine total soluble salts. Soil particle size distribution was determined by the hydrometer method as described by Bouyocoucos (1951).

For each ant nest and reference area, soil surface characteristics of bare ground, gravel (2–64 mm in diameter), cobble (65–256 mm), and boulder (>256 mm) were visually quantified using 10% increments.

Water infiltration rates were measured by using PVC pipe, 5.5 cm in diameter and 9.5 cm tall. This pipe was open at both ends and was gently tamped into the disc and reference soils to a depth of 2 cm to prevent leakage, and then 50 mL of water was poured into the pipe. Time taken for the water to disappear completely into the soil surface was recorded with a stop-watch.

Approximately 1.5 L of water, acting as an artificial rain, was manually poured through a perforated 13-cm disk, with perforations being evenly spaced on a 0.1-cm grid. The disk was placed 1.0 m aboveground. Total delivery time was 1 min for the water to be dispensed on the nest or soil surface and to create precipitation at a cloudburst level (Brotherson and Rushford 1983). A sudden heavy precipitation is significant due to its impact on surface-water runoff and fluvial erosion. Depth of water penetration was measured once the water had soaked into the soil.

Surface-water runoff was measured by recording the downslope and across-slope spread of water that was artificially rained onto study sites (Brotherson and Rushforth 1983). The area of water spread from these 2 slope measurements was computed using the formula for the area of an ellipse.

Soil movement was assessed by estimating the amount of soil moved through fluvial erosion during a measured rain. The following index was used: 1 = no appreciable movement; 2 = moderate movement, up to 10% of soil being displaced; and 3 = heavy movement, between 10% and 20% of soil being displaced (Brotherson and Rushforth 1983).

Paired *t* tests (Analytical Software 1994) were performed to compare differences between properties, surface characteristics, and moisture status of disc (nest) and adjacent reference soils. Student's *t* tests (Analytical Software 1994) were conducted to compare differences between terrace and slope habitats (geomorphic surfaces). Mean values are presented with standard errors, and statistical significance was determined at the 5% level.

## RESULTS

Mean distance between ant nests and nearest shrubs was  $164.0 \pm 15.6$  cm. Mean ant nest diameter was  $88.9 \pm 10.7$  cm ( $n = 217$ ). Moisture content, bulk density, and compaction of

nest soils decreased ( $P \leq 0.05$ ; Table 1) compared to adjacent reference soils in the *L. tridentata*-dominated shrubland. However, percent pore space, soil organic matter content, and soil temperatures increased ( $P \leq 0.05$ ) in nest soils compared to reference soils. Soil pH, salinity, and texture (percentages of sand, silt, and clay) did not differ between nest and reference soils ( $P > 0.05$ ; Table 1).

Percent bare soil and rock (gravel, cobble, and boulder) cover did not differ ( $P > 0.05$ ; Table 2) between nest and reference soils. A relatively high percent ground cover of bare soil and a low percent cover of rock were observed in both nest and reference soils.

Moreover, nest soils increased ( $P \leq 0.01$ ; Table 3) the water infiltration rate and depth of water penetration during a measured rain compared to reference soils at both terrace and slope habitats. Between the 2 geomorphic surfaces, infiltration rates ( $t = -10.38$ ,  $df = 216$ ,  $P \leq 0.0001$ ) and depth of water penetration ( $t = 7.06$ ,  $df = 216$ ,  $P = 0.0001$ ) were greater in terrace than slope habitat. However, nest soils decreased the area of water spread as well as the downslope and across-slope water spread (surface-water runoff) in both geomorphic surfaces during the artificial rain ( $P \leq 0.05$ ; Table 3). Water-borne soil movement (fluvial erosion) was reduced at terrace habitat compared to slope habitat ( $t = -4.04$ ,  $df = 216$ ,  $P = 0.003$ ). Yet, fluvial erosion did not differ between nest and reference soils despite the occurrence of a minor fluvial erosion in both soils ( $P > 0.05$ ; Table 3).

## DISCUSSION

*Pogonomyrmex rugosus* colonies alter certain soil properties as well as soil surface and moisture characteristics in southern Nevada. Viable *P. rugosus* nests modified a number of edaphic parameters.

Water relations of *P. rugosus* colonies are not well documented. Soil moisture is an important source of colony water, and workers have clear preferences for moist soil (Rissing 1988). *Pogonomyrmex rugosus* conserves soil moisture by removing transpiring plants (Rissing 1988). However, soil moisture content declines significantly in nest soils compared to adjacent reference soils (Table 1). Low moisture content in nest soils is expected if changes in vegetation cover and evapotranspiration rates

TABLE 1. Chemical and physical properties (mean  $\pm$   $s_{\bar{x}}$ ,  $n = 217$ ) of ant nest and adjacent reference (nonnest, 4 m beyond nest) soils in the *L. tridentata*-dominated shrubland. Soil moisture, organic matter, and texture (sand, silt, and clay) are expressed in percentages.

Soil property	Ant nest	Reference	Paired <i>t</i> test	
			<i>t</i> -value	<i>P</i> -value
Moisture (%)	1.1 $\pm$ 0.3	1.8 $\pm$ 0.4	-10.82	0.0000
Temperature ( $^{\circ}$ C)				
At soil surface	24.7 $\pm$ 1.2	22.9 $\pm$ 0.8	3.59	0.0058
At 15 cm below	26.3 $\pm$ 0.7	24.4 $\pm$ 0.5	3.72	0.0048
Bulk density (g cm <sup>-3</sup> )	1.3 $\pm$ 0.1	1.5 $\pm$ 0.1	-6.00	0.0002
Compaction (g cm <sup>-2</sup> )	6.0 $\pm$ 0.3	6.8 $\pm$ 0.3	-3.87	0.004
Pore space (%)	47.2 $\pm$ 4.6	43.4 $\pm$ 3.1	11.11	0.0000
Organic matter (%)	3.1 $\pm$ 0.4	2.4 $\pm$ 0.2	8.80	0.0000
pH	7.8 $\pm$ 0.1	7.9 $\pm$ 0.1	-1.34	0.213
Salinity (mmho cm <sup>-1</sup> )	0.3 $\pm$ 0.03	0.3 $\pm$ 0.01	-0.50	0.626
Sand (%)	77.6 $\pm$ 1.4	78.7 $\pm$ 1.5	-2.19	0.056
Silt (%)	19.3 $\pm$ 1.2	19.5 $\pm$ 1.0	-2.24	0.052
Clay (%)	3.1 $\pm$ 0.3	2.8 $\pm$ 0.2	2.09	0.066

TABLE 2. Percent ground cover of bare soil, gravel, cobble, and boulder (mean  $\pm$   $s_{\bar{x}}$ ,  $n = 217$ ) in ant nest and adjacent reference (nonnest, 4 m beyond nest) soils in the *L. tridentata*-dominated shrubland.

Soil surface variable (%)	Ant nest	Reference	Paired <i>t</i> test	
			<i>t</i> -value	<i>P</i> -value
Bare soil	35.6 $\pm$ 4.2	32.3 $\pm$ 3.8	1.57	0.151
Gravel	48.7 $\pm$ 4.7	52.1 $\pm$ 3.1	-1.81	0.104
Cobble	11.0 $\pm$ 1.4	10.2 $\pm$ 1.1	2.09	0.066
Boulder	4.7 $\pm$ 0.1	5.4 $\pm$ 0.1	-2.10	0.065

TABLE 3. Moisture characteristics (mean  $\pm$   $s_{\bar{x}}$ ,  $n = 217$ ) of ant nest and adjacent reference (nonnest, 4 m beyond nest) soils on 2 distinct geomorphic surfaces in the *L. tridentata*-dominated shrubland.

Moisture parameter	Ant nest	Reference	Paired <i>t</i> test	
			<i>t</i> -value	<i>P</i> -value
Infiltration (seconds)				
Terrace	184.7 $\pm$ 11.7	212.4 $\pm$ 10.3	-5.78	0.0000
Slope	239.1 $\pm$ 12.5	263.9 $\pm$ 11.8	-5.04	0.0000
Depth of water penetration (cm)				
Terrace	3.7 $\pm$ 0.02	3.0 $\pm$ 0.01	7.13	0.0001
Slope	3.1 $\pm$ 0.01	2.4 $\pm$ 0.01	7.36	0.0000
Downslope spread (cm)				
Terrace	71.1 $\pm$ 4.2	81.3 $\pm$ 4.1	-4.24	0.0022
Slope	83.8 $\pm$ 5.2	94.0 $\pm$ 4.4	-4.89	0.0002
Across slope spread (cm)				
Terrace	68.6 $\pm$ 4.0	77.5 $\pm$ 4.0	-2.70	0.025
Slope	76.2 $\pm$ 4.2	88.9 $\pm$ 5.4	-3.42	0.008
Area of spread (cm <sup>2</sup> )				
Terrace	3828.8 $\pm$ 435.9	4961.1 $\pm$ 442.0	-14.86	0.0000
Slope	5012.7 $\pm$ 701.3	6560.0 $\pm$ 740.8	-17.23	0.0000
Soil movement				
Terrace	1.2 $\pm$ 0.01	1.3 $\pm$ 0.01	-1.63	0.137
Slope	1.4 $\pm$ 0.01	1.5 $\pm$ 0.01	-1.66	0.132

result from constant ant activities. Reduced water content may be due to numerous tiny openings at nest entrances on the soil surface that dry, aerate, and loosen soils more quickly in *Pinus ponderosa* and *P. monophylla*-*J. osteosperma* stands of New Mexico (Carlson and Whitford 1991).

In this study tiny openings on the soil surface caused by ant activities were also likely to lower soil compaction and bulk density and to raise soil temperature at 15 cm beneath ant colonies. A lack of dense vegetation also increased soil temperatures. Percent pore space increased significantly in nest soils relative to adjacent reference soils (Table 1). Soil excavation by *P. barbatus* (harvester ant) may have increased average soil pore size (Wagner et al. 1997). Sandy soils normally show a range of 35%–50% pore space (Brady 1974), which concurs with this study. Pore space of soils generally contains air and water, and this space consists of macropores that allow ready movement of air and water (Davidson and Fox 1974). The decrease in soil compaction and bulk density, along with the increase in macropore space and soil temperature, may result in greater evaporative losses of soil moisture and less potential storage of soil water at depth.

Soil organic matter was higher in nests than surrounding reference soils (Table 1). In numerous excavations of *P. rugosus* colonies, decomposing plant materials in shallow nest chambers were observed; these would increase organic content of nest soils (Wagner et al. 1997). Elevated organic matter content may relate to accumulation and retention of waste plant materials and, to a lesser extent, turn-overs and metabolic wastes of the ants (Carlson and Whitford 1991). However, soil pH and salinity did not vary significantly between nest and adjacent reference soils (Table 1). Mandel and Sorenson (1982) found no pH difference for *P. occidentalis* mounds that occurred in alkaline soils compared to adjacent reference soils.

Soil texture (percent sand, silt, and clay) also did not vary significantly between nest and reference soils (Table 1), which corresponds with Carlson and Whitford's (1991) study. Despite significant publications and contributions in the past regarding the presence of ants that alter certain soil properties, no comparative data are available because a number of soil physical and chemical properties have

not been measured in the *L. tridentata*-dominated shrublands in southwestern deserts.

A high percentage of bare soil cover and a low percentage of rock cover were observed on the surface of nest and reference soils throughout much of my study site (Table 2). Previous studies of *P. rugosus* in the *L. tridentata*-dominated shrublands did not report rock size and abundance, which are 2 major components of soil surface characteristics in this study. In New Mexico rock content may affect a variety of other soil attributes including infiltration, porosity, water-holding capacity, and erodibility (Carlson and Whitford 1991).

In this study significantly lower compaction and bulk density of nest soils, partially due to subterranean cavities and runways around the nest entrances, improved aeration and water infiltration without regard to geomorphic surfaces (Table 3). Dean and Yeaton's (1993) study in South Africa demonstrated that infiltrability of soils is influenced by many factors: organic matter, pore size, texture, and slope. Higher water infiltrability is expected on ant nests where soils contain significantly more organic matter and are less compacted than reference soils (Dean and Yeaton 1993).

Significantly lower surface-water runoff was detected in nest than surrounding reference soils because nest soils absorbed more water during and shortly after a measured cloudburst in this study (Table 3). Similarly, water disappeared significantly faster into the surface of nest soils than reference soils irrespective of geomorphic surface. Fluvial erosion was significantly greater for the slope than terrace site. A small movement of soil occurred when water traveled rapidly downslope during a cloudburst, perhaps due to a lack of abundant rocks on the soil surfaces. A minor fluvial erosion led to partial destruction of upper portions of vertical subterranean tunnels beneath nest entrances in this study. More surface-water runoff and fluvial erosion would be expected if this cloudburst had a much longer duration, higher frequency, and greater intensity.

The terrace site had significantly greater depth of water penetration compared to the slope site in this study (Table 3). With increased infiltration and reduced surface-water movement, deeper penetration of water into the soil occurs (Brotherson and Rushforth 1983). Viable ant nests appeared to have a protective

influence on the soil in terms of significantly reducing surface-water runoff, enhancing water infiltrability, and increasing depth of water penetration, presumably due to multiple subterranean cavities and runways.

Although the total area covered by active *P. rugosus* colonies is relatively small, localized influences of subterranean *P. rugosus* on soil properties and on soil surface and moisture characteristics are evident. *Pogonomyrmex rugosus* significantly modifies a number of edaphic attributes including soil properties, water infiltration, water storage, and surface-water runoff in the *L. tridentata*-dominated shrubland in southern Nevada.

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## C<sub>3</sub> AND C<sub>4</sub> SPECIES CHANGES IDENTIFIED BY δ<sup>13</sup>C VALUES OF SOIL ORGANIC MATTER IN A COLORADO PRAIRIE

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**ABSTRACT.**—We measured carbon isotope signatures (δ<sup>13</sup>C) from 0–10 cm and 10–20 cm soil depth intervals for grassland soils near Boulder, Colorado. These grasslands included tall-, short-, and mixed-grass prairies that were grazed, ungrazed, or hayed. Soils exhibited δ<sup>13</sup>C signatures consistent with observations that current sites are a mix of C<sub>3</sub> and C<sub>4</sub> species, with C<sub>3</sub> plants more abundant in mixed-grass than in native tall- or shortgrass prairies. The δ<sup>13</sup>C signatures were not significantly different for grassland types; however, management treatments (grazing, no grazing, haying) significantly influenced changes in soil δ<sup>13</sup>C signatures from the 0–10 cm to 10–20 cm soil depth intervals. We observed a correlation ( $r = 0.63$ ) between isotopic values of surface soils and percent native species in total vegetation cover. Overall, the community type with the lowest percentage of nonindigenous species cover had the most enriched δ<sup>13</sup>C signature.

Sites currently grazed by prairie dogs, cattle, or both herbivores had stronger C<sub>3</sub> signatures, indicating that grazing may have increased C<sub>3</sub> plant productivity in these communities at the expense of C<sub>4</sub> grasses. This finding differs from studies of native shortgrass steppe where grazing has the opposite effect on the relative abundance of these 2 functional groups of plants. This result, along with the correlation between C<sub>3</sub> isotopic values and nonnative vegetation abundance, provides evidence that management practices that maintain dominance of C<sub>4</sub> grasses should be encouraged.

*Key words:* δ<sup>13</sup>C, C<sub>3</sub>, C<sub>4</sub>, carbon, grassland, Colorado, prairie.

Human activities have caused wide-scale alteration of grassland communities. Cattle grazing, irrigation, and fire suppression have been practiced along the Front Range of Colorado for about 130 yr. In addition, many nonindigenous plant species have been introduced into the area (Bennett 1997). Increased atmospheric deposition of inorganic nitrogen (Williams et al. 1996), in conjunction with increases in atmospheric CO<sub>2</sub> and climatic changes, are also believed to be influencing ecosystem processes of grasslands that historically contained both C<sub>3</sub> and C<sub>4</sub> species (e.g., Wedin and Tilman 1996, Tieszen et al. 1997).

Bennett (1997) completed a survey of grassland plant communities around Boulder, Colorado, and found higher abundances of C<sub>3</sub> plants in these areas than previously reported (Vestal 1914). The significance of a shift in vegetative composition in temperate grassland from C<sub>4</sub> to C<sub>3</sub> species dominance implies changes in several ecosystem characteristics that affect soil characteristics and subsequent plant species composition and productivity (Seastedt 1995, Wedin and Tilman 1996).

Soil organic matter contains a record of the relative composition of C<sub>3</sub> and C<sub>4</sub> species (O'Leary 1981). Atmospheric CO<sub>2</sub> is composed of approximately 1.1‰ <sup>13</sup>C and 98.9‰ <sup>12</sup>C (O'Leary 1981, Farquhar et al. 1989). During photosynthetic CO<sub>2</sub> fixation, plants discriminate against the heavier isotope, <sup>13</sup>C, while favoring the lighter isotope, <sup>12</sup>C (O'Leary 1988). C<sub>3</sub> plants discriminate against <sup>13</sup>CO<sub>2</sub> to a greater extent than do C<sub>4</sub> plants, resulting in distinctly different ranges of δ<sup>13</sup>C values for C<sub>3</sub> and C<sub>4</sub> plants (O'Leary 1981, Dzurec et al. 1985, Farquhar et al. 1989, Ehleringer et al. 1991, Wang et al. 1993). δ<sup>13</sup>C values for C<sub>3</sub> plants are between –23‰ and –34‰, with an average of –26‰; C<sub>4</sub> plant values are between –9‰ and –17‰ and have an average of –12‰ (O'Leary 1988). Average difference in δ<sup>13</sup>C values between C<sub>3</sub> and C<sub>4</sub> plants is therefore about 14‰ (Dzurec et al. 1985, Wang et al. 1993).

Decomposition further modifies isotopic values. Respiratory CO<sub>2</sub> is lower in <sup>13</sup>C than is soil organic matter, and there is usually a detectable increase in <sup>13</sup>C abundance in older organic matter originating from C<sub>3</sub> sources

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(Nadelhoffer and Fry 1988). Long-term decomposition rates of  $C_3$  and  $C_4$  plant substrates are unknown, which adds some uncertainty to the analyses. However, the relatively large difference in carbon isotope signatures of the 2 plant groups should dominate soil organic matter signatures (Dzurec et al. 1985, Kelly et al. 1993, Boutton 1996). Assuming that soil organic matter is derived from past plant associations and not deposited as loess, we can therefore estimate relative historical  $C_3$  and  $C_4$  species abundances by assuming that the isotopic signature is correlated to relative productivity of each plant group (Dzurec et al. 1985, Wang et al. 1993).

Average age of soil carbon in temperate grassland soils is variable. As a general rule, less than half of soil organic matter is composed of recalcitrant materials, humus, and precursors of humus that may average over 1000 yr in age. The remainder is composed of relatively young material produced in the last decades (Parton et al. 1996). Older carbon is also found deeper in the soil (e.g., Tiezen et al. 1997). Identifying the photosynthetic pathway source of this carbon therefore provides information on the historical composition of the area as well as an indication of how much the current community may differ from the past.

$C_4$  species comprise most native grass species in the Boulder area (Bennett 1997). They have historically dominated both tallgrass and shortgrass prairies and are a significant component of mixed-grass prairie (Brown 1989). We hypothesize that (1) the tallgrass prairie will exhibit the strongest  $C_4$  carbon isotopic signature because this community type is believed to have the strongest dominance of warm-season ( $C_4$ ) grasses; and (2) given that all nonnative plants currently abundant in the Boulder area are  $C_3$  species, we expect the strongest  $C_3$  carbon isotopic signature will be found in nonnative vegetation areas. To test these hypotheses, we used carbon isotope signatures of soil organic matter as an index of change in the community composition of  $C_3$  and  $C_4$  plant species (e.g., Boutton 1991). We also evaluated whether isotopic signatures in the soil would identify functional shifts in vegetation due to grazing and haying activities.

#### STUDY SITE AND METHODS

Plots were sampled in Boulder Open Space grasslands (ca 40°N, 105°W, 1645 m elevation)

used in Bennett's (1997) study of grassland diversity. Precipitation averages about 46 cm per year, and soils are mostly cobbly clay loams or sandy clay loams classified as Aridic Argiustolls (Moreland and Moreland 1975). These grasslands were formed on alluvial and colluvial deposits generated from Pleistocene outwash from the Front Range. Parent materials are of igneous or metamorphic composition and are noncarbonaceous. Shale sites or sites with suspected carbonate materials were excluded from the study. Native vegetation in the area ranges from tallgrass sites dominated by *Andropogon gerardii* ( $C_4$ ) and *Panicum virgatum* ( $C_4$ ), to mixed-grass sites dominated by *Agropyron smithii* ( $C_4$ ), *Stipa comata* ( $C_3$ ), and *Koeleria pyramidata* ( $C_4$ ), and grazed mixed-grass areas with extensive *Bouteloua gracilis* ( $C_4$ ) and *Buchloe dactyloides* ( $C_4$ ). These native grasses are often accompanied or dominated by nonnative  $C_3$  species such as *Bromus* spp., *Poa pratensis*, and *Alyssum minus* (Bennett 1997). Bennett's data were summarized by Craig et al. (in press), who found that tall-, short-, and mixed-grass prairies consisted of 45%, 44%, and 29%, respectively, nonindigenous plant species. Hay meadows on former tall- and mixed-grass prairies averaged 85% nonnative species in terms of percent vegetation cover.

Plots were located in areas that were (1) grazed by cattle, prairie dogs, or both herbivores; (2) hayed; or (3) in enclosures where there was no grazing or haying for about the last decade. We classified plots as either mixed-grass or tallgrass prairie. A subset of the mixed-grass sites had vegetation characteristics consistent with shortgrass steppe, but we lacked sufficient replicates of these sites for a separate analysis.

Soil cores of 1.7-cm diameter to a depth of 20 cm were obtained at each site. Of the 66 plots surveyed by Bennett (1997), only 42 could be sampled in this manner. Sites with shale substrate were excluded from analysis because of high  $CaCO_3$  content. We assumed there was very little or no  $CaCO_3$  at sites with soils derived from noncarbonaceous parent material. Each soil core was divided into samples 0–10 cm deep and 10–20 cm deep. Soil samples were air-dried, and the dry soil was shaken onto a series of increasingly smaller-diameter sieves. Visible particulate debris such as



roots and rocks was manually removed. Samples were ground to a fine powder and combusted in a VG Isochron mass spectrophotometer to measure the amount of  $^{13}\text{C}$  present.

Results here are expressed in standard  $\delta^{13}\text{C}$  notation where

$$\delta^{13}\text{C}\text{‰} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3$$

and  $R = ^{13}\text{C}/^{12}\text{C}$  (Craig 1957). All samples are reported relative to the international PDB standard (O'Leary 1988). Repeated measurements of a soil standard yielded a precision of 0.1‰. We performed two 2-way analysis of variance (ANOVA) procedures to test for isotopic differences attributable to grassland type and land use treatment. We compared average isotopic value for the entire 20-cm profiles (weighted equally for each horizon) in 1 analysis, and in the 2nd we tested for changes in  $\delta^{13}\text{C}$  values between the 0–10 cm and 10–20 cm cores related to grassland type and land use effect. This 2nd test assumed that larger differences in the top-to-bottom  $\delta^{13}\text{C}$  values would potentially identify more recent changes in the functional composition of grasslands. Younger carbon is assumed to dominate surface horizons, while older, more recalcitrant forms of carbon occupy lower horizons (Nadelhoffer and Fry 1988). We used the Student-Newman-Keuls multiple range test when significant differences were detected to identify cell differences in land use type (SAS 1988).

We also used a Pearson's correlation analysis to relate our soil isotope values with summary findings from Bennett's (1997) vegetation analysis. Isotopic values from each plot were correlated with the value of native plants as percent of total vegetation cover.

## RESULTS

The 0–10 cm depth interval averaged  $\delta^{13}\text{C}$  values of about  $-21\text{‰}$ , with a range from  $-16.3\text{‰}$  to  $-23.8\text{‰}$ , while soils at lower depths exhibited a less negative  $\delta^{13}\text{C}$  signature and ranged from  $-13.8\text{‰}$  to  $-22.7\text{‰}$  (Table 1). Surprisingly, soils with the highest  $^{13}\text{C}$  content were from ungrazed mixed-grass sites. Grazed mixed-grass sites with or without prairie dogs, or sites identified as potential shortgrass sites, all showed similar values (Table 1).

Hay meadows are dominated by nonnative  $\text{C}_3$  grasses (Bennett 1997) and therefore were expected to have a stronger  $\text{C}_3$  influence than soils of native grasslands; this trend was evident (Table 1). Grazing also produced significantly different  $\delta^{13}\text{C}$  values than ungrazed sites (SNK test; Fig. 1). Isotope values of grazed mixed-grass sites indicated a larger  $\text{C}_3$  increase than did grazed tallgrass sites (Fig. 1), which produced a marginally significant ( $P = 0.06$ ) interaction effect between treatment and prairie type.

Differences in isotopic abundance between upper (0–10 cm) and lower (10–20 cm) soil depths showed no effect due to plant community type, but did show a significant effect of treatment type ( $F_{2,36} = 9.94$ ,  $P < 0.001$ ) and a strong interaction effect ( $F_{2,36} = 5.53$ ,  $P = 0.008$ ) between community and treatment. Of the plant communities, tallgrass prairie showed the largest changes in isotopic abundance between upper and lower soil depths (Table 1). While this difference for tallgrass communities was maximized for hay meadows, the difference was minimized in hay meadows of mixed-grass sites, thereby producing the interaction (Table 1).

TABLE 1. Carbon isotope signatures from 0–10 and 10–20 cm deep soil samples from grasslands near Boulder, Colorado. Values are means with standard errors in parentheses.

Grassland	Treatment	Number of samples	Soil depth (cm)		Difference (top–bottom)
			0–10	10–20	
Tallgrass	Ungrazed	4	-20.6 (0.5)	-17.4 (0.2)	3.1 (0.4)
	Grazed	3	-22.6 (1.3)	-20.2 (1.7)	2.4 (0.5)
	Hay meadow	5	-23.7 (0.6)	-19.0 (0.6)	4.7 (0.5)
Mixed-grass	Ungrazed	10	-16.3 (1.4)	-13.8 (1.6)	2.5 (0.5)
	Grazed (total)	13	-20.9 (0.6)	-18.3 (0.9)	2.6 (0.5)
	(with prairie dogs)	6	-20.5 (1.2)	-17.4 (1.7)	3.0 (1.0)
	(without prairie dogs)	7	-22.1 (0.6)	-19.2 (1.4)	2.9 (0.8)
	(shortgrass)	3	-20.3 (0.9)	-18.8 (0.7)	1.5 (0.2)
	Hay meadow	7	-23.8 (0.3)	-22.7 (0.3)	1.0 (0.3)

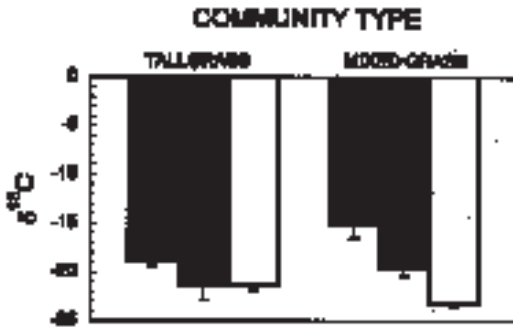


Fig. 1. Carbon isotopic values for soils from tallgrass and mixed-grass sites near Boulder, Colorado. Treatments include ungrazed areas (shaded bars), grazed areas (hatched bars), and hayfields (clear bars). Vertical hatched bars designate 1 standard error.

We observed a positive correlation between isotopic values and percent exotic vegetation at each site (Fig. 2). This relationship exists for the entire data set ( $r = 0.62$ ), as well as when hayfields were excluded from the analysis ( $r = 0.63$ ).

#### DISCUSSION

Changes in plant species composition can produce feedbacks that further alter ecosystem components (D'Antonio and Vistousek 1992, Bowman and Steltzer 1998). In particular, the shift from  $C_4$  to  $C_3$  species dominance in temperate grasslands is thought to be associated with higher levels of nitrogen availability (Wedin and Tilman 1996), which would benefit nitrogen-loving species, including many weeds. Understanding how changes in land use practices have affected particular grassland communities is difficult because the effects of one practice are often compounded with those of others. Collectively, these changes have undoubtedly created a new environment for remaining plant communities. At a minimum, these communities are clearly outside the historical range of variability in natural disturbance agents (such as fire) responsible for the vegetation composition occurring prior to European settlement (e.g., Hobbs and Huenneke 1992, Swanson et al. 1993).

We reject our 1st hypothesis that tallgrass communities in the Boulder area would exhibit the strongest  $C_4$  carbon isotope signature. Average isotopic signatures observed in soils from

the Boulder area indicate that  $C_3$  grasses are present in all community types. Indeed,  $\delta^{13}C$  values were very different from the average of  $-13\text{‰}$  reported for tallgrass soils in eastern Kansas (Smith and Johnson 1997). We conclude instead that Front Range tallgrass areas likely had a higher  $C_3$  species component than their eastern counterparts.

The more depleted  $\delta^{13}C$  values in surface soils are consistent with increases in  $C_3$  species contribution to soil organic matter. These results correlated with Bennett's (1997) findings, lending support to his suggestion of an overall shift in community dominance from  $C_4$  to  $C_3$  species in the grasslands around Boulder. We therefore accept our 2nd hypothesis that the  $C_3$  carbon isotopic signature is associated with nonnative ( $C_3$ ) vegetation. These observations are also consistent with other studies that suggest a trend toward more  $C_3$ -dominated grasslands in North America (Tieszen et al. 1997). Causal mechanisms for these changes remain unidentified, but atmospheric nitrogen enrichment, fire suppression, and the introduction of a large number of nonindigenous  $C_3$  plants into the region could all contribute to the trend.

Results from this study suggest that we need to reconsider our preconceptions regarding the historic composition of tallgrass, mixed-grass, and shortgrass communities. Strongest  $C_4$  signatures in soils were not found in tallgrass sites, but in areas of currently ungrazed, mixed-grass prairie. These sites appear to have a higher contribution of warm-season  $C_4$  grasses than the tallgrass areas. Grazing by cattle, prairie dogs, or both species has increased the relative abundance of  $C_3$  species in all sites, but particularly in mixed-grass sites (Fig. 1). In the Boulder area, grazing in tallgrass prairie is often restricted to winter or early spring, which would favor the persistence of warm-season  $C_4$  grasses. Nevertheless, our data suggest that this grazing regime has resulted in an increase in relative  $C_3$  productivity.

Prairie dog colonies are known to favor forb growth over grasses (e.g., Whicker and Detling 1988) and should therefore enhance the  $C_3$  carbon isotopic signature. However, grazing by ungulates has been reported to enhance  $C_4$  species abundance in more xeric grasslands (Mulchunas et al. 1989, Frank et al. 1995). Our results indicate a consistent effect of grazing toward  $C_3$  species dominance. While interpre-

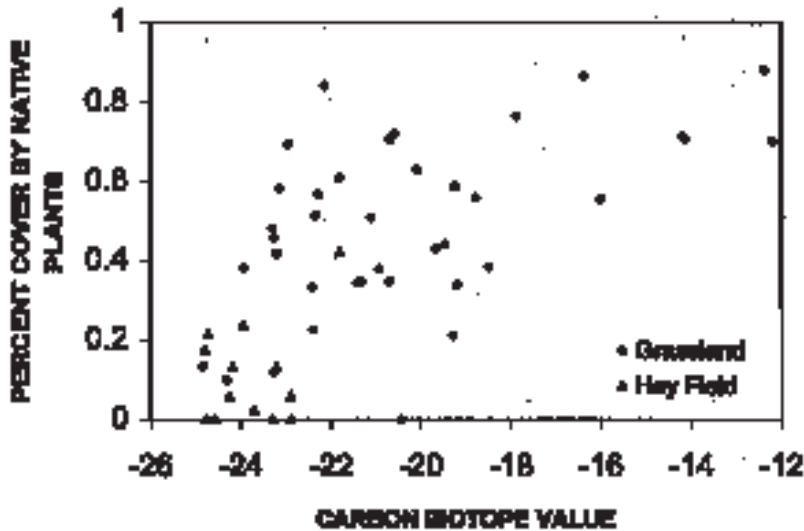


Fig. 2. Correlation between surface (0–10 cm) soil  $\delta^{13}\text{C}$  signatures and native plant abundance as percentage of total vegetation cover. Square symbols are from hayfields; diamonds are from tall-, mixed-, and shortgrass prairie.

tations remain speculative, the increase in non-indigenous, largely  $\text{C}_3$  species such as cheatgrass (*Bromus tectorum*) and a variety of forbs on these lands (e.g., Bennett 1997, Reeve-Morgahan and Seastedt 1999) is hypothesized as the causal mechanism for the soil carbon isotope grazing response observed in the Boulder area. Indeed, the community type with the highest contribution of  $\text{C}_4$  carbon to the soil, the mixed-grass prairie, correlated with the lowest percentage composition of non-indigenous species (29% vs. over 44% for all other sites) reported by Craig et al. (in press).

Changes in plant community composition will likely affect community productivity, soil carbon storage, and other ecosystem properties that can impact surviving prairie grasslands around the Boulder area. If the dominance of native, warm-season grasses in these systems is a priority management goal, more proactive measures to enhance  $\text{C}_4$  grasses in this area are warranted.

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OREOHELICES OF UTAH, I. REDISCOVERY OF THE UINTA  
MOUNTAINSNAIL, *OREOHELIX EUREKENSIS UINTA* BROOKS, 1939  
(STYLOMMATOPHORA: OREOHELICIDAE)

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ABSTRACT.—*Oreohelix eurekensis uinta* had not been found since its original discovery and had never been reported as a living taxon, and this had led to speculation that it is extinct. However, searches for *O. e. uinta* had been confounded by multiple errors in the original definition of the type locality. The type locality has now been relocated and is here redefined, and *O. e. uinta* is reported for the 1st time as a living taxon. Although the holotype has been lost, existing specimens believed to be paratypes have been examined, and correction of errors in the literature concerning its size and proportions is provided. *O. e. uinta* has been detected only in a surprisingly small area (~0.03 ha) where potential threats to its continued existence are evident.

*Key words:* *Oreohelix eurekensis uinta*, *Uinta mountainsnail*, mollusks, gastropods, Utah, Uinta Mountains.

The Uinta mountainsnail, *Oreohelix eurekensis uinta*, was described by Brooks (1939) based on material collected at a single locality in northeastern Utah in the 1930s by E.R. Eller, but this taxon had not been found since its original discovery. Although searches for this taxon were conducted in 1992 (Clarke 1993, Clarke and Hovingh 1994), the type locality could not be relocated and the snail was not found. Clarke and Hovingh (1994) reported that vegetation in the area they thought to be the type locality of *O. e. uinta* had “been recently destroyed by fire with the object of improving grass cover for sheep” and commented that this “[b]urning of vegetation may have extirpated the snail population and this subspecies may be extinct.”

No attempts to relocate *O. e. uinta* other than that of Clarke and Hovingh (1994) have been reported. Clarke and Hovingh (1994) asserted that “[d]uring a comprehensive molluscan survey of the Uinta Mountains in 1939–1941 by Woolstenhulme (1942) no specimens of this subspecies were found.” However, Woolstenhulme’s (1942) work was, as stated by its author, a preliminary rather than comprehensive report and, despite its misleading title, largely does not pertain to the Uinta Mountains but deals mainly with the Wasatch Mountains to the west and non-mountainous areas both south and north of the Uinta Mountains.

Woolstenhulme’s (1942) report, in fact, provides very few records from localities actually within the Uinta Mountains.

In reviewing the scant literature (Brooks 1939, Pilsbry 1939) pertaining to *O. e. uinta*, we became convinced that, since the time of its description, no adequate effort had been made to find this taxon and speculation regarding its extinction (Clarke and Hovingh 1994) was premature, despite the fact that no living examples had been reported. Our goals, then, were to relocate the type locality with the objective of finding at least dead material (shells) and to search for living representatives of *O. e. uinta*, as well as to clarify and to expand, as much as possible, knowledge of this taxon.

#### METHODS

In the type description of *O. e. uinta*, Brooks (1939) stated the type locality as “on Hominy Creek, R. 1 W., T. 3 S., 3 miles north Uinta Special Meridian, near Whiterocks, Uinta Co., Utah.” There are, however, several errors in this locality statement. Although the spelling of Uintah County used by Brooks (1939) is incorrect, this is a commonly encountered error resulting from confusion with the spelling of the Uinta Mountains and one that does not impede understanding. However,

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since the Uintah Special Meridian (also misspelled by Brooks [1939]) runs north and south, not east and west, the phrase “3 miles north Uinta Special Meridian” is nonsensical. Furthermore, “T. 3 S.” is grossly incorrect, producing a locality far to the south of Hominy Creek.

While Clarke and Hovingh (1994) failed to note any of these errors in Brooks' (1939) statement of the type locality, they did claim, incorrectly: “The name Hominy Creek does not appear on topographic maps.” The name Hominy Creek indeed does appear on 2 USGS 7.5-minute topographic maps, Ice Cave Peak, Utah (1965) and Pole Creek Cave, Utah (1965), and it also appears, misspelled as “Hominy Creek,” on the USGS 30 × 60-minute topographic map Dutch John, Utah-Colo.-Wyo. (1981).

Solutions to problems created by errors in the type description came from the discovery that Hominy Creek exists—and is mapped—and is not an older name for some other water body such as the Whiterocks River as Clarke and Hovingh (1994) believed. From this came the realization that the township designation “R. 1 W., T. 3 S.,” although wrong, is not completely inexplicable: R1W having been correctly derived from the Uintah Special Meridian and T3S having been incorrectly derived from the Salt Lake Meridian. Furthermore, if “3 miles west” of the Uintah Special Meridian is substituted for the nonsensical “3 miles north,” a reasonable locality is produced.

Corroboration of these conclusions came from the further discovery of an earlier publication by Brooks. Three years before publication of the type description, Brooks (1936) had announced the find of an undescribed *Oreohelix*, which at that time he referred to as a new species rather than a new subspecies, reportedly collected in 1935 rather than 1933 as he wrote later in the type description (Brooks 1939), and stated the locality of its collection as “Hominy Creek near Whiterocks, R. 1 W, T. 2 N, Uinta [*sic*] Special Meridian.” Although not a very precise locality, it is not, except for the minor error in spelling, erroneous or self-contradicting, and of particular importance is the correctly designated township: R1W, T2N, Uintah Special Meridian.

Guided by this earlier locality designation (Brooks 1936) combined with the necessary corrections to the locality stated in the type

description (Brooks 1939), in July 1998 we went to Hominy Creek, where we searched for *O. e. uinta* at 13 locations along the length of the creek, from near its source in Duchesne County to its mouth, the confluence of Hominy Creek and Farm Creek, in Uintah County.

## RESULTS AND DISCUSSION

At one of the 13 collecting stations along Hominy Creek, we were successful in finding *O. e. uinta*, of which we collected 84 dead shells as well as 3 live individuals on 10 July 1998, and we have compared these new specimens with Brooks' specimens from the type locality.

### Type Specimens

In the type description of *O. e. uinta*, Brooks (1939) wrote: “Type in coll. Carnegie Mus., paratype in coll. Acad. Nat. Sci., Philadelphia.” John E. Rawlins of the Carnegie Museum of Natural History (letter, 6 January 1999) advised us:

The holotype of that name [*Oreohelix eurekensis uinta* Brooks, 1939], although supposedly at the Carnegie Museum, could not be found despite three thorough searches that included all of our known material in the family. . . . Further, our records do not reveal a catalog or accession number for anything under that name. . . . I checked the records and correspondence files carefully, and there is no evidence that this primary type was borrowed . . . and not returned.

We examined the single lot of *O. e. uinta* that is in the collection of the Academy of Natural Sciences of Philadelphia, catalogue number 164004, which contains 9 specimens that evidently are Brooks' paratypes, despite his use of the singular “paratype” (Brooks 1939). Labels associated with these 9 specimens match closely the collection data reported by Brooks (1939) in the type description, including all locality errors, and provide the exact date of collection, 21 June 1933, which had been variously reported by Brooks (1936, 1939) as 1935 and 1933. Of these 9 specimens, the smallest individual may have been alive at the time of collection, as evidenced by the epiphragm covering the aperture when we examined it, although Brooks (1936, 1939) made no mention of any live material. The other 8 specimens appear to have been dead when collected, most of them rather obviously so. The vial

containing the 9 specimens had been divided, using a plug of cotton, into 1 group of 3 specimens in the bottom and another group of 6 higher in the vial. The 3 specimens in the bottom are the largest of the series, and they match the 3 shells illustrated in Pilsbry's (1939) Figure 348. Clarke and Hovingh (1994) reproduced Pilsbry's (1939) photographs of these 3 specimens, which they referred to as the "holotype" even though Pilsbry (1939) did not identify them as being type material. The shell that agrees with the one figured by Pilsbry in ventral view (lower left, Figure 348 in Pilsbry 1939), in addition to having a chipped aperture that matches that of the figured ventral view, still had a foreign, seemingly unnatural substance—presumably glue or wax used to hold it in position for photographing—adhering to the spire when we examined it. The 2 other specimens also agree with Pilsbry's photographs in various details (e.g., a small "scar" in the margin of the shell shown in dorsal view).

Brooks' (1939) measurements of the holotype, "[h]eight 8 mm., diam. 4.2 mm.," cannot be correct for an individual of the species *O. eurekaensis*—or for any member of the genus *Oreohelix* in which "[t]he shell is . . . usually depressed but varying from discoidal to pyramidal . . ." as defined by the author of this genus (Pilsbry 1905, 1939). While accepting the diameter of the holotype reported by Brooks (1939), Clarke and Hovingh (1994) believed that 2 typographical characters had been omitted from Brooks' (1939) statement of height and suggested that the actual measurement of shell height intended by Brooks was "probably 2.8" mm. However, Clarke and Hovingh's (1994) correction of the measurements of the holotype of *O. e. uinta* would make it only a little more than half the size of typical *O. e. eurekaensis* (see Pilsbry 1939) and would assign to *O. e. uinta* proportions that are very different from those of *O. e. eurekaensis* (i.e., *O. e. uinta* would be proportionately much higher spired). The more parsimonious explanation concerning the problematical measurements of *O. e. uinta* reported in the type description is that they were merely transposed, Brooks' (1939) intention having been: height 4.2 mm, diameter 8 mm. Measurements of the presumed paratypes (ANSP 164004), particularly the 3 figured by Pilsbry (1939), confirm this.

We have deposited 10 of the newly collected topotypes of *O. e. uinta* in the malacological collection of the Academy of Natural Sciences of Philadelphia (ANSP 401983).

#### Type Locality

The site at which we relocated *O. e. uinta*, and which we propose as a redefinition of the type locality of this taxon, is:

Utah, Duchesne County, south slope of the Uinta Mountains, T2N, R1W, SE  $\frac{1}{4}$  of SE  $\frac{1}{4}$  of SE  $\frac{1}{4}$  of section 4 (Uintah Special Meridian); along Hominy Creek  $\frac{1}{4}$  km upstream from "The Hole"; 13.8 km N and 5.3 km W of Whiterocks; 2645 m elevation.

It should be noted that this redefinition places the type locality in Duchesne County, not Uintah County as stated in the type description (Brooks 1939). This locality is, however, only 1.4 km west of the Uintah County line, and we believe the collector of the type material, Eller, was actually in Duchesne County in 1933 when he collected the type material. Importantly, the locality is precisely 3.00 miles west of the Uintah Special Meridian, while the type description states, as discussed above, that the type locality is "3 miles north Uinta Special Meridian," which supports our *a priori* conclusion that "west" rather than "north" was meant by Brooks (1939).

We found *O. e. uinta* only in a remarkably small area. The 4 farthest outlying shells (all dead) defined a quadrangle about  $14 \times 18 \times 28 \times 19$  m—an area of approximately 342 m<sup>2</sup> (~0.03 ha). Of the 3 live individuals, 2 were under the same rock, only a few centimeters apart, and the other was under a rock about 7 m away. The area of greatest concentration of shells was probably less than 1/10th of the total area in which shells were detected. Habitat somewhat similar to that found to be inhabited by *O. e. uinta* covered an area estimated to be at least 1 ha in the immediate vicinity, but we were unable to detect the presence of *O. e. uinta* beyond the limits mentioned above.

#### Habitat

The site where we located *O. e. uinta* was a relatively open, 45°, south-southwest-facing slope of broken limestone and loam. The sparse plant cover of the small area inhabited by *O. e. uinta* was predominantly chokecherry (*Prunus virginiana*), rose (*Rosa* cf. *woodsii*),

serviceberry (*Amelanchier* cf. *alnifolia*), pine (*Pinus* sp.), Douglas-fir (*Pseudotsuga menziesii*), thistle (*Cirsium* sp.), and wax currant (*Ribes cereum*), although we identified 9 other species of forbs and 2 other species of shrubs that were also present. Quaking aspen (*Populus tremuloides*) and sagebrush (*Artemisia* sp.) were prominent plants of the surrounding parts of the same slope, but only seedlings of these 2 plants were present within the area occupied by *O. e. uinta*; this was, in fact, the only noticeable difference between the area inhabited by *O. e. uinta* and the surrounding, seemingly uninhabited, but similar, area.

#### Associated Gastropods

Although we found and collected many species of gastropods during the course of our search for *O. e. uinta* at the 13 collecting stations along Hominy Creek, which included a wide array of habitats, we found very few molluscan taxa in close association with *O. e. uinta* at the single station where it occurs. The most common of these snail associates of *O. e. uinta* was its much larger congener the Rocky Mountain snail, *Oreohelix strigosa*, a very widespread and abundant snail in Utah, of which we found 155 dead shells and 6 live individuals within the area occupied by *O. e. uinta*; that is, *O. strigosa* was approximately twice as numerous, by counts of both live and dead individuals, as *O. e. uinta* in the small area where *O. e. uinta* occurs. The association of these 2 oreohelices is very close indeed, for under the same small rock that 2 of the living *O. e. uinta* were found, there was a live *O. strigosa* only 7 cm from 1 of the live individuals of *O. e. uinta*.

The few other snails found in association with *O. e. uinta* were each represented by very few individuals (fewer than 10 each, mostly dead shells); they were the Rocky Mountain column (*Pupilla blandi*), the variable vertigo (*Vertigo gouldi*), a species of vallyonia (*Vallyonia* cf. *cyclophorella*), the forest disc (*Discus whitneyi*), the striate disc (*Discus shimekii*), the brown hive (*Euconulus fulvus*), the amber glass (*Nesovitrea electrina*), and the western glass-snail (*Vitrina pellucida*).

#### Conservational Considerations

Despite the fact that *O. e. uinta* had never been reported as extant, it was formerly a Category 2 candidate taxon, one

for which information now in possession of the [U.S. Fish and Wildlife] Service indicates that proposing to list as endangered or threatened is possibly appropriate, but for which persuasive data on biological vulnerability and threat are not currently available (U.S. Fish and Wildlife Service 1994),

until Category 2 was eliminated by the U.S. Fish and Wildlife Service on 28 February 1996. It is designated a "species of special concern" on the state's Utah Sensitive Species List (Utah Division of Wildlife Resources 1998).

The site inhabited by *O. e. uinta* is within the Ashley National Forest. Despite the moderately high elevation of the locality, cattle were conspicuously present in the area, and there was ample evidence of their use of the site where we found *O. e. uinta*. Because the inhabited site is steep, dry, and highly erodible, trampling and grazing by cattle could be devastating to the habitat of the snails, if not to the snails themselves; furthermore, grazing in this area removes plant cover, adding to the destabilization of the slope, altering the immediate habitat, and removing important food sources for these snails.

Timber harvest is a potential threat to *O. e. uinta*. Even though the particular patch of habitat occupied by the snails is not covered by arborescent growth, the surrounding area is, there being large conifers along Hominy Creek only 18 m from the lower edge of the inhabited portion of the slope, as well as scattered aspens on much of the slope itself.

We have communicated with personnel of the U.S. Forest Service regarding the rediscovery of *O. e. uinta*, and they have expressed their interest in taking action to protect the site of its occurrence.

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## EGG MASS DEPOSITION BY ARIZONA TOADS, *BUFO MICROSCAPHUS*, ALONG A NARROW CANYON STREAM

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*Key words:* *Bufo microscaphus*, *dispersion*, *breeding site selection*.

Declining amphibian populations in the arid southwestern United States have prompted increased efforts to understand the reproductive behavior of desert anurans, particularly those species in restricted habitats (Sullivan 1989, Corn 1994). The Arizona toad, *Bufo microscaphus*, is confined in southwestern Utah to tributaries of the Virgin River drainage (Price and Sullivan 1988). Like most desert anurans, *B. microscaphus* is an explosive breeder (Wells 1977, Sullivan 1992); however, unlike many other toads, which deposit their eggs in still ponds and lakes, it prefers to lay eggs in the flowing water of a perennial or semi-permanent stream. Water quality and breeding behavior are influenced by many physical and biological variables so that choice of a nesting site may not be simply by chance. The questions we consider here are: Do mating pairs select a particular portion of the habitat to deposit their eggs, and, if so, what factors might explain site selection?

We observed egg deposition by Arizona toads in Oak Creek, Zion National Park, between 26 April and 9 May 1998. Oak Creek is a narrow (1–3 m in width), shallow, intermittent stream (<0.5 m in depth at its deepest point). In many places stream banks rise 3–4 m above the flow. The streambed consists of various mixtures of sandy soil and rock, and stream bank vegetation ranges from sparse shrubs and grasses to thick shrubs and trees with large, branching canopies. Egg masses were counted along a 1750-m transect marked every 50 m with labeled surveyor's tape. The transect began near the parking lot of the visitors center and research complex (section 1) and continued upstream (to section 36); we did

not survey the entire stream prior to setting up the transect but merely chose a portion that was convenient for frequent visitation and nocturnal sampling. We also assumed the stream flow was perennial throughout the sampling area.

Blair (1955) reported a female typically deposits about 4500 eggs. We observed these in long, gelatinous strings that were usually found in irregular masses in pools and other parts of the stream where flow is minimal. Each egg mass was marked with a numbered flag and its section recorded. Between 1010 and 1330 h on 26 April 1999, the 1st day egg masses were found in the creek, the following measurements were taken at the beginning of each of 36 sections in the transect: temperature (°C) and percent of dissolved oxygen (DO measured with a YSI model 55), pH (taken with a pHep 3, Hanna Instruments), water depth (cm) in the middle of the egg mass, number of streamside pools (>1 m in diameter and 4 cm in depth), distance (m) to the nearest tree, and percent canopy covering the stream channel estimated by simply viewing 5 areas per section and averaging percentages for each section. The choice of these independent variables was based on factors known to affect both development of embryos and larvae and the energetics of finding mates (Wells 1977, Rome et al. 1992, Shoemaker et al. 1992). From April to August 1999, we also surveyed the entire transect on 7 evenings, marking (by toe clipping) the number of adult and juvenile toads seen in each section.

Twenty-one egg masses were deposited in 11 contiguous sections (24–34) of the transect; obviously, masses were not distributed randomly

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along the stream (mean number of egg masses per section = 0.58, Poisson  $\chi^2 = 76.7$ ,  $df = 35$ ,  $P < 0.001$ ) but were concentrated in particular sections (variance to mean ratio = 2.19, Moristia's index of dispersion = 3.089; Brower and Zar 1984). Although in previous years adults were seen all along the stream transect (Breck Bartholomew and Mary Hunnicutt personal communication), most were found in the same areas as the egg masses (numbers of adults in sections 24–34, mean = 18.5, range = 6–33, vs. those in sections 1–23, 35–36, mean = 4.0, range = 0–16; Mann-Whitney test, 2-tailed  $P < 0.001$ ). During the breeding period in April, we saw toads only in sections 24–34, the area of egg mass deposition; in June and July adults were found in sections 1–34. A summer flood followed by stream drying in sections 1–12 seemed to further restrict toads to upstream sections of the transect.

Number of pools and water temperature best explained number of egg masses per section (multiple regression, number of egg masses =  $7.08 + 0.60$  [number of pools] +  $0.38$  [water temperature],  $R^2 = 0.74$ ,  $P < 0.001$ ). Number of egg masses per section was negatively and significantly correlated with percent canopy (Pearson product-moment correlation =  $-0.40$ ,  $P < 0.01$ ,  $N = 36$ ). Significant intercorrelation among independent variables was negative for canopy cover and distance ( $-0.44$ ,  $P < 0.01$ ) to the nearest tree, number of pools ( $-0.34$ ,  $P < 0.05$ ), and temperature ( $-0.75$ ,  $P < 0.001$ ). Water temperature and both distance to the nearest tree ( $0.41$ ,  $P < 0.01$ ) and number of pools ( $0.34$ ,  $P < 0.05$ ) were positively correlated. Depth of stream (mean = 7.7 cm,  $s = 3.3$  cm) and pH (mean = 7.3,  $s = 0.10$ ) were relatively constant along the stream.

If *B. microscaphus* in Oak Creek chose sections for laying eggs, those 11 sites were characterized by an abundance of pools (mean = 6.3,  $s = 2.7$ , range 2–10). Twenty-five sections without egg masses had less than half the average number of pools per section (mean = 3.1,  $s = 1.6$ , range = 0–6). Pools have less flow than the stream, so breeding male toads may more easily detect movement by an approaching female (Sullivan 1992). Egg masses also have little chance of being washed downstream (except during flash flooding) when laid in a pool. Pools may be more numerous in sections with egg masses because trees and their roots

are farther from the stream (mean = 5.0 m,  $s = 3.7$  m, range = 2–15 m) than they are in sections without egg masses (mean = 4.2 m,  $s = 3.8$  m, range = 1–20 m). Without tree roots to hold the soil, erosion and subsequent meandering of the stream course can occur. Sections of the stream with egg masses were warmer (mean =  $16.5^\circ\text{C}$ ,  $s = 0.5^\circ\text{C}$ , range =  $15.7^\circ\text{--}17.1^\circ\text{C}$ ) than sections without egg masses (mean =  $12.3^\circ\text{C}$ ,  $s = 2.2^\circ\text{C}$ , range =  $9.6^\circ\text{--}16.7^\circ\text{C}$ ). They also had less tree canopy cover (mean = 8.2%,  $s = 9.8\%$ , range = 0–20%) than those sections without eggs (mean = 52.8%,  $s = 36.9\%$ , range = 0–95%). Warmer temperature shortens development time to metamorphosis in anuran embryos (e.g., Noland and Ultsch 1981); however, finding that eggs are preferentially laid in warmer pools may be irrelevant. If water temperature influences site selection and mating takes place at night, then variation in temperature among stream sections would be expected at night; these measurements were not taken. Toads preferred to lay eggs in open-canopy pools with photosynthetic algae that raised dissolved oxygen levels, in contrast to ponds with closed canopies and heavy leaf litter, the decomposition of which consumed oxygen (Werner and Glennemeier 1999). A similar relationship probably does not explain selection of breeding sites along our stream zone. We found no significant correlation between number of egg masses and dissolved oxygen in the stream. Actually, average dissolved oxygen concentration at egg mass sites in pools (mean = 65.8,  $s = 10.3$ ,  $N = 22$ ) was lower than for those measurements in the adjacent stream (mean = 77.3,  $s = 1.8$ ,  $N = 11$ ; Mann-Whitney test, 2-tailed  $P < 0.001$ ).

Other breeding species and the presence of predators may affect nesting site selection (e.g., Petranka et al. 1994, Skelly 1996). We observed both red-spotted toads, *Bufo punctatus*, and canyon treefrogs, *Hyla arenicolor*, breeding in the same sections as *B. microscaphus*. In addition, we noted the presence of predatory insect larvae in many pools. Understanding the extent to which interspecific competition or predation affects site selection, as well as the determination of causal relationships between nest site selection and other potentially explanatory variables, must await either comparative (natural) studies among populations in similar habitats or experimental manipulations of variables.

It is entirely possible that we may have overlooked factors critical to the final site for egg deposition that are not represented in our limited choice of physical and biological variables. The deposition of eggs may simply be a function of where females emerge from hibernacula in response to calling males that wander up and down the stream, or to subtle aspects of stream bank terraces, either of which may have little relationship to male or female choice, and for which we took no measurements (S. Sweet personal communication).

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A CONFIRMED RECORD OF THE EPHEMEROPTERA GENUS  
*BAETISCA* FROM WEST OF THE CONTINENTAL DIVIDE  
AND AN ANNOTATED LIST OF THE MAYFLIES  
OF THE HUMBOLDT RIVER, NEVADA

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ABSTRACT.—The mayfly *Baetisca lacustris* is reported from the Humboldt River, Nevada, based on 3 relatively mature nymphs collected in 1997 and 2000. An annotated list of the mayfly fauna of the Humboldt River is given, which includes the section from Elko to Winnemucca.

*Key words:* mayflies, Ephemeroptera, *Baetisca*, Humboldt River, Nevada.

In their recent revision of the genus *Baetisca*, Pescador and Berner (1981) indicate that they were unable to verify the presence of the genus at any locality west of the Continental Divide. Although *B. columbiana* Edmunds was described from the Columbia River near Pasco, Washington (Edmunds 1960), the type, which is at the California Academy of Sciences, is the only known specimen and has not been recollected. An old historical record for California (Eaton 1883–1888) also has not been confirmed.

Recently, 3 relatively mature *Baetisca* nymphs were found in some benthic samples taken in the Humboldt River in north central Nevada. Two of these nymphs were examined by M.L. Pescador and verified as *Baetisca lacustris* McDunnough. This species is widespread in North America, and the nearest known record is from the Laramie River in Albany County, Wyoming, east of the Continental Divide. Consequently, it now seems possible that *Baetisca* may occur in the far west at several localities.

Over the last 10 years much collecting of aquatic insects has occurred in Nevada. A study on the stonefly (Plecoptera) fauna by R.W. Baumann and A.L. Sheldon is nearing completion, and several studies on the benthic fauna of the Humboldt River drainage are being conducted. The mayfly fauna of the state is poorly known, and even though the potential mayfly fauna was addressed (Allen

and Murvosh 1991), few published records exist. Thus, it was deemed useful to produce a list of the species that have been verified from the Humboldt River to date.

The Humboldt River has its headwaters in the Jarbridge, Ruby, and nearby mountain ranges in northeast–north central Nevada. However, our list is limited to the mainstream of the Humboldt River from just below the confluence of the North Fork, east of Elko, to the junction of Rose Creek, immediately west of Winnemucca. Although most records are based on nymphs, some also have been collected as adults, and 1 species, *Siphonurus occidentalis* (Eaton), is known only from a large series of adults found on the Dunphy bridge.

LIST OF MAYFLIES FROM THE  
HUMBOLDT RIVER, NEVADA

BAETIDAE

- Acentrella insignificans* (McDunnough)
- Baetis tricaudatus* Dodds
- Camelobaetidius warreni* (Traver and Edmunds)
- Centroptilum bifurcatum* McDunnough
- Fallceon quilleri* (Dodds)

Since the important study of *Baetis* larvae of North America (Moriyama and McCafferty 1979), several closely related genera have been recognized that were formerly included under the genus *Baetis*. The 5 species recorded

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belong to 5 different genera and represent the present classification (Lugo-Ortiz and McCafferty 1998). These species are widespread in western North America and are relatively common in the Humboldt River drainage.

#### EPHEMERELLIDAE

*Ephemerella inermis* Eaton

Widely distributed in the Intermountain West, this species extends east to Nebraska and south to Texas, and so its presence in the river would be expected (Allen and Edmunds 1965).

#### EPHEMERIDAE

*Ephemera simulans* Walker  
*Hexagenia limbata* (Serville)

These 2 burrowing mayflies are widely distributed in western North America (McCafferty 1994), but because actual records are few, the following Humboldt River sites are noted.

*Ephemera simulans*: Elko Co., Carlin; Eureka Co., above Barth and below Harney.  
*Hexagenia limbata*: Elko Co., Carlin; Eureka Co., Dunphy and Shoshone; Lander Co., Argenta, Blue House Slough, and above Rock Creek.

#### HEPTAGENIIDAE

*Heptagenia elegantula* (Eaton)  
*Rhithrogena undulata* Banks  
*Stenonema terminatum* (Walsh)

These species are present in warmer rivers of the West (Bednarik and McCafferty 1979, Bednarik and Edmunds 1980). *Heptagenia elegantula* was collected only occasionally, but the other 2 species were commonly found wherever suitable habitats existed.

#### LEPTOPHLEBIIDAE

*Choroterpes albiannulata* McDunnough  
*Paraleptophlebia debilis* (Walker)  
*Traverella albertana* McDunnough

The *Choroterpes* and *Traverella* species are commonly found in larger, warmer rivers of western North America (Jensen 1966). However, *P. debilis* appears more sensitive to environmental perturbation and has been found only at 3 localities: Eureka Co., Dunphy; Humboldt Co., 26 Ranch near Mote and Christiansen Dam bridge.

#### SIPHONURIDAE

*Siphonurus occidentalis* (Eaton)

Nymphs were not collected even though benthic samples were taken from numerous stations over a 10-yr period. A large series of adults was obtained on a bridge at the following locality: Eureka Co., Dunphy, 7 June 2000.

Nymphs are good swimmers and spend much of their life in the more lentic areas along the river margins.

#### LEPTOHYPHIDAE

*Tricorythodes minutus* Traver

This species is very common throughout the entire drainage and ranges throughout western North America and to the Northeast (McCafferty 1999).

#### POLYMITARCIDAE

*Ephoron album* (Say)

This common western and midwestern species (McCafferty 1994) is the most abundant burrowing mayfly in the drainage. It occurs from Elko County to Lander County.

#### CAENIDAE

*Caenis latipennis* Banks

Provonsa's (1990) revision of the *Caenis* of North America does not list any species from Nevada. However, *C. latipennis* was described from Washington and it is widely distributed. It is found at the following localities in the Humboldt River: Eureka Co., Palisade Canyon, Shoshone; Lander Co., Rock Creek confluence; Humboldt Co., 26 Ranch near Mote, Comas Gauging Station above Golconda.

#### BAETISCIDAE

*Baetisca lacustris* McDunnough

This taxon is recorded for the first time in Nevada from the following localities: Nevada, Eureka Co., Humboldt River at Shoshone, 13 November 1997, 2 nymphs; Eureka Co., Humboldt River at Dunphy, 3 March 2000, 1 nymph.

Although this list of species known to occur in the Humboldt River might not be complete, the addition of 19 species, many of which are new state records from Nevada, is

useful. Additional collecting in the North Fork and some of the major tributaries of the Humboldt River may increase the list. Specimens are deposited at the Monte L. Bean Life Science Museum, Brigham Young University, Provo, Utah, and C.P. Gillette Museum, Colorado State University, Fort Collins, Colorado.

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## BOOK REVIEW

### **Singing Stone, a Natural History of the Escalante**

**Canyons.** Thomas Lowe Fleischner. University of Utah Press, Salt Lake City, Utah. 1999. \$17.95, paperback. ISBN 0-87480-619-4.

I enjoyed reading this book. The author has gained much knowledge of the Escalante Canyons area and is willing to share his enthusiasm for the natural beauty one can find there.

The structure of the book is logical, with 2 main groups of chapters: an introductory chapter woven around the geology of the area, followed by a chapter relating to biology, and then a historical chapter concerning various groups of humans that have been in the area. This group of chapters is followed by a chapter summarizing range policy considering both local and national scales and another addressing recreational issues impacting the area in ways that were perhaps unanticipated. This final chapter also summarizes at least some of the author's views on environmentalism and the current debate concerning wilderness and roadless areas in the West. I was pleased with his attempt to open the issue to discussion. He outlined the issues he perceives, and while it is clear what the author personally feels about human uses of the Escalante Canyons, he is equally clear about his assessment of why opponents to his views voice their concerns.

The closing paragraph of this 2nd group of chapters summarizes quite succinctly the previous many pages with the author's view:

The world casts its eye toward the Escalante Country and values its scenic beauty. More and more seekers come, hungry for fun. Local residents try earnestly to make peace with the values and influences of outsiders. Gaunt cows of flesh and blood begin to be replaced by cash cows of the tourist industry—motels, gas stations, souvenir, and gear shops. This new industry, based on this new valuing of the Escalante Country, may provide a sustainability that has eluded this hidden corner of the American dream. Or it may yield problems of its own. The future, as has always been the case, cannot be foretold.

While the future “cannot be foretold,” the author shares with us his opinions about what might generally be expected by highlighting the past, from a geologic, biologic, and historic summary, which is easy to follow. Additionally, the author voices a plea, in several places in the Prologue and Epilogue, for more people to consider studies of “natural history” for the values they offer to humans—humans which he and others sense are becoming more and more detached from the natural world.

The book itself is adequately sturdy. Notes and References sections provide the opportunity for scholars, both casual and serious, to pursue primary literature and assess the author's views objectively. The section Taxonomy of Species Mentioned in Text will allow casual natural historians a chance to communicate using scientific names of a few of the thousands of species that occur in the Escalante Country. Others might want longer lists of species in the area, but that information can be found elsewhere and is often cited in the References section.

I was somewhat disappointed with the choice and reproduction of maps in the front of the book. They lack contrast and detail that could have been possible by choosing other, or drawing new, maps. As produced, they fail to communicate the amazing topography and complexity of the country this author so obviously loves.

I would recommend this book to potential readers from all factions that love the Escalante Country. It offers a chance to see how the area has affected the life of one who may have views differing from their own. I feel that the author was successful in expressing his opinion without becoming overly condescending or apologetic. It is an easy book to read.

As an added note, I will search these canyons personally for the alcove, exact location not given, which has so impressed Thomas Lowe Fleischner through the years.

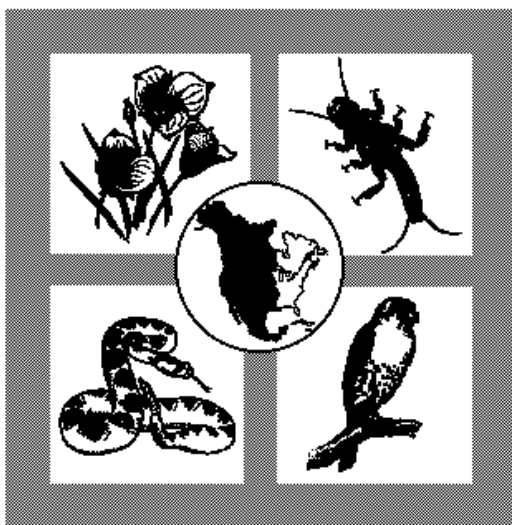
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# Western North American Naturalist

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