

A CLASSIFICATION OF AQUATIC PLANT COMMUNITIES WITHIN THE NORTHERN ROCKY MOUNTAINS

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ABSTRACT.—A synecological study of aquatic macrophyte plant communities was conducted across northern Idaho and western Montana during the summers of 1997, 1998, and 1999. A total of 111 natural and man-made water bodies were sampled based on a stratification of environmental variables thought to influence plant species distribution (i.e., elevation, landform, geology, and water body size). Plant species foliar cover data were used to develop a hierarchical, floristic-based community type classification with TWINSPLAN and DECORANA software. Six planmergent (conspicuous portion of vegetative plant body on the water surface) and 24 submergent (vegetative plant body found primarily underwater) community types were identified. Multivariate analysis indicated that all community types displayed significant differences in plant species composition, and the Sorensen's floristic similarity between communities averaged 10% for planmergent and 8% for submergent types. Canonical correspondence analysis was used to inspect relationships between abiotic factors and plant species abundance. Results of this analysis indicated some relationships between species distributions and abiotic factors; however, chance introduction of plant species to water bodies is a process considered to be equally important to the presence of the community types described.

Key words: aquatic plant communities, aquatic macrophyte vegetation, ecological classification, synecological study, vegetation classification.

Aquatic plant communities are widely distributed throughout the Northern Rockies, occurring in both natural and man-made water bodies of glaciated landscapes such as lakes, ponds, reservoirs, and low-velocity streams. The ecological value of these communities is twofold. First, they enhance a variety of processes in aquatic ecosystems such as oxygen production, substrate stabilization, nutrient cycling, improved water quality, and phytoplankton reduction (Nichols 1986, Scheffer 1998, Jurgens and Jeppeson 1997). Additionally, these communities provide habitat for aquatic fauna, nesting sites for waterfowl, and forage for large ungulates such as moose (Scheffer 1998, Lodge et al. 1997, Nichols 1986, Fraser et al. 1982).

Despite the importance of aquatic plant communities to ecosystem function and species habitat, they have received relatively little attention in the scientific literature. To date most research concerning mesic plant communities within the Northern Rockies has focused primarily on wetland and riparian types (Hansen et al. 1995); however, no classification system exists for aquatic plant communities. Even for the western United States, work on

aquatic plant community classification has been largely descriptive, with little supporting field data (Schuyler 1984, Sawyer and Keeler-Wolf 1995). The primary objective of this paper is to provide a quantitative classification of aquatic macrophyte plant communities for the United States portion of the Northern Rockies. The classification scheme presented is hierarchical and designed to nest within the national wetland and deep-water habitat system first proposed by Cowardin et al. (1979) and later modified for the Northern Rockies by Rabe and Chadde (1994). Specifically, our aquatic plant community classification describes important types at the subclass and dominant levels of these previous classification schemes. Our classification provides a much needed tool for future land management activities within lacustrine and riverine systems.

METHODS

Study Sites

We sampled 111 water bodies or sites across northern Idaho and western Montana during the summers of 1997, 1998, and 1999 (Fig. 1). Site selection was based on “subjective sampling

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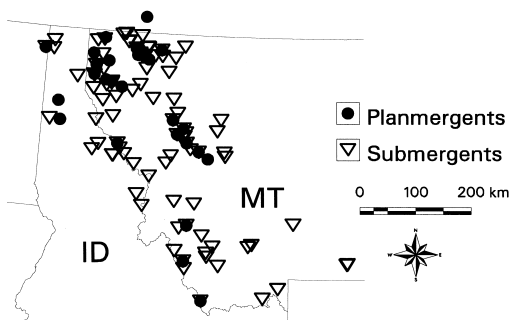


Fig. 1. Location of sampled water bodies used in developing a classification of aquatic plant communities for the Northern Rocky Mountains.

without preconceived bias” as described by Mueller-Dombois and Ellenberg (1974). Our objective was to describe representative aquatic plant communities for the study area. Accordingly, we stratified our sample to ensure that we characterized the following environmental factors that might influence species distributions: elevation (sites ranged from 628 to 2667 m), landform (valley bottoms to cirque basins), geology, and water body size. Six water bodies with less than 3-m visibility were visited but not sampled because we felt that the chance of missing a plant species or misreading associated measurements was too great in such situations.

Field Data

Sampling at each site was conducted along a water depth gradient that began where shoreline terrestrial vegetation ended and proceeded to a depth where aquatic plant species disappeared and the substrate was unvegetated. Sampling of the aquatic plant communities present along these transects was made within a 405-m² macroplot following ECO-DATA vegetation sampling procedures routinely used by the USDA Forest Service, Northern Region (USDA, Forest Service 1992). We sampled 169 macroplots in the 111 water bodies studied. The number of macroplots sampled along each water body transect ranged from 1 to 3, depending on the number of communities present at different depths. SCUBA equipment was used extensively in field sampling.

Vegetation information collected at each macroplot included a complete list of all macrophyte plants present, as well as their average height and foliar cover. Taxonomies used

in the identification of vascular plant species included Fassett (1940), Hitchcock and Cronquist (1973), Dorn (1984), Borman et al. (1997), and Douglas et al. (1994), in decreasing order of usage. We identified mosses and algae by the taxonomies of Lawton (1971) and Prescott (1978), respectively. Macrophyte plants were defined in this study as all vascular and moss species, as well as 2 genera of algae (i.e., *Chara* spp. and *Nitella* spp.). Voucher specimens were collected for each plant species within a macroplot with representative samples of each species deposited at the MRC in Missoula, MT.

Abiotic information collected at each macroplot included elevation; minimum and maximum water depth; water temperature, pH, and conductivity within 15 cm of the substrate bottom; and total nitrogen, organic carbon, and available phosphorus (USDA NRCS 1996) within a 15-cm-deep surface core of the water body substrate.

Data Analysis

In a previous hierarchical classification of aquatic plant communities, Schuyler (1984) identified 3 life form groupings: pleustophytes (free floating plants such as *Lemna* sp.), emergents (terrestrial wetland communities), and benthophytes (plants with their basal portion in or on the water body substrate). Of these life forms, we sampled only benthophytes in this study. Schuyler further broke down benthophytes into 2 growth form types or associations: submergents (vegetative plant body parts found primarily underwater) and planmergents (conspicuous portion of vegetative plant body on the water surface). In our classification we first split sample data into submergent and planmergent groupings. For each grouping we then analyzed data concerning macroplot species presence and abundance using TWINSpan and DECORANA software (Hill 1979a, 1979b).

Two-Way INDicator SPecies ANALysis (TWINSpan) was used to develop initial aquatic plant community classifications for the macroplots based on species lists and associated foliar cover values. TWINSpan is a polythetic, divisive, hierarchical classification technique similar to the Braun-Blanquet classification method that emphasizes indicator species and the production of an arranged species-sample data matrix (Gauch 1982). Macroplots

were tentatively assigned to a community type based on their TWINSpan cluster assignment. Each macroplot was then inspected to see if it contained abundances of indicator plant species similar to those of other samples in its assigned community type. Macroplots displaying low similarity to other samples in their community type were reassigned to a different community type when appropriate. Detrended Correspondence Analysis (DECORANA; Hill and Gauch 1980), which produces a complementary ordination of species and samples to TWINSpan, was also used in the identification of sample outliers and final community type classification.

We used the multivariate statistical analysis program of SPSS (Norusis 1985) to detect floristic differences between community types and to identify indicator plant species for the classification. A Sorenson floristic similarity coefficient (Gauch 1982) was calculated between each community type to determine the number and abundance of plant species in common. Relationships between abiotic factors and plant species composition of macroplots were described using canonical correspondence analysis (CCA; ter Braak and Prentice 1988). CCA selected the linear combination of abiotic factors that best explained sample-species variability along 4 ordination axes. Significance of the regression between species and abiotic data was tested against the possibility of random association by comparing the *F*-ratio with 99 unrestricted Monte Carlo permutations of sampled data. Abiotic data were standardized to have a mean of zero and unit variance, and CCA species scores reflected weighted mean sample scores in this analysis.

RESULTS

Community Type Classification

We identified 24 submergent and 6 planmergent community types in this study (Table 1) using TWINSpan and DECORANA software (Hill 1979a, 1979b). This software, however, does not indicate whether such community types differ significantly in their vegetation composition. In testing the hypothesis that our plant communities differed in vegetation composition, we utilized 2 analysis procedures: multivariate analysis of species abundance (MANOVA) and percent similarity based

on species richness and abundance using Sorenson's similarity coefficient. Results of our MANOVA analysis indicated that all plant communities within the submergent and planmergent growth form groupings differed significantly from each other in average vegetation composition, as interpreted at a 95% confidence level. Additionally, these communities displayed low floristic Sorenson similarity scores, ranging from 0% to 37% (with an average of 10%) within planmergent community types, and 0% to 48% (with an average of 8%) within submergent community types. Given the fact that floristic similarity scores can range between 0% (no species in common) and 100% (all species and their abundance the same), we conclude that our classification of aquatic plant communities was effective in describing types with different floristic characteristics. A complete description of plant species constancy and cover, as well as floristic similarity, is available for our aquatic community types from the senior author.

A variety of plant species were effective in discriminating between the planmergent and submergent community types identified in this study. The plant species presented in our key to aquatic community types (Table 1) were also the primary indicator species of the TWINSpan and MANOVA analyses. These results suggest that forb species tend to have greater significance than graminoid, moss, or algal species in determining plant community types.

We used a foliar canopy cover of 10% or greater in our key to aquatic plant communities (Table 1) because this cover level was optimum in separating overall floristic differences between most of the community types studied. Canopy cover levels of 5%–20% have commonly been used in other classification keys for riparian and wetland communities (Youngblood et al. 1985, Hansen et al. 1995); accordingly, we felt that the 10% cover level used in this study was appropriate given previous research efforts. However, when using the key presented in Table 1, a person should first establish a visual depth transect to determine the number of plant communities present and their representative locals within a water body based on total species composition and abundance criteria. If this is not done, a community may be misidentified. For example, *Potamogeton praelongus* is primarily a deep-water

TABLE 1. Key to the 30 aquatic benthophyte plant communities identified in this study. (In using this key, observe the following procedure: If the majority of the photosynthetic biomass is at the water surface, select the first community type with 10% or more cover of the indicator species listed under the planmergent community types. If the majority of the photosynthetic biomass is below the water surface, select the first community type with 10% or more cover of the indicator species listed under the submergent community types.)

Code	Community type name	Sample size	Indicator species foliar cover	
			Average	Range
Planmergent				
NUPLUT	<i>Nuphar lutea</i>	20	31	10–60
BRASCH	<i>Brasenia schrebrei</i>	3	20	10–30
POLAMP	<i>Polygonum amphibium</i>	3	40	10–60
SPAANG	<i>Sparganium angustifolium</i>	2	15	10–20
POTNAT	<i>Potamogeton natans</i>	6	13	10–20
NYMODO	<i>Nymphaea odorata</i>	1	90	—
Submergent				
SCISUB	<i>Scirpus subterminalis</i>	4	33	10–70
POTPRA	<i>Potamogeton praelongus</i>	13	44	10–90
POTAMP	<i>Potamogeton amplifolius</i>	12	40	10–80
HIPVUL	<i>Hippuris vulgaris</i>	3	50	20–70
POTRIC	<i>Potamogeton richardsonii</i>	15	19	10–60
POTPEC	<i>Potamogeton pectinatus</i>	4	70	50–90
POTPUS	<i>Potamogeton pusillus</i>	11	35	10–90
POTFIL	<i>Potamogeton filiformis</i>	6	30	10–80
POTGRA	<i>Potamogeton gramineus</i>	1	20	—
POTFOL	<i>Potamogeton foliosus</i>	1	40	—
POTEPI	<i>Potamogeton epihydrus</i>	5	16	10–30
POTALP	<i>Potamogeton alpinus</i>	5	16	10–20
POTROB	<i>Potamogeton robbinsii</i>	5	42	10–90
POTCRI	<i>Potamogeton crispus</i>	2	75	60–90
ELEACI	<i>Eleocharis acicularis</i>	2	50	40–60
ISOBOL	<i>Isoetes bolanderi</i>	9	36	10–50
ELOCAN	<i>Elodea canadensis</i>	7	37	10–90
ELONUT	<i>Elodea nuttallii</i>	2	35	20–50
NITELL	<i>Nitella</i> spp.	5	36	20–60
CHARA	<i>Chara</i> spp.	18	69	10–90
HETDUB	<i>Heteranthera dubia</i>	1	20	
RANAQU	<i>Ranunculus aquatilis</i>	1	20	—
MYRIOP	<i>Myriophyllum</i> spp.	1	10	—
DREEXA	<i>Drepanocladus exannulatus</i>	2	50	10–90

species; however, it sometimes can be found in shallow water with enough coverage to be keyed in Table 1, despite the fact that it may be found with much higher abundance at greater depths within the same water body. Ideally, a person should use both the key presented in Table 1 and the constancy/cover tables developed in this study in identifying different aquatic plant communities present within a given water body.

Canonical Correspondence Analysis

Results of our stepwise regression analysis indicated that different abiotic variables assumed different importance in explaining the cumulative amount of species-environmental variability within macroplot samples

from both the submergent and planmergent community types (Table 2). The abiotic variables listed in Table 2 accounted for 8% and 20% of the species-sample variability in our CCA analysis of submergent and planmergent community types, respectively. The species-environment relationship was significantly different from random for all 4 CCA axes ($P = 0.01$), accounting for 73% of all explained variation within submergent plant communities, and 77% of all variation within planmergent plant communities.

Ordination of species and environmental data along the first 2 CCA axes demonstrates different gradients between submergent and planmergent communities. For submergent community types, the 1st CCA axis was most significantly related to water conductivity

TABLE 2. Cumulative amount of total species—environmental variability accounted for by different abiotic variables based on a stepwise regression analysis.

Planmergent communities		Submergent communities	
Variable	Cumulative variance explained (%)	Variable	Cumulative variance explained (%)
Water-pH	17	Water-Conductivity	20
Sediment-Phosphorus	29	Sediment-Carbon	36
Water-Conductivity	40	Elevation	50
Sediment-Carbon	53	Water-Average depth	63
Sediment-Nitrogen	65	Water-pH	74
Elevation	76	Sediment-Nitrogen	85
Water-Max depth	89	Water-Max depth	91
Water-Average depth	100	Water-Min depth	96
		Sediment-Phosphorus	100

(interser correlation = 0.57) and elevation (interser correlation = -0.55). The 2nd CCA axis was primarily related to average water depth (interser correlation = 0.43). The 1st CCA axis for planmergent communities, however, was most strongly related to average water depth (interser correlation = 0.24) and elevation (interser correlation = -0.41). The 2nd CCA axis primarily described a water chemistry gradient of phosphorus (interser correlation = -0.64) and conductivity (interser correlation = -0.62). Descriptive statistics for selected abiotic and biotic variables are presented by community type in Tables 3 and 4.

DISCUSSION

Our classification of aquatic plant communities provides the first quantitative characterization of aquatic plant communities within the Northern Rocky Mountains. We used a floristic-based method for community type classification in this study. Ideally, we would have preferred to develop a site-potential classification for aquatic communities based on an understanding of seral community relations and indicator species associated with "climax" plant communities. Such classification schemes are important to land managers and have been widely used in the characterization of forest habitat types (Daubenmire 1952, 1968, Pfister et al. 1977) and rangeland sites (Hironaka et al. 1983, Mueggler and Stewart 1980, RISC 1983). We were unable to develop a site potential-based classification in this study simply because we do not understand the seral relations between the plant communities described. Accordingly, we thought it important to first describe communities according to floristic

similarities without undue concern regarding successional status. This approach resulted in a floristic-based classification of communities, which has been shown to approximate site potential-based classifications of habitat types in other research (Komarkova 1983, Jensen et al. 1988).

A factor that complicates seral plant community description in aquatic systems relates to concepts of island biology. Island biology as described by MacArthur and Wilson (1967) and Lomolino et al. (1989) states that the presence or absence of a species in an isolated environment or "island" is primarily a function of chance introduction, establishment, loss, and reintroduction. In our opinion, each of the water bodies in our study is an island. Accordingly, the aquatic macrophyte plants described are primarily dependent on birds, mammals, boats, and trailers for dispersal from one water body to another, unless they are downstream of another source area. Because of this, chance appears to play a major role in determining species presence or absence across our samples. Despite this fact, we were still able to discern general trends across the community types.

Planmergent communities were primarily restricted to ponds, small lakes, and sheltered bays of larger lakes. These communities have little tolerance for wave action and boat traffic and tend to be absent in areas of heavy recreational use. The POTNAT community type (ct) is considered to be the most resistant planmergent community to these types of disturbance. The POLAMP ct is unique in that it was always found in recently disturbed aquatic environments or in ones with naturally fluctuating water levels. The NUPLUT ct, the most

TABLE 3. Average values for selected abiotic attributes by planmergent and submergent community types.

Community types	Sample size	Elev. (m)	Slope (%)	Water depth (cm)		Water pH	Water conductivity (μS/cm)	Organic carbon (%)	N (%)	P (ppm)
				Min.	Max.					
Planmergent										
BRASCH	3	831	2	51.8	161.5	6.7	47	10.6	1.0	0.8
NUPLUT	20	1140	6	56.4	163.1	7.2	176	21.5	1.6	1.6
NYMODO	1	701	5	91.4	243.8	8.0	210	—	—	—
POLAMP	3	1449	5	51.8	143.3	7.3	240	14.9	1.3	1.7
POTNAT	6	1300	3	36.6	137.2	7.7	188	17.9	1.2	2.1
SPAANG	2	1710	11	45.7	91.4	7.5	35	12.1	1.0	0.4
Submergent										
CHARA	18	1316	15	207.3	484.6	7.8	279	10.8	1.1	0.9
DREEXA	2	1908	80	152.4	457.2	7.7	10	8.5	0.8	2.7
ELEACI	2	1978	5	30.5	106.7	7.6	30	27.0	1.2	1.9
ELOCAN	7	1093	23	125	368.8	7.8	170	2.8	0.4	0.8
EIONUT	2	2030	1	106.7	320	7.4	60	—	—	—
HETDUB	1	1021	30	30.5	274.3	7.6	210	8.6	0.7	1.1
HIPVUL	3	1104	2	70.1	131.1	7.8	180	2.9	0.5	2.7
ISOBOL	9	1988	8	57.9	277.4	7.5	29	8.4	0.8	0.5
MYRIOP	1	1943	0	30.5	91.4	7.1	10	—	—	—
NITELL	5	1692	26	335.3	719.3	7.4	56	10.8	1.3	0.5
POTALP	5	1904	7	91.4	213.4	7.7	60	13.8	1.2	0.2
POTAMP	12	1275	28	118.9	347.5	7.3	99	13.2	1.0	0.7
POTCRI	2	1361	5	167.6	426.7	7.6	180	—	—	—
POTEPI	5	1866	7	121.9	243.8	7.4	16	20.0	1.8	0.2
POTFIL	6	1731	19	40.5	208.2	7.3	163	11.2	0.9	0.6
POTFOL	1	768	0	91.4	243.8	8.0	530	43.2	3.2	2.0
POTGRA	1	1113	150	61	426.7	8.0	370	4.1	0.3	0.6
POTPEC	4	1301	1	45.7	128	8.0	515	10.4	1.2	0.5
POTPRA	13	1371	12	256	502.9	7.5	148	10.9	1.0	0.6
POTPUS	11	1561	4	149.4	283.5	7.5	86	11.4	1.1	0.3
POTRIC	14	1355	12	91.4	265.2	7.6	153	3.8	0.4	1.5
POTROB	5	1234	14	256	554.7	7.1	80	8.7	0.9	2.3
RANAQU	1	1615	20	213.4	426.7	7.6	140	—	—	—
SCISUB	4	1041	3	91.4	198.1	7.8	382	12.4	1.1	1.6

widely observed planmergent community across the study area, occupied sites with relatively high organic carbon values (Table 3).

Across the submergent communities, we found that POTPRA and POTROB ct's consistently occupied the deepest substrate zones. CHARA and NITELL ct's (which are algal communities) were sometimes observed at deeper depths; however, they were just as commonly found in shallow depth environments (Table 3). NITELL and POTEPI ct's were found in water with a conductivity $< 100 \mu\text{S}/\text{cm}$, while the CHARA ct was found where conductivity was $> 100 \mu\text{S}/\text{cm}$. Plant communities most likely to be found in moving water were HIPVUL, POTPEC, and POTRIC.

From our transect data we found that macrophyte plant species diversity generally decreased with increasing depth. This same trend also occurred as elevation of water bodies increased. Segal (1971) also made similar

observations in his study of aquatic macrophytes, concluding that species diversity and community diversity decrease as the environment becomes more extreme. Our transect data also indicated that plant community diversity was often maximized within areas of water inflow into lakes and ponds. Additionally, the position of the thermocline was important to the zonation of aquatic communities, with most types stopping at this zone or experiencing an abrupt change in community composition.

Only 2 plant communities were named after nonnative species in this study. *Nymphaea odorata* is from North America; however, its native range is east of our study area (Fasset 1940). Usually when this species is found, its floating leaf canopy coverage is commonly so high that light is severely diminished beneath its canopy. Consequently, species diversity and abundance are greatly reduced when the NYMODO ct is present. The other nonnative

TABLE 4. Average values for selected vegetation attributes by planmergent and submergent community types.

Community types	Spp. richness	Community height (cm)	Foliar cover (%)				
			Graminoids	Forbs	Ferns	Moss	Algae
Planmergent							
BRASCH	4.0	—	13	33	0	0	27
NUPLUT	7.0	—	1	36	0	1	11
NYMODO	5.0	—	1	90	0	0	0
POLAMP	6.0	—	0	53	0	20	30
POTNAT	5.2	—	0	30	0	0	27
SPAANG	4.0	—	2	20	2	0	0
Submergent							
CHARA	3.0	15	0	2	0	2	69
DREEXA	1.0	4	0	0	0	50	0
ELEACI	3.5	6	40	0	0	2	0
ELOCAN	4.7	45	0	10	0	0	6
EIONUT	1.0	100	0	35	0	0	0
HETDUB	5.0	30	0	30	0	0	1
HIPVUL	4.0	30	0	80	0	0	0
ISOBOL	2.1	4	0	0	36	4	0
MYRIOP	1.0	10	1	10	0	0	0
NITELL	3.0	30	0	6	0	1	38
POTALP	3.0	15	16	34	0	0	18
POTAMP	3.2	100	0	44	0	0	0
POTCRI	3.5	180	0	90	0	0	0
POTEPI	3.0	20	1	22	9	12	0
POTFIL	3.4	40	4	30	0	0	16
POTFOL	5.0	60	0	60	0	0	3
POTGRA	5.0	30	0	30	0	0	60
POTPEC	2.5	60	0	70	0	0	42
POTPRA	3.0	300	0	56	0	0	8
POTPUS	5.3	70	2	55	0	1	21
POTRIC	5.5	120	1	39	0	0	15
POTROB	3.0	60	0	44	0	0	0
RANAQU	1.0	30	0	20	0	0	0
SCISUB	5.2	30	30	13	0	0	18

community we observed is named after *Potamogeton crispus*. This species was found only in reservoirs where it dominated the community type structure.

With regard to the genus *Myriophyllum*, the 2 species described were *M. verticillatum* and *M. sibiricum*. These species were rarely found in flower, making them difficult to identify. Because of this, we used only the genus name in our community type classification.

CONCLUSIONS

Our classification of aquatic plant communities within the Northern Rocky Mountains is by necessity largely descriptive. To date little, if any, attention has been given to describing synecological relations of these communities. Additionally, the autecological relations of many aquatic macrophyte plant species are also poorly understood.

Given the importance of these communities to aquatic system function and species habitat, it is imperative that more scientific studies be conducted. The sensitivity of these communities to eutrophication, boat use, altered flows, and introduced exotic species suggests that little time still remains for scientific study and maintenance of these systems. The permanent plots used in this study provide a needed baseline for future monitoring efforts. The classification developed in this study provides a useful communication tool for future land management activities within aquatic environments.

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TREE GROWTH AND REGENERATION RESPONSE TO CLIMATE AND STREAM FLOW IN A SPECIES-RICH SOUTHWESTERN RIPARIAN FOREST

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ABSTRACT.—We studied the influence of climate variables, stream flow, and topography on regeneration and growth of several riparian tree species (*Acer negundo*, *Alnus oblongifolia*, *Fraxinus velutina*, *Juglans major*, *Platanus wrightii*, *Populus fremontii*, *Salix* spp.) at an unregulated perennial stream, West Clear Creek, in central Arizona. A pulse of seedling regeneration occurred for *Alnus*, *Fraxinus*, *Platanus*, *Populus*, and *Salix* in 1995 and 1996 following high winter and spring surface flows in 1993 and high spring surface flow in 1995. In contrast, little regeneration occurred for *Acer* and *Juglans* under these conditions. Most seedlings occurred at the active channel topographic location, and few seedlings occurred at abandoned channel, gravel-boulder bar, and bench locations. Relationships between environmental variables and annual radial stem growth varied among species and between constrained and unconstrained reaches. High spring or winter surface flows were negatively related to growth of *Acer*, *Alnus*, and *Platanus*, whereas high spring surface flow was positively related to growth of *Fraxinus*. Positive relationships between precipitation and growth occurred only for *Fraxinus* and *Juglans*, suggesting greater use of surface soil water by these species. Annual radial growth was high for *Platanus* and *Alnus*, medium for *Acer* and *Fraxinus*, and low for *Juglans*. Overall, the tree species in our study responded individually, rather than collectively, in regeneration and growth to changes in stream flow and climatic variables.

Key words: Arizona, *Acer negundo*, *Alnus oblongifolia*, climate, dendrochronology, *Fraxinus velutina*, *Juglans major*, *Platanus wrightii*, *Populus fremontii*, regeneration, riparian, *Salix*, tree ring, stream flow.

Riparian areas are physically linked to and dependent upon perennial, ephemeral, or intermittent surface or subsurface waters (Arizona State Parks 1994). These areas provide critical habitat for wildlife and vegetation across the United States (Brinson et al. 1981) and are important for maintaining regional biodiversity (Naiman et al. 1993). Riparian areas in the southwestern United States support forests that resemble the mesophytic humid forests that were widespread in the Early Tertiary era (Minckley and Brown 1982). The development of a drier climate after this era in the Southwest limited riparian forests to sites with dependable water sources (Minckley and Brown 1982). More recently, southwestern riparian forests have been depleted by human impacts such as flow regulation, dewatering, groundwater pumping, and grazing (Johnson and Haight 1984, Swift 1984, National Research Council 1992, Rood and Mahoney 1993, Stromberg 1993, Busch and Smith 1995, Stromberg et al. 1996). Given the high value and increasing scarcity of southwestern riparian forests,

factors that influence the regeneration and growth of riparian trees need to be better understood.

Flooding and resulting geomorphic changes in riparian ecosystems often cause changes in their biotic communities (Vannote et al. 1980). For example, recruitment of riparian *Populus* species has been linked to high surface flows in western North America (Everitt 1968, Brady et al. 1985, Howe and Knopf 1991). High flows scour openings along stream banks, widen floodplains, and deposit alluvium, thus creating extensive open fluvial surfaces for recruitment of pioneer trees such as *Populus* (Stromberg et al. 1991, 1993, Scott et al. 1997, Stromberg 1997). Moreover, seedfall for many riparian trees coincides with spring flooding (Everitt 1968, McBride and Strahan 1984, Fenner et al. 1985, Bock and Bock 1989, Siegel and Bock 1990, Stromberg 1993, Friedman et al. 1995). Further, overland flows created by spring flooding can promote seedling establishment by providing a moist seedbed for germination (Bock and Bock 1989, Stromberg 1997).

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Survival of riparian tree seedlings can be influenced by environmental factors such as temperature, pH, and salinity (Siegel and Bock 1990), as well as their location on the floodplain. Optimal germination sites for long-term survival of riparian trees are at elevations high enough on the floodplain to protect the substrate and new seedlings from scouring, yet low enough to provide direct contact with moist sediments (McBride and Strahan 1984, Stromberg et al. 1991, 1993, Scott et al. 1997, Stromberg 1997). Riparian forests also have been shown to develop successfully in abandoned channels created by fluctuating seasonal flows (Brady et al. 1985). Further, the topography of the floodplain may also affect long-term survival of riparian trees. Trees growing in broad floodplains may suffer lower mortality during high flows than those growing in narrow, constrained reaches due to high flow velocity and inundation in narrow reaches (Palik et al. 1998, Friedman and Auble 1999).

Most research on southwestern riparian forests has concentrated on low-elevation forests dominated by trees in the genera *Populus* and *Salix* and has focused on the impacts of stream flow or groundwater regulation by humans (e.g., Brady et al. 1985, Stromberg and Patten 1990, 1991, 1996, Howe and Knopf 1991, Stromberg et al. 1991, 1993, 1996, Stromberg 1993, 1997, Busch and Smith 1995, Cooper et al. 1999, Shafroth et al. 2000, Horton and Clark 2000, Horton et al. 2001). Factors that affect regeneration and growth of species-rich riparian forests of higher elevations in the Southwest (Brown 1982, Szaro 1990) are poorly understood, and yet these forests are widespread in the region and may be increasingly threatened by anthropogenic impacts as human populations grow in the Southwest. Our study addressed the influences of topographic location, stream flow, and climatic variables on regeneration and growth of several riparian tree species (*Acer negundo*, *Alnus oblongifolia*, *Fraxinus velutina*, *Juglans major*, *Platanus wrightii*, *Populus fremontii*, and *Salix* spp.) growing in a relatively pristine, species-rich riparian forest along an unregulated perennial stream in central Arizona, West Clear Creek.

We addressed the following hypotheses. First, high stream flow promotes seedling regeneration of all these tree species. Second, seedling density would be distributed unevenly across different topographic locations, with

the greatest densities occurring in abandoned channels, low benches, and adjacent to the active channel. Third, seedling density and annual radial growth of all species would be greater in unconstrained areas of the floodplain compared with bedrock-constrained areas. Fourth, annual radial growth of all tree species would be correlated with stream flow and climate characteristics. Specifically, we expected positive correlations between growth rate and surface flow and precipitation based on the premise that tree growth in the southwestern United States is often strongly limited by water availability (Fritts 1974). We also expected negative correlations between growth and air temperature during the growing season because high temperatures would limit photosynthesis due to high vapor pressure deficit, as shown for *Acer negundo* at a perennial stream near our study site (Kolb et al. 1997). Last, we hypothesized that radial growth rate would differ among species.

METHODS

Study Site

The study location is West Clear Creek, a free-flowing perennial stream within the sub-Mogollon region (Minckley and Brown 1982) of the Colorado Plateau in central Arizona (Fig. 1). West Clear Creek flows approximately 48 km through a deep canyon to its confluence with the Verde River. The geology of the watershed comprises sedimentary rocks overlain with basalt in some areas. Elevations in the West Clear Creek watershed range from approximately 2300 m to 945 m. Our study site is located at the Bull Pen U.S. Geological Survey gaging station (lat. 34°32'19", long. 111°41'36", in NW1/4, NW1/4, sec 11, T13N, R6E, Yavapai County, Hydrologic Unit 15060203) 14.5 km east of Camp Verde and 17.7 km upstream of the mouth in the Coconino National Forest at 1106 elevation (Fig. 1).

Surface flow at West Clear Creek varies seasonally. Between 1969 and 1992 average monthly base flow varied between 0.42 and 0.57 m³ sec⁻¹ from May through January (Galusky 1994). Surface flows were highest in February and March due to runoff from snowmelt and averaged 1.13 m³ sec⁻¹ (Galusky 1994). Temperatures at highest elevations in the watershed (Happy Jack Ranger Station, Coconino National Forest) average 7.8°C annually,

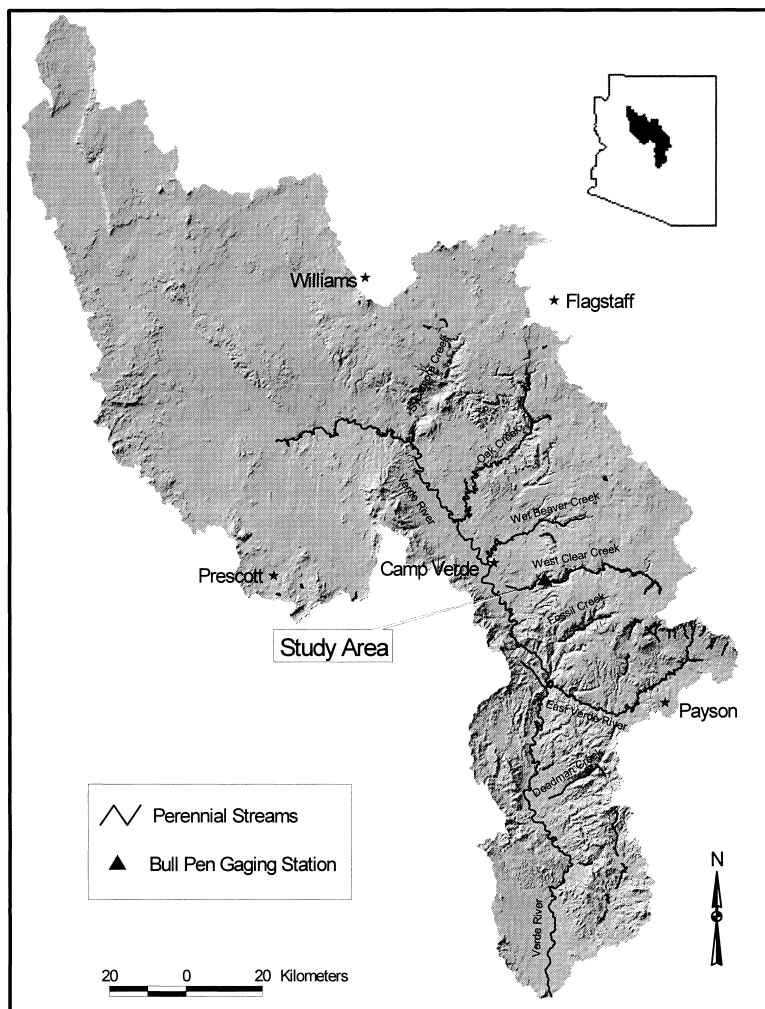


Fig. 1. Location of West Clear Creek and the study area in the Verde River Watershed, Arizona.

17.2°C in July, and -2.8°C in January (Western Regional Climate Center). Average annual precipitation at the highest elevations is 68.6 cm, which includes an average of 223.5 cm of snowfall. Temperature at Beaver Creek Ranger Station (Coconino National Forest), which is located within approximately 15 km of the study site at a similar elevation to the lower parts of the watershed, averaged 16.7°C annually, 27.2°C in July, and 6.7°C in January (Western Region Climate Center). Average annual precipitation at the Beaver Creek Ranger Station is 40.6 cm, which includes only a few centimeters of snowfall per year (Galusky 1994).

A variety of biotic communities occur in the West Clear Creek watershed. In upland parts of the watershed (elevations >1823 m), *Pinus ponderosa* dominates (Plan West Associates 1994). Between elevations of 1822 m and approximately 1372 m, *Pinus edulis*, *Juniperus scopulorum*, *J. deppeana*, *J. osteosperma*, and *J. monosperma* woodland communities (Minckley and Brown 1982) dominate. The lowest upland elevations of the watershed (<1372 m elevation) support interior chaparral and desert scrub communities (Galusky 1994). The interior canyon of West Clear Creek supports a deciduous broadleaf forest of riparian trees typical of mid-elevation, warm temperate,

riparian ecosystems in Arizona (Minkley and Brown 1982). The riparian tree species at our study site include *Acer negundo*, *Alnus oblongifolia*, *Fraxinus velutina*, *Juglans major*, *Platanus wrightii*, *Populus fremontii*, *Salix* spp., and a few *Amorpha fruticosa*, *Robinia neomexicana*, and *Tamarix chinensis*.

Field Sampling

We conducted all field sampling in October and November 1996. Our study area included the riparian forest corridor from approximately 760 m upstream to 100 m downstream of the Bull Pen gaging station. At the gaging station, West Clear Creek was characterized by a broad, unconstrained floodplain and a shallow braided channel of sand and cobbles. Approximately 360 m above the gaging station, the canyon narrows and forms a bedrock-constrained narrow channel characterized by little sediment accumulation.

Because West Clear Creek supports a continuous riparian forest, we used a systematic sampling approach with a randomly placed origin to sample trees. We established transects beginning 100 m below the gaging station. In all, 8 transects were established, 4 in the constrained reach and 4 in the unconstrained reach. Of the 8 total transects, 7 were above the gaging station and 1 was below. With this placement, flow data from the gaging station could be used reliably for all transects. We oriented each transect parallel to the stream channel, choosing the side with the broadest floodplain to maximize the number of trees available for sampling. Therefore, the width of each transect varied and included the riparian forest from the edge of the active stream channel to its outer edge. All transects were 20 m long and spaced 100 m apart. However, we did not sample upper peripheral terraces that were characterized by a mixture of xeric shrubs and old, decaying riparian trees with rotten centers.

We recorded the species, diameter at breast height (dbh), and topographic location of every tree in all transects. The following topographic location descriptors were used: active channel, abandoned channel, gravel-boulder bar, first bench, and second bench. We defined the active channel as the area directly adjacent to the stream bank characterized by shallow (<10 cm deep), low-velocity surface flow that covered fine sediments and small cobbles. The

abandoned channel location was an older stream channel that was dry at low flows but had recently been within the active channel prior to high flows which rerouted the stream. Abandoned channels were lower in elevation than gravel-boulder bars or benches. Gravel-boulder bars were remnant alluvial bars, deposited during recent high flows. These bars, elevated at least 1 m above stream base flow, were composed of large cobbles and boulders; fine sediment was generally absent. The first bench location included stream banks immediately adjacent to the active channel; it was characterized by fine sediments deposited among cobbles. This location was raised above the stream base flow up to 1 m. Finally, second bench described the terrace above and peripheral to the first bench location. These areas were raised 1 m or more above stream base flow and were covered in sand, fine sediment, and cobbles.

We established smaller plots within each transect to sample seedlings. These plots were positioned along the upstream border of the transect and were 5 × 5 m in size. We counted and recorded the species, age, and topographic location of all seedlings in these plots. This sampling occurred at each topographic location where seedlings occurred. Therefore, 1 transect could have up to 4 seedling plots, 1 for each topographic location. We aged seedlings by visual observation of terminal bud scars. We practiced this technique of estimating seedling age by comparing ages estimated from bud scars with counts of tree rings from increment cores taken at the soil surface.

Tree Ring Measurement

We excavated each tree with a dbh >5 cm to expose the root collar and extracted 2 increment cores spaced 90° apart just above the root collar to ensure accurate determination of the date of regeneration (Sigafoos 1964, Scott et al. 1997). The cores were prepared for analysis using standard dendrochronological techniques (e.g., Schweingruber 1988). We measured the width of annual growth rings under 20X magnifying power with an automated computer counter accurate to the nearest 0.01 mm. Any cores with questionable rings were evaluated by 2 other experienced people. We cross-dated growth rings of all trees using skeleton plotting (Stokes and Smiley 1968, Schweingruber 1988) and made

modifications to the tree-ring database for obvious missing or false rings.

To standardize annual radial growth of each tree, we divided radial growth in each year by the mean annual radial growth over all years for that tree (Stromberg and Patten 1990). We developed annual radial growth indices for each species for the period between 1964 and 1996 averaged over transects, topographic locations, reaches, and streamwide. Trees <5 years old were excluded from the indices. The number of radial growth increments used to develop the indices varied among years, sites, and species because of differences in spatial occurrence and age among trees. The number of streamwide cores used for the indices was greater for *Fraxinus velutina* ($n = 27\text{--}60$, depending on year) and *Alnus oblongifolia* ($n = 21\text{--}40$) than for *Acer negundo* ($n = 3\text{--}13$), *Juglans major* ($n = 1\text{--}8$), and *Platanus wrightii* ($n = 6\text{--}8$; Fig. 2).

Hydrologic and Climatic Variables

We obtained flow data for the Bull Pen gaging station (number 09505800) from the U.S. Geological Survey (U.S. Geological Survey 2000). These data included daily flow records from October 1964 through October 1996. Climate data were obtained from the Western Regional Climate Center, Desert Research Institute, on CD-ROM for the Beaver Creek Ranger Station (climate station number 020670, 1164 m elevation), located approximately 15 km from the study site and at a similar elevation. The climate data included precipitation and temperature summaries from 1964 through 1996. From the National Oceanic and Atmospheric Administration, we obtained Palmer Drought Severity Index (PDSI; Palmer 1965) values for the region of our study location. PDSI values show departures from average soil water availability. Increasing drought severity results in decreasing (more negative) PDSI values.

Data Analysis

SAS (Version 6.12, SAS Institute Inc., Cary, NC, USA) and SPSS (Version 9.0, SPSS Inc., Chicago, IL, USA) statistical software were used for all analyses. We evaluated the effect of stream reach and species on seedling density and mature-tree radial growth rate (nonstandardized) of the 5 most prevalent riparian tree

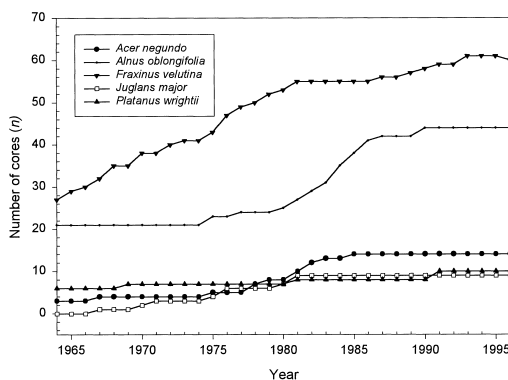


Fig. 2. Number of cores (n) for 5 tree species in 1996 at West Clear Creek used to develop streamwide standardized growth indices.

species (*Alnus oblongifolia*, *Fraxinus velutina*, *Platanus wrightii*, *Populus fremontii*, and *Salix* spp.) using 2-factor, fixed-effects ANOVAs. Factors in the ANOVAs were species, reach, and their interaction. A Tukey multiple-range test was used to compare means among species using a significance level of $P \leq 0.05$. For seedling density this analysis was limited to the active channel location because >90% of all seedlings were located there (Table 1).

We developed 28 environmental variables (Table 2) to describe variations in temperature, precipitation, and stream flow for West Clear Creek between 1965 and 1996. We examined the relationships between these environmental variables and standardized annual radial stem growth of *Acer negundo*, *Alnus oblongifolia*, *Fraxinus velutina*, *Juglans major*, and *Platanus wrightii* averaged streamwide and over constrained and unconstrained reaches separately using forward multiple regression that allowed testing of the independent influence of each variable on growth (Neter et al. 1996). Coefficients of partial determination (r^2) were considered significant at $P \leq 0.05$.

Finally, we constructed a histogram that showed the number of trees that established for each species in each year and West Clear Creek's seasonal flow regime from 1966 through 1996. Using this histogram, we graphically evaluated the relationship between stream flow characteristics and the date of establishment of 7 tree species (*Acer negundo*, *Alnus oblongifolia*, *Fraxinus velutina*, *Populus fremontii*, *Juglans major*, *Platanus wrightii*, and *Salix* spp.) Because we aged only living trees, and because of our inability to account for trees

TABLE 1. Distribution of seedlings of different species in 1996 at 3 topographic locations along West Clear Creek. Totals are combined across constrained and unconstrained reaches.

Species	Total seedlings counted	Topographic location	Total seedlings at each location	% of total for location
<i>Acer negundo</i>	1	Active channel	1	100
<i>Alnus oblongifolia</i>	877	Abandoned channel	70	7.98
		Active channel	807	92.02
<i>Amorpha fruticosa</i>	3	Active channel	3	100
<i>Fraxinus velutina</i>	356	First bench	12	3.37
		Abandoned channel	16	4.49
		Active channel	328	92.13
<i>Juglans major</i>	1	Abandoned channel	1	100
<i>Platanus wrightii</i>	161	Abandoned channel	6	3.73
		Active channel	155	96.27
<i>Populus fremontii</i>	285	Abandoned channel	4	1.40
		Active channel	281	98.60
<i>Robinia neomexicana</i>	1	First bench	1	100
<i>Salix</i> spp.	102	Active channel	102	100
<i>Tamarix chinensis</i>	5	Active channel	5	100

swept away during past floods, this analysis was limited to a visual interpretation of the number of sampled trees that established during different years.

RESULTS

Seasonal Stream Flow and Recruitment of Riparian Trees

Our analysis of the relationship between seedling establishment and seasonal stream flow revealed evidence of frequent germination between 1966 and 1992 by *Acer negundo*, *Alnus oblongifolia*, *Fraxinus velutina*, *Juglans major*, and *Platanus wrightii* (Fig. 3). Seedling establishment of all species was low the first (1993) and second (1994) springs after a winter high-flow event in 1993 that scoured the West Clear Creek channel (Fig. 3). In spring of 1993 only 12 individuals of all species established, and in spring of 1994 only 13 individuals of all species established on our plots. However, the winter of 1995 had low winter flow followed by a moderately high spring flow, and these conditions produced 486 *Alnus oblongifolia*, 99 *Fraxinus velutina*, 85 *Platanus wrightii*, 214 *Populus fremontii*, and 63 *Salix* spp. seedlings on our plots. An additional 392 *Alnus oblongifolia*, 250 *Fraxinus velutina*, 76 *Platanus wrightii*, 70 *Populus fremontii*, and 39 *Salix* spp. seedlings established on these plots in 1996. In contrast, no *Juglans major* and only 1 *Acer negundo* seedling established on our plots in 1995 and 1996 (Fig. 3).

TABLE 2. Environmental variables used in multiple regression analyses. Chronologies for 1965 through 1996 were developed for each variable.

Variables
Winter precipitation (1 October–31 January)
Spring precipitation (1 February–30 April)
Summer precipitation (1 May–30 June)
Monsoon precipitation (1 July–30 September)
Annual precipitation (1 October–30 September)
Winter mean maximum 24-hour temperature (1 October–31 January)
Spring mean maximum 24-hour temperature (1 February–30 April)
Summer mean maximum 24-hour temperature (1 May–30 June)
Monsoon mean maximum 24-hour temperature (1 July–30 September)
Winter mean minimum 24-hour temperature (1 October–31 January)
Spring mean minimum 24-hour temperature (1 February–30 April)
Summer mean minimum 24-hour temperature (1 May–30 June)
Monsoon mean minimum 24-hour temperature (1 July–30 September)
Mean winter temperature (1 October–31 January)
Mean spring temperature (1 February–30 April)
Mean summer temperature (1 May–30 June)
Mean monsoon temperature (1 July–30 September)
Winter surface flow (1 October–31 January)
Spring surface flow (1 February–30 April)
Summer surface flow (1 May–30 June)
Monsoon surface flow (1 July–30 September)
Annual surface flow (1 October–30 September)
Maximum winter surface flow (1 October–31 January)
Maximum spring surface flow (1 February–30 April)
Maximum summer surface flow (1 May–30 June)
Maximum monsoon surface flow (1 July–30 September)
Maximum annual surface flow (1 October–30 September)
Palmer Drought Severity Index (PDSI)

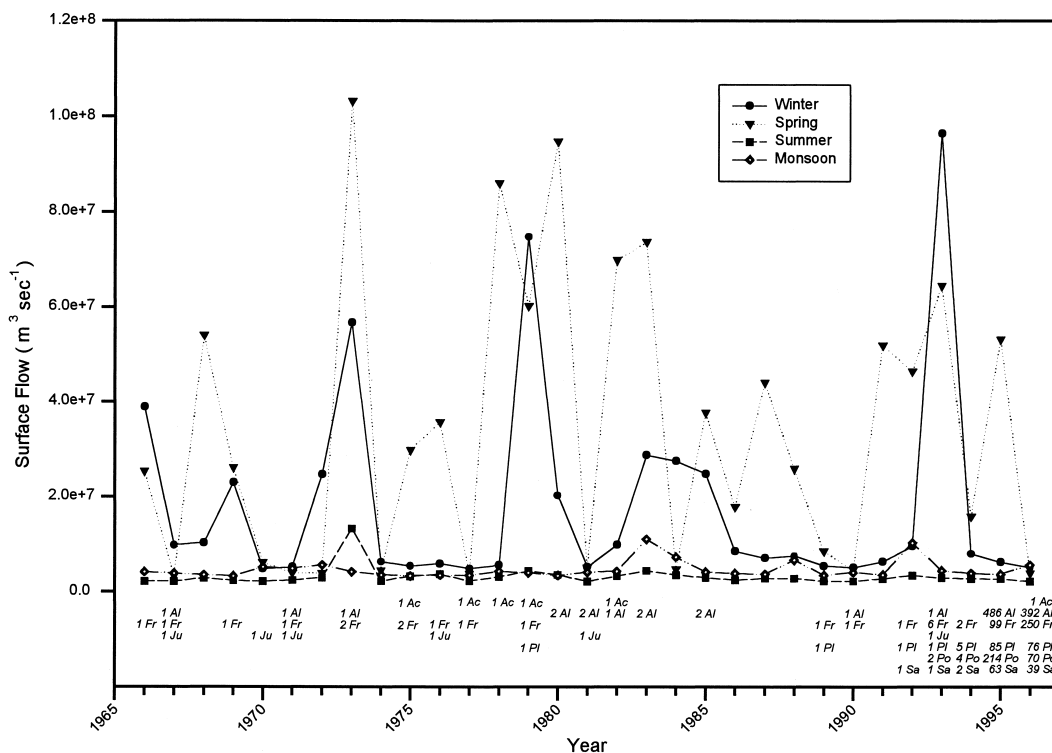


Fig. 3. Seasonal surface flow ($\text{m}^3 \text{sec}^{-1}$) for winter (1 October–31 January), spring (1 February–30 April), summer (1 May–30 June), and monsoon (1 July–30 September) periods from 1965 through 1996 at West Clear Creek. Numbers and codes above the x-axis show the number of individuals that established for 7 tree species (Ac = *Acer negundo*, Al = *Alnus oblongifolia*, Fr = *Fraxinus velutina*, Ju = *Juglans major*, Pl = *Platanus wrightii*, Po = *Populus fremontii*, Sa = *Salix* spp.) for each year.

Seedling Density

The active channel was the preferred location for seedling recruitment, with 92% of *Alnus oblongifolia* seedlings, 92% of *Fraxinus velutina* seedlings, 96% of *Platanus wrightii* seedlings, 99% of *Populus fremontii* seedlings, and 100% of *Salix* spp. seedlings occupying that topographic location (Table 1). Seedling density at the active channel location differed significantly among species ($P = 0.005$) but not between constrained and unconstrained reaches ($P = 0.13$). Further, the reach \times species interaction was not significant ($P = 0.404$), indicating a similar effect of reach on seedling density for each species. Mean seedling density along the active channel was highest for *Alnus oblongifolia*, intermediate for *Fraxinus velutina* and *Populus fremontii*, and lowest for *Platanus wrightii* and *Salix* spp. (Table 3).

Radial Growth

Of 28 environmental variables tested (Table 2), several were significantly related to annual

TABLE 3. Mean seedling density (number individuals m^{-2}) in 1996 along the active channel topographic location of 5 tree species averaged over constrained and unconstrained reaches at West Clear Creek. Means followed by the same letter do not differ significantly ($P \leq 0.05$) with Tukey's Multiple Range test.

Species	Mean density	s
<i>Alnus oblongifolia</i>	4.04 ^a	1.13
<i>Fraxinus velutina</i>	1.64 ^{a,b}	0.69
<i>Platanus wrightii</i>	0.78 ^b	0.33
<i>Populus fremontii</i>	1.41 ^{a,b}	0.56
<i>Salix</i> spp.	0.51 ^b	0.21

variation in standardized radial stem growth. Growth of *Acer negundo* streamwide was significantly ($P = 0.026$) and negatively related to high spring surface flow (Table 4), which accounted for 16% of the yearly variability in growth. *Acer negundo* growth streamwide was also negatively related to summer mean maximum temperature (partial $r^2 = 0.29$, $P = 0.0007$; Table 4); this pattern also occurred at

TABLE 4. Results of forward multiple regression analyses for 5 tree species at West Clear Creek using standardized tree-ring indices averaged streamwide from 1965 through 1996 as the dependent variable and 28 environmental independent variables.

Species	Environmental variable	Partial r^2	Slope direction	P
<i>Acer negundo</i>	Summer mean maximum temp.	0.2885	—	0.0007
	Spring surface flow	0.1578	—	0.0269
	Monsoon mean temp.	0.0584	+	0.0743
	Winter precipitation	0.0561	+	0.0923
<i>Alnus oblongifolia</i>	Monsoon mean minimum temp.	0.0980	+	0.0863
<i>Fraxinus velutina</i>	Mean winter temp.	0.2570	—	0.0036
	Summer precipitation	0.1494	+	0.0129
<i>Juglans major</i> ^a	Winter mean maximum temp.	0.1845	+	0.0121
	Palmer Drought Severity Index	0.1569	+	0.0334
	Mean spring temperature	0.0745	—	0.0862
<i>Platanus wrightii</i>	Maximum spring surface flow	0.0951	—	0.0913

^aFound only at the constrained reach.

TABLE 5. Results of forward multiple regression analyses for 5 tree species at West Clear Creek using standardized tree-ring indices averaged over the constrained reach from 1965 through 1996 as the dependent variable and 28 environmental independent variables.

Species	Environmental variable	Partial r^2	Slope direction	P
<i>Acer negundo</i>	Annual surface flow	0.1510	—	0.0307
	Summer mean maximum temp.	0.1469	—	0.0222
	Monsoon mean max. temp.	0.1027	+	0.0406
<i>Alnus oblongifolia</i>	Maximum winter surface flow	0.1524	—	0.0299
	Summer mean maximum temp.	0.0851	+	0.0879
	Monsoon mean max. temp.	0.0769	—	0.0932
	Mean monsoon temp.	0.0715	+	0.0937
<i>Fraxinus velutina</i>	Mean winter temp.	0.2050	—	0.0105
	Summer precipitation	0.1924	+	0.0058
<i>Juglans major</i>	Winter mean maximum temp.	0.1845	+	0.0121
	Palmer Drought Severity Index	0.1569	+	0.0334
	Mean spring temp.	0.0745	—	0.0862
<i>Platanus wrightii</i>	None	—	—	—

the constrained reach (partial $r^2 = 0.15$; $P = 0.022$; Table 5). *Acer negundo* growth was negatively related to annual surface flow in the constrained reach only (partial $r^2 = 0.15$, $P = 0.031$; Table 5), a response similar to the negative relationship between spring surface flow and growth of *Acer negundo* streamwide (Table 4). *Acer negundo* growth at the constrained reach was positively related to monsoon season mean maximum temperature (partial $r^2 = 0.103$, $P = 0.041$; Table 5). None of the 28 environmental variables tested was significantly

($P \leq 0.05$) related to *Acer negundo* growth at the unconstrained reach (Table 6).

Growth of *Fraxinus velutina* was negatively related to winter mean temperature streamwide (partial $r^2 = 0.26$, $P = 0.0036$; Table 4) and at the constrained reach (partial $r^2 = 0.21$, $P = 0.011$; Table 5). Summer precipitation was positively related to growth of *Fraxinus velutina* streamwide (partial $r^2 = 0.15$, $P = 0.013$; Table 4) and at the constrained reach (partial $r^2 = 0.19$, $P = 0.0058$; Table 5). Growth of *Fraxinus velutina* at the unconstrained reach

TABLE 6. Results of forward multiple regression analyses for 5 tree species at West Clear Creek using standardized tree-ring indices averaged over the unconstrained reach from 1965 through 1996 as the dependent variable and 28 environmental independent variables. *Juglans major* was found only at the constrained reach.

Species	Environmental variable	Partial r^2	Slope direction	P
<i>Acer negundo</i>	Maximum summer surface flow	0.1180	—	0.0585
<i>Alnus oblongifolia</i>	None	—	—	—
<i>Fraxinus velutina</i>	Maximum spring surface flow	0.1360	+	0.0247
	Monsoon surface flow	0.1249	+	0.0512
	Palmer Drought Severity Index	0.0900	—	0.0840
<i>Juglans major</i> ^a	—	—	—	—
<i>Platanus wrightii</i>	Maximum spring surface flow	0.1314	—	0.0450
	Maximum monsoon surface flow	0.0965	—	0.0719

^aFound only at the constrained reach.

was significantly related to only a single environmental variable, maximum spring surface flow, which was positively related to growth (partial $r^2 = 0.14$, $P = 0.025$; Table 6).

Juglans major growth at the constrained reach was positively related to PDSI (partial $r^2 = 0.16$, $P = 0.033$; Table 5). Winter mean maximum temperature was also positively related to *Juglans major* growth at the constrained reach (partial $r^2 = 0.18$, $P = 0.012$; Table 5), which was the only reach where *Juglans major* occurred. The only variable significantly related to growth of *Platanus wrightii* was maximum spring surface flow at the unconstrained reach (partial $r^2 = 0.13$, $P = 0.045$; Table 6), where growth was lower when spring surface flows were high. The only variable significantly related to growth of *Alnus oblongifolia* was maximum winter surface flow at the constrained reach (partial $r^2 = 0.15$, $P = 0.03$; Table 5), where growth was lower when maximum winter surface flows were high.

Average annual radial stem growth (non-standardized) differed significantly among species ($P < 0.001$) and reaches ($P < 0.001$), and the species \times reach interaction was significant ($P < 0.001$). Radial growth averaged over reaches was significantly higher for *Alnus oblongifolia* and *Platanus wrightii* than for *Acer negundo*, *Fraxinus velutina*, and *Juglans major* (Table 7). Radial growth averaged over all species was greater at the unconstrained reach (mean = 5.75 mm, $s = 0.39$) than the constrained reach (mean = 2.43 mm, $s = 0.45$). Further, the significant reach \times species interaction indicates that differences in radial growth

TABLE 7. Mean annual radial growth (mm) from 1965 through 1996 at West Clear Creek for 5 tree species averaged over constrained and unconstrained reaches at West Clear Creek. Means followed by the same letter do not differ significantly ($P \leq 0.05$) with Tukey's Multiple Range test.

Species	Mean annual radial growth	s
<i>Acer negundo</i>	2.49 ^a	0.84
<i>Alnus oblongifolia</i>	5.29 ^b	0.47
<i>Fraxinus velutina</i>	2.62 ^a	0.39
<i>Juglans major</i>	1.18 ^a	1.04
<i>Platanus wrightii</i>	6.57 ^c	0.74

between reaches varied among species. Specifically, growth of *Alnus oblongifolia* and *Platanus wrightii* was significantly higher at the unconstrained versus the constrained reach, whereas reach had little effect on radial growth of *Acer negundo* and *Fraxinus velutina* (Fig. 4).

DISCUSSION

We hypothesized that high surface flow events are necessary to recruit seedlings of all tree species at our West Clear Creek study site. However, we could evaluate this hypothesis only for seedling recruitment that followed the 1993 and 1995 floods because the 1993 flood removed many existing younger trees (T.E. Kolb personal observation, unpublished photo documentation by U.S. Geological Survey) and may have removed entire age classes of some tree species. Large numbers of *Alnus oblongifolia*, *Fraxinus velutina*, *Platanus*

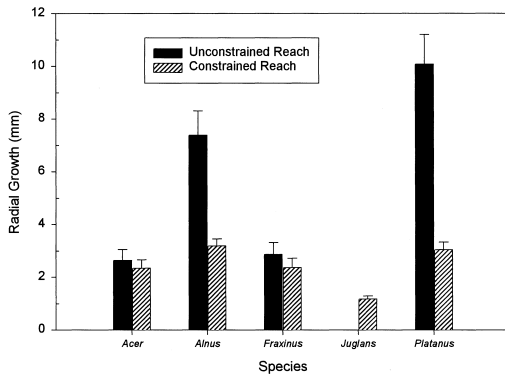


Fig. 4. Average annual radial stem growth (1965–1996) for the 5 most prevalent mature tree species at constrained and unconstrained reaches of West Clear Creek. Bars indicate 1 s. Note: *Juglans* was not found at the lower reach.

wrightii, *Populus fremontii*, and *Salix* spp. seedlings established in 1995 and 1996, suggesting that germination and establishment of these species were promoted by the high winter and spring surface flows in 1993 or the high spring surface flow in 1995. In contrast, there was only 1 *Juglans major* seedling on our plots, and it germinated in 1993 in an abandoned channel. Similarly, we observed only 1 *Acer negundo* seedling, which germinated in 1996 in an abandoned channel. These observations suggest that regeneration of *Juglans major* and *Acer negundo* at our study site was not stimulated by the high surface flow events of 1993 and 1995 as were *Alnus oblongifolia*, *Fraxinus velutina*, *Platanus wrightii*, *Populus fremontii*, and *Salix* spp. Our results on regeneration of *Populus fremontii* and *Salix* spp. are consistent with other research in the western United States on these species that has documented an increase in seedlings following high surface flows (Howe and Knopf 1991, Stromberg et al. 1991, 1993, Scott et al. 1997, Stromberg 1997).

We also hypothesized that topographic location and stream reach would influence recruitment of riparian trees at West Clear Creek. We found that *Acer negundo*, *Alnus oblongifolia*, *Fraxinus velutina*, *Platanus wrightii*, *Populus fremontii*, and *Salix* spp. regenerated almost exclusively at the active channel topographic location (>90% for all seedlings). The nearly exclusive active channel preference was unexpected because other research in Arizona riparian forests has documented that high

winter surface flows with slowly subsiding spring runoff increased sediment deposition and provided a moist seedbed along peripheral floodplains which then facilitated seedling recruitment in abandoned channels and along upper stream benches (Bock and Bock 1989, Stromberg 1997). West Clear Creek had high winter surface flows that inundated all topographic locations 3 years before our sampling (1993); thus, we expected to find more seedlings at the abandoned channel and first bench topographic locations.

The flood that occurred in December 1993 at West Clear Creek scoured the floodplain and reduced the density of mature trees, thus providing openings along the active floodplain for future seedling recruitment. However, this high winter flow also might have scoured and removed more sediment than it deposited. Additionally, the 1993 flood was a spike winter flood in which flows increased and decreased rapidly. Insufficient soil moisture during early summer months along peripheral topographic locations, such as abandoned channels and benches, may have prevented seedling establishment at all topographic locations except the active channel where seedling roots were in direct contact with saturated soil (Bock and Bock 1989, Stromberg 1997). This interpretation is consistent with other research that has shown the importance of magnitude and timing of floods in reestablishing riparian trees (e.g., McBride and Strahan 1984, Stromberg et al. 1991, 1993, Scott et al. 1997, Stromberg 1997).

We expected greater seedling density along the unconstrained reach compared with the bedrock-constrained reach. This expectation is consistent with research on other riparian systems showing that higher stream velocity in narrow entrenched channels at constrained reaches restricts sediment deposition and therefore offers little habitat for seedling establishment (Palik et al. 1998). However, our results did not support these findings. At West Clear Creek we found similar seedling density between constrained and unconstrained reaches for *Alnus oblongifolia*, *Fraxinus velutina*, *Platanus wrightii*, *Populus fremontii* and *Salix* spp. More than 90% of seedlings occurred at the active channel location, and this location was similar in width at both the constrained and unconstrained reaches. Therefore, we conclude that recent seedling recruitment (1993–

1996) at our study site was not influenced by bedrock constraints because the locations where most seedlings occurred did not differ in size between reaches.

We also hypothesized that seedling density would differ among tree species. We found that seedling density of *Alnus oblongifolia* was significantly higher than densities of *Acer negundo*, *Juglans major*, *Platanus wrightii*, and *Salix* spp. at the active channel topographic position where most seedlings occurred. We suspect that the lower density of *Platanus wrightii* was due to less widespread seed distribution compared to *Alnus oblongifolia*, as *Platanus wrightii* seedlings typically establish in clumps at the location of seed drop (Bock and Bock 1989). Also, we suspect that the lower density of *Salix* spp. seedlings was largely due to fewer mature trees. In fact, we did not include *Salix* spp. in the growth analysis because no mature trees occurred on our plots. *Acer negundo* and *Juglans major* were fairly common mature trees at our sites (both were included in the growth analysis), but seedlings of these species were extremely rare on our plots (1 each) compared to other species. Kolb et al. (1997) observed that most small *Acer negundo* trees at a site similar to West Clear Creek (Oak Creek) originated from sprouting by mature, flood-damaged trees, suggesting an important role of asexual regeneration for *Acer negundo* in frequently flooded southwestern riparian forests.

We hypothesized that annual growth of riparian trees at West Clear Creek would be correlated with stream flow characteristics. We found that high stream flow during the growing season was negatively related to annual growth for *Acer negundo* streamwide, and at both constrained and unconstrained reaches. This finding suggests that growth of *Acer negundo* is sensitive to inundation, which is consistent with research by Friedman and Auble (1999), who documented increased mortality of *Acer negundo* saplings with extended flood inundation on the Gunnison River, Colorado. Moreover, high surface flows at West Clear Creek were also negatively associated with annual growth of *Alnus oblongifolia* (constrained reach) and *Platanus wrightii* (unconstrained reach). Other studies (Reily and Johnson 1982, Astrade and Begin 1997) have also reported negative effects of prolonged saturation and limited root oxygenation on annual

radial growth of riparian trees. Further, inundating flows could have greater negative impacts on riparian trees growing along constrained versus unconstrained reaches due to deeper water and greater physical damage from debris moving in floodwater caused by higher water velocity (Palik et al. 1998).

The only positive relationship between stream flow and annual radial growth in our study occurred for *Fraxinus velutina*. Given the arid climate of our study site, why did this relationship not occur for more species? Stromberg and Patten (1991) showed that the strongest, positive correlation between radial growth of *Populus* spp. and stream flow occurred in areas where low flows were not sufficient to meet tree water requirements. In areas where tree water requirements were met by low flows, there was a low correlation between radial growth and stream flow. In their study (Stromberg and Patten 1991), stream diversions abated high flows, and thus the negative effect of high flow was not tested. At West Clear Creek a consistent perennial base flow likely supplied ample water to most trees, except perhaps *Fraxinus velutina*; thus, high stream flows did not increase water availability to trees.

We also conclude that temperature can be an important influence on annual growth of riparian trees at West Clear Creek. High temperature was significantly and negatively related to streamwide annual radial growth of *Acer negundo* during the dry, early summer months, but it was positively related to growth of *Acer negundo* during the wetter, late-summer monsoon season (constrained reach). Perhaps the detrimental effect of high temperature on *Acer negundo* growth in early summer was ameliorated by more humid conditions during the late-summer monsoon season. Consistent with this idea, Kolb et al. (1997) reported that photosynthesis of *Acer negundo* was negatively affected by high vapor pressure deficit at a riparian site similar to West Clear Creek. High temperatures and low humidity in the dry, early summer season would lead to very high vapor pressure deficits, thus reducing photosynthesis and assimilate available for growth. Streamwide annual radial growth of *Fraxinus velutina* was negatively related to winter mean temperature, suggesting poor growth following warm winters, perhaps because of high respiratory losses of stored

carbohydrates. In contrast, growth of *Juglans major* was positively related to winter mean maximum temperature, suggesting greater growth following warmer winters. Perhaps warm winter temperatures increase subsequent growth of this species because of reduced incidence of xylem cavitation caused by freezing (Kozlowski et al. 1991). Overall, our results suggest that temperature plays an important role in the growth of some riparian trees at West Clear Creek, and that this role depends on species sensitivity to temperature and the season during which temperature extremes occur.

Our hypothesis that tree growth would be positively correlated with precipitation was supported only for *Fraxinus velutina* and *Juglans major*. For *Fraxinus velutina*, growth was positively related to summer precipitation streamwide and at the constrained reach. For *Juglans major*, growth was positively related to PDSI values at the constrained reach. One explanation is that because roots of these species at the constrained reach did not contact groundwater, precipitation thus was an important water source. In addition, *Juglans major* in our study grew only on upper benches away from the active channel, where lack of contact with saturated soil and perhaps groundwater may have made it more susceptible to drought than other species that grew closer to the stream. Our explanations are consistent with other research documenting the influence of recent precipitation on riparian tree growth increases when water is not available from other sources (Reily and Johnson 1982, Stromberg and Patten 1990). In contrast to *Fraxinus velutina* and *Juglans major*, growth of *Acer negundo*, *Alnus oblongifolia*, and *Platanus wrightii* was not strongly related to precipitation or PDSI, suggesting greater use of stream or groundwater by these species.

Our expectation that annual radial growth would vary among species was supported by greater growth for *Alnus oblongifolia* and *Platanus wrightii* than for *Fraxinus velutina*, *Juglans major*, and *Acer negundo*. Differences in radial growth rate of these species might be caused by a tradeoff between allocation of carbon to fast growth (i.e., wide rings) versus dense wood, or they might reflect differences in life history strategy (Grime 1979, Loehle 1988). Additionally, fast growth of *Alnus oblongifolia* might be caused by its symbiotic

nitrogen-fixing relationship with actinomycete fungi (Aber and Melillo 1991), which does not occur in the other species we studied. Riparian restoration programs in the Southwest that include tree establishment should consider *Alnus oblongifolia* and *Platanus wrightii* because of their fast growth.

We expected faster tree growth at the unconstrained reach due to more favorable growing conditions such as closer proximity to alluvial groundwater (Reily and Johnson 1982, Stromberg and Patten 1996) and deeper fine sediments from prior high flows (Palik et al. 1998). However, we found that the effect of stream reach on growth varied among species. *Alnus oblongifolia* and *Platanus wrightii* had significantly higher annual radial growth at the unconstrained reach than at the constrained reach, whereas growth of *Acer negundo* and *Fraxinus velutina* did not differ between reaches. Thus, the fastest growing species, *Alnus oblongifolia* and *Platanus wrightii*, responded more dramatically to changes in resource availability than the slower growing species, *Acer negundo* and *Fraxinus velutina*.

CONCLUSIONS

Environmental requirements for seedling establishment varied among tree species at West Clear Creek. A pulse of seedling establishment occurred in 1995–96 for *Alnus oblongifolia*, *Fraxinus velutina*, *Platanus wrightii*, *Populus fremontii*, and *Salix* spp. following high winter and moderate spring surface flows in 1993, and high spring surface flow in 1995. In contrast, little seedling establishment occurred for *Acer negundo* and *Juglans major* under these conditions despite the common occurrence of mature trees. Most seedlings of all species occurred at the active channel topographic location, with few seedlings at abandoned channel, gravel-boulder bar, and bench locations. Our study did not address the environmental conditions necessary for reproduction of riparian trees by sprouting, although this may be an important factor in the reestablishment of riparian forests at some sites (e.g., Kolb et al. 1997).

Relationships between environmental variables and annual radial growth varied among species and between constrained versus unconstrained stream reaches for some species. Relationships with annual radial growth were

most consistent with surface flow. Surface flows were negatively related to growth of *Acer negundo*, *Alnus oblongifolia* (constrained reach), and *Platanus wrightii* (unconstrained reach), whereas spring surface flows were positively related to growth of *Fraxinus velutina* (unconstrained reach). Precipitation or PDSI was positively related to growth only for *Fraxinus velutina* and *Juglans major*, suggesting greater reliance on water in surface soil by these species. In several cases yearly variations in temperature appeared to influence the growth of these riparian trees, and this influence varied among species and seasons. Overall, annual radial growth was high for *Platanus wrightii* and *Alnus oblongifolia*, medium for *Acer negundo* and *Fraxinus velutina*, and low for *Juglans major*. Of the 28 environmental variables we considered, no category of variable (stream flow, temperature, precipitation) equally affected annual radial growth of all species. Thus, tree species at our study site on West Clear Creek responded individually rather than collectively to changes in stream flow and climatic variables.

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DIET AND FOOD-NICHE BREADTH OF BURROWING OWLS (*ATHENE CUNICULARIA*) IN THE IMPERIAL VALLEY, CALIFORNIA

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ABSTRACT.—Burrowing Owls (*Athene cunicularia*) occupy intensively managed agricultural areas within the Imperial Valley of California, where they occur at high densities relative to other areas in the state, and yet reproductive rates are often low. Understanding diet and food-niche breadth may lead to insights into factors contributing to their poor reproductive performance. We tested the relative contribution of sex, year, and season on diet composition and food-niche breadth from analyses of stomach contents of adult Burrowing Owls ($n = 53$). Orthoptera dominated the diet; it accounted for 58.9% of the total number of prey items in all stomachs and was found in 98.2% of all samples. Rodents, a source of potentially limiting dietary calcium, were found in only 2 stomachs. We detected yearly and seasonal effects on estimated food-niche breadth. Mean food niche for the breeding season was broader (antilog of Shannon's index: 2.38 ± 0.15) and more even (Pielou's index: 0.67 ± 0.06) than for the nonbreeding season (1.83 ± 0.13 , 0.49 ± 0.07 , respectively) partially because of a greater frequency of Araneida, Isopoda, Lepidoptera, and Solpugida in the diet during the breeding season. Mean food-niche breadth for 1997 (2.25 ± 0.23) was broader than during 1994, 1995, and 1996 (2.07 ± 0.23 , 1.98 ± 0.20 , and 1.82 ± 0.40 , respectively) because of a greater frequency of Araneida, Dermaptera, Isopoda, Lepidoptera, and Solpugida. These results, and auxiliary diet information, suggest rodents were infrequent in the diet of Burrowing Owls in the Imperial Valley and may help explain their lower reproductive success relative to other areas of California.

Key words: diet, food-niche breadth, *Athene cunicularia*, Burrowing Owl, California, Imperial Valley.

Much published information exists on food habits of the Burrowing Owl (*Athene cunicularia*) throughout most of its range (Thomsen 1971, Marti 1974, MacCracken et al. 1985, Brown et al. 1986, Thompson and Anderson 1988, Barrows 1989, Schmutz et al. 1991, Green et al. 1993, Haug et al. 1993, Plumpton and Lutz 1993). However, all researchers identified prey from regurgitated pellets and/or remains found at the nest burrow. The unreliability of data collected from pellet analyses is well documented (Coulombe 1971, Thomsen 1971, MacCracken et al. 1985, Haug et al. 1993, Plumpton and Lutz 1993). Differential consumption of prey, decomposition rate of remains, and age- or sex-based differences in foraging may bias pellet collections. We had the unique opportunity to examine stomach contents from owls collected over both nonbreeding and breeding seasons, from 4 separate years, and from both sexes. These owls were collected from the Imperial Valley of California, where little is known about the

ecology and food habits of the Burrowing Owl (Coulombe 1971). Recent studies have suggested that the Imperial Valley is unique in that the Burrowing Owl occurs at some of the highest densities in the state, and yet it often has low reproductive success (Rosenberg and Haley in press). To provide insights into the species' reproductive biology and poor reproductive performance in the Imperial Valley, we explored variation in diet and food-niche breadth.

A broad food niche indicates high numbers of prey species nearly equally distributed in the diet. Conversely, a narrow food niche indicates relatively few prey species and unequal prey distribution. Most species have broad food niches, sacrificing efficiency in use of a narrow range of resources (specialization) for the ability to use a wide range of resources (generalization). Several researchers (Gleason and Craig 1979, Barrows 1989, Green et al. 1993, Haug et al. 1993) have suggested that Burrowing Owls are food generalists and

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opportunists. Opportunistic predators may take prey according to relative prey abundances (Murdoch and Oaten 1975, Hegazi 1981, Jaksic et al. 1981, Village 1982, Jaksic 1989, Korpimäki 1992) or may choose food items that yield the greatest net energy (MacArthur and Pianka 1966, Pulliam 1974, Stephens and Krebs 1986, McKnight and Hepp 1998). Food items also may be utilized on the basis of certain limiting nutrients (e.g., protein, calcium, sodium) necessary during times of increased energetic or nutrient requirements (Krebs et al. 1983, Edwards 1997).

Our objectives were to estimate and compare the food-niche breadth and diet composition of Burrowing Owls between sexes, seasons, and years.

STUDY AREA

The U.S. Fish and Wildlife Service provided specimens (none was killed for the study) recovered in 1994–1997 from an area surrounding an electric fence that borders the Calipatria State Prison, California, about 40 km north of the Mexico border (56 m below sea level). Owls were inadvertently killed from the electric fence prior to modifications. The habitat is an intensively managed agricultural matrix and includes roads, canals, ditches, and agricultural fields, similar to most of the agricultural areas of the Imperial Valley (Rosenberg and Haley in press). The temperature can reach 49°C during the summer; average annual rainfall is 6.5 cm. Principal crops during the study were alfalfa (*Medicago sativa*), Sudan grass (*Sorghum bicolor*), and row crops such as onions (*Allium cepa*) and sugar beets (*Beta vulgaris*). Burrowing Owls nested on banks of the canals and ditches.

METHODS

Diet Analyses

We assumed that our sample was representative of Burrowing Owls in the Imperial Valley. The habitat in which these birds were collected is almost entirely composed of agricultural fields and is representative of the Imperial Valley. Because Burrowing Owls in the Imperial Valley forage up to 2 km from the nest site during the breeding season and probably farther during the nonbreeding season (Rosenberg and Haley in press), the foraging

area of the owls in our sample includes an area larger than that from which they were collected.

Specimens with intact stomachs that were absent of maggots and severe desiccation or decay were included in our study. Specimens were kept frozen at –10°C until necropsied. Age of owls was determined by plumage characteristics (Haug et al. 1993); only owls ≥70 days of age were used in this study. We determined sex by examining gonads and classified specimens as breeding (March–August) or nonbreeding (September–February) based on collection date. Although stimuli for onset of egg laying are unknown (Haug et al. 1993), egg laying begins in March in hot, arid environments (Martin 1973, Rosenberg and Haley in press). Completion date of the breeding season varies, although August is typically the last month of nesting activity in this region (Rosenberg and Haley in press).

Prey items in stomach contents were identified to order; minimum number of prey items ingested was estimated by counting sclerotized fragments, including heads, mandibles, and elytra. Although pooling prey into order categories risks underestimating niche breadth (Greene and Jaksic 1983), finer taxonomic resolution of prey was difficult because of digestion and paucity of information available on invertebrate fauna of the area. Coleoptera was undoubtedly underestimated because the exoskeleton/elytra were generally in many small pieces, making quantification of prey items difficult. Because rodents were found infrequently (3.8% of all samples), they were excluded from analyses of sex, seasonal, and annual patterns of prey order but were included in the estimation of food-niche breadth and evenness.

Statistical Analyses

To describe the diet and to evaluate seasonal and sex changes in diet composition, we estimated mean number of items of each prey order per stomach for each sex, season and year, percent of total items for each prey order, and percent frequency of occurrence. We estimated dietary diversity by calculating food-niche breadth and dietary evenness for females ($n = 36$) and males ($n = 17$). We calculated breadth of food niches with the antilog of Shannon's index because it is readily interpretable and is linearly related to the number

of prey categories in the sample (Alatalo and Alatalo 1977). The possible breadth of the food niche for this sample was 1.00 to 8.00. We calculated dietary evenness by using Pielou's (1969) index. Evenness values ranged from 0.00 to 1.00, approaching 1.00 as prey proportions in the diet became equal.

To evaluate factors affecting diet composition and food-niche breadth, we sought models to approximate effects (Burnham and Anderson 1998) supported by our empirical data. We used analysis of variance (SAS 1990) and examined 10 models over 2 different response variables, examined separately, niche breadth and prey order. The most complex model allowed the response variables (niche breadth and prey order) to vary over time (by season and year), by sex, and with an interaction between season and sex effects. Intermediate models included sex, season, and year; sex, season, and sex with season interaction; sex and season; sex and year; and season and year. Our simplest models were 1-variable models consisting of sex, season, year, and a null model of only an intercept term. To evaluate all models and to select our best approximating model, we used the least-squares method of Akaike's Information Criterion with small-sample (2nd-order) bias adjustment (AIC_c) because our sample size was small with respect to the number of estimated effects (Burnham and Anderson 1998). Models were ranked and compared by use of AIC_c differences (Δ_i) and Akaike weights (w_i). AIC_c differences were calculated:

$$\Delta_i = AIC_{c,i} - \min AIC_c$$

where $AIC_{c,i}$ is the AIC_c value for the i th model in a suite of candidate models being compared and $\min AIC_c$ is the minimum value among those models. To interpret the relative likelihood of a model, we calculated Akaike weights:

$$w_i = \frac{\exp(-0.5\Delta_i)}{\sum_{r=1}^R \exp(-0.5\Delta_r)}$$

where Δ_i is the AIC_c difference for model i and R is the set of models. Akaike weights sum to 1 and provide a measurement for the "weight of evidence in favor of Model i as being the actual best model" (Burnham and Anderson 1998). It follows that the larger the

Δ_i , the smaller w_i will be and the less plausible is Model i as being the best model. Situations arose where several models were weighted similarly; all models within a relative likelihood of 2 of the best model were considered in making inferences. All values reported in the Results section are $\bar{x} \pm s_{\bar{x}}$.

RESULTS

Diet Composition

Araneida, Coleoptera, Dermaptera, Isopoda, Lepidoptera, Orthoptera, Rodentia, and Solpugida were identified in the diet. The average number of individual prey items per stomach was 46.8 ± 3.5 ; one breeding-season male had 113 individual prey items in its stomach. A breeding female with an egg almost fully developed in the oviduct had only mollusk shells, white pebbles, rodent bones, and Coleoptera chitin in its stomach.

Orthoptera was the dominant prey order based on prey numbers and frequency of occurrence (Table 1). Frequency of occurrence of Coleoptera, Dermaptera, and Solpugida was high, but number of individuals per stomach was low (Table 1). Rodentia and Isopoda were rare in the diet by both number and frequency of occurrence (Table 1).

The weights of several models were extremely close for both Isopoda ($w = 0.11$ – 0.25) and Solpugida ($w = 0.15$ – 0.31), indicating no best approximating model for these 2 orders. However, the null model for these 2 orders was not heavily weighted (Isopoda: $w = 0.01$, Solpugida: $w = 0.00$). The models with the greatest weight included sex and year effects for Isopoda and season and year effects for Solpugida. A greater number of Isopoda were consumed by males, and Solpugida was taken more during the breeding season; a greater number of both were consumed during a single year (Table 2). The models of sex and year, and sex, season, and year, were heavily weighted for Araneida ($w = 0.38$ and 0.24 , respectively) and Dermaptera ($w = 0.45$ and 0.20 , respectively). Males consumed a greater number of Araneida and Dermaptera than females, a greater number of both were consumed during the breeding season, and a greater number were consumed during a single year (Table 2). Consumption of Coleoptera and Lepidoptera was most affected by season and year (Coleoptera: $w = 0.38$; Lepidoptera:

TABLE 1. Composition of Burrowing Owl stomach contents ($n = 53$) collected in the Imperial Valley, California, 1994–1997.

Prey order	Number/stomach ^a		% of total ^b	Frequency of occurrence (%) ^c
	$\bar{x} \pm s_{\bar{x}}$	Range		
Araneida	1.2 ± 0.5	0–21	4.9	31.5
Coleoptera	2.0 ± 0.6	0–25	8.2	51.9
Dermaptera	2.5 ± 0.7	0–26	10.6	64.8
Isopoda	0.6 ± 0.6	0–32	2.5	3.7
Lepidoptera	1.4 ± 0.6	0–29	5.7	14.8
Orthoptera	13.9 ± 2.3	0–55	58.9	98.2
Rodentia	0.04 ± 0.03	0–1	0.2	3.7
Solipugida	2.1 ± 0.9	0–5	9.1	40.7

^aNumber of individuals of each taxa counted in Burrowing Owl stomachs.^bPercent composition of the diet for each taxa, estimated as $x_i/\bar{x} * 100$, where x_i is the number of individuals of the i th prey order and \bar{x} is the total number of prey for all orders.^cPercent of stomachs in which we found ≥ 1 individual of the given prey order.TABLE 2. Mean number ($\bar{x} \pm s_{\bar{x}}$) of prey items per stomach for the Burrowing Owl, Imperial Valley, California, 1994–1997.

Effect	n	Prey order						
		Araneida	Coleoptera	Dermaptera	Isopoda	Lepidoptera	Orthoptera	Solipugida
Sex								
female	36	0.61 ± 0.21	1.72 ± 0.72	1.74 ± 0.40	0.03 ± 0.03	0.17 ± 0.06	11.33 ± 2.44	2.76 ± 1.24
male	17	2.41 ± 1.34	2.65 ± 0.93	4.09 ± 1.83	1.88 ± 1.88	0.12 ± 0.08	19.21 ± 5.03	0.82 ± 0.29
Season								
breeding	20	2.15 ± 1.06	3.10 ± 0.81	2.60 ± 1.29	1.60 ± 1.60	3.65 ± 1.60	15.10 ± 4.17	4.43 ± 2.11
nonbreeding	33	0.61 ± 0.35	1.36 ± 0.76	2.42 ± 0.72	0.03 ± 0.03	0.06 ± 0.06	13.11 ± 2.82	0.76 ± 0.35
Year								
1994	12	1.67 ± 0.96	0.50 ± 0.19	1.50 ± 0.61	0.08 ± 0.08	0	9.38 ± 3.21	1.58 ± 0.93
1995	20	0.25 ± 0.12	2.95 ± 1.31	1.95 ± 0.61	0	0.50 ± 0.41	13.30 ± 4.35	0.55 ± 0.22
1996	4	0	1.25 ± 0.48	1.50 ± 0.74	0	0	20.75 ± 7.64	1.00 ± 0.71
1997	17	2.24 ± 1.23	2.18 ± 0.84	4.06 ± 1.84	1.88 ± 1.88	3.82 ± 1.84	16.06 ± 4.41	4.68 ± 2.49

$w = 0.57$), with a greater number consumed during the breeding season, and with a single year of high consumption (Table 2). Consumption of Orthoptera was affected by sex and year ($w = 0.49$), with a greater number consumed by males and during a single year (Table 2).

Food-Niche Breadth

Food-niche breadth was narrow and uneven, demonstrating selection for a few taxa (Table 3). Although the model with season and year effects was selected as the best approximating model based on Akaike weights ($w = 0.45$), it was less than twice as likely as the next best model of sex and season effects ($w = 0.26$). Food-niche breadth tended to be broadest during the breeding season and during a single year and was slightly broader for males than for females (Table 3). Although model selection evidence did not support a sex with season interaction model ($w = 0.03$ to 0.05),

estimates of the mean were suggestive of a small effect. Males tended to have a slightly broader food niche during the breeding season (2.75 ± 0.33 , $n = 6$) than females (2.33 ± 0.24 , $n = 14$), and the sexes had similar food-niche breadths during the nonbreeding season (1.77 ± 0.24 for $n = 11$ males and 1.88 ± 0.17 for $n = 22$ females).

DISCUSSION

Diet Composition

The dominance of Orthoptera in the diet of Burrowing Owls in the Imperial Valley was maintained regardless of season or year or consumption of alternative prey types. Jaksic (1989) suggests that opportunistic predators may show a disproportionately large consumption of most abundant prey after a search image has been formed. The conditions necessary for ideal Orthoptera habitat, including warm, dry surroundings with plenty of green

TABLE 3. Food-niche breadth and evenness of the Burrowing Owl, Imperial Valley, California, 1994–1997.

	<i>n</i>	Food-niche breadth		Evenness	
		$\bar{x} \pm s_{\bar{x}}$	Range	$\bar{x} \pm s_{\bar{x}}$	Range
Overall	53	2.07 \pm 0.19	1.00–3.93	0.56 \pm 0.05	0–1.00
Females	36	2.05 \pm 0.14	1.00–3.78	0.55 \pm 0.05	0–1.00
Males	17	2.12 \pm 0.22	1.00–3.93	0.58 \pm 0.05	0–1.00
Breeding season	20	2.45 \pm 0.19	1.00–3.93	0.67 \pm 0.06	0–1.00
Nonbreeding season	33	1.84 \pm 0.14	1.00–3.66	0.49 \pm 0.07	0–1.00
1994	12	2.07 \pm 0.23	1.00–3.66	0.64 \pm 0.10	0–1.00
1995	20	1.98 \pm 0.20	1.00–3.62	0.54 \pm 0.09	0–1.00
1996	4	1.82 \pm 0.40	1.00–2.62	0.38 \pm 0.17	0–0.70
1997	17	2.25 \pm 0.23	1.00–3.93	0.56 \pm 0.08	0–0.97

food, bare ground, and water (Dempster 1963), are met in the Imperial Valley agricultural matrix. With year-round irrigation and growth of crop plants, Orthoptera could reproduce all year. We observed dense populations of Orthoptera that served as a continual prey base for the Burrowing Owl.

Rodents represented only 0.2% of the total prey found in stomachs from this study and were the only vertebrates identified in the diet. In comparison, rodents and other vertebrate prey from previous studies represented 8% (Marti 1974, Colorado), 10% (Green et al. 1993, Oregon and Washington), 14% (Brown et al. 1986, Oregon), 20% (Jaksic and Marti 1981, Chile), 30% (Jaksic and Marti 1981, California), 35% (Schmutz et al. 1991, Alberta), 41% (Thomsen 1971, California), and 52% (Plumpton and Lutz 1993, Colorado) of the total prey. The difference in the proportion of vertebrate prey apparent between this study and previous studies may be partially accounted for by sampling methods, i.e., regurgitated pellets and stomach contents. Smaller and/or more easily digestible prey items could be discovered in stomach contents and overlooked or not discovered in regurgitated pellets. Past researchers (Jaksic and Marti 1981, Green et al. 1993) have concluded that the greater proportion of vertebrate prey reflects differential prey availability. We also attribute the low frequency of rodents in the diet and the differences between the Imperial Valley diet and other diets to differential prey availability, which is affected by habitat and weather differences. The only time rodents seemed to contribute more to the diet than revealed by our stomach analyses was after a field burn when we observed a greater accumulation of rodent remains

around owl burrows (Rosenberg and Haley in press). Additionally, owls responded much quicker to our traps that use mice (*Mus musculus*) as an attractant than at any of our other study sites in California (Rosenberg personal observation). This suggests that Burrowing Owls consume this larger, calcium- and protein-rich prey item when it is available to them. The year-round cultivation and flood method of irrigation is probably inhospitable to rodents, maintaining populations to a presumably low density.

Calcium is an essential nutrient for birds and is especially limiting for egg-laying females and growing young (St. Louis and Breebaart 1991). Birds that normally consume calcium-deficient diets, such as those containing insects, often augment dietary calcium by selectively consuming items rich in this element during times of greater physiological need (St. Louis and Breebaart 1991). The presence of calcium-rich food items in the stomach of one breeding female supports the hypothesis that female Burrowing Owls seek calcium-rich items during egg laying in the Imperial Valley. These calcium-rich items, such as mollusk shells, may be difficult to locate, causing eggs with thin shells to be laid. However, eggshell thickness of Burrowing Owls in the Imperial Valley is similar to that of other California populations (Gervais et al. 2000), suggesting that calcium may not be limiting. St. Louis and Breebaart (1991) suggested that when dietary calcium is insufficient, birds produce smaller clutches. The scarcity of rodents and other calcium-rich food items in the diet and the smaller average clutch size relative to other California populations (Rosenberg and Haley in press) leads us to hypothesize that calcium

is a limiting factor for Burrowing Owls in the Imperial Valley, thus affecting clutch size and reproductive rates. A recent study by Haley (2002) lends support to this hypothesis; Burrowing Owl productivity in the Imperial Valley is greater when the diet is supplemented with rodents. These results may also support an alternative protein-limitation hypothesis. Recent literature suggests that clutch and egg size may be greater for protein-supplemented females (Williams 1996, Nager et al. 1997).

Food-Niche Breadth

A narrow food niche is expected for the Burrowing Owl; the small body size of this predator, 150 gm (Haug et al. 1993), suggests that they are not capable of consuming a large array of prey types and sizes (Barclay and Brigham 1991, Marti et al. 1993). We expected seasonal and year-to-year variation in the diet because of changing seasonal energy needs and because of differential prey availability, palatability, accessibility, and profitability (Tome 1994, Smith and Remington 1996). Because opportunistic predators may select prey relative to prey abundance, we expected food niches to broaden during the breeding season when more prey species are likely available and more abundant. We also expected food-niche to broaden during the breeding season because, as speculated by Smith and Remington (1996), individuals may decrease prey selectivity when they experience elevated requirements such as those imposed on adult birds during egg production and chick rearing. We predicted food niches would narrow during the nonbreeding season when fewer prey species are likely available and when consumers do not need to meet nutrient and energetic requirements of raising offspring. We predicted a broader food niche for males than for females during the breeding season when females remain close to the nest to care for young (Haug et al. 1993). Males forage farther from the nest (Thompson and Anderson 1988), potentially encountering a wider variety of prey species. Although the male brings food to the female, it is likely less diverse than what he encounters. We expected similar food-niche breadth between sexes of this monomorphic species during the nonbreeding season when females are not caring for eggs or young and are free to forage farther from the nest for longer periods of time.

Consistent with our expectations, we detected strong seasonal and yearly effects on food-niche breadth, and a competing model indicated a sex effect. Burrowing owls consumed a greater diversity of prey, especially Araneida, Isopoda, Lepidoptera, and Solpugida, during the breeding season and during 1997. The seasonal and yearly variations in the diet that we detected were presumably because of differential annual and seasonal prey availability, palatability, accessibility, and profitability. However, in the absence of prey abundance data, we cannot make any conclusions regarding the mechanisms that led to temporal variation.

Males are known to provide food to females and offspring during the breeding season (Haug et al. 1993), thus foraging farther from the nest and for longer periods of time than females. During the nonbreeding season, both sexes can potentially forage equal distances and for equal time periods. We expected food-niche breadth to be broader for males than females during the breeding season and to be similar for the sexes during the nonbreeding season. Our results were consistent with this prediction; however, given the sample sizes, the evidence was not strong. Regardless of season, we found evidence that males had a broader niche breadth than females. Males consumed a greater number of Araneida, Coleoptera, Dermaptera, Isopoda, and Orthoptera than females. Differences in food-niche breadth between the sexes of birds is mainly because of sexual size dimorphism (Selander 1966, Storer 1966, Earhart and Johnson 1970, Halley and Gjershaug 1998). However, Burrowing Owls are monomorphic (Earhart and Johnson 1970) or only slightly dimorphic (Plumpton and Lutz 1994) in body size, suggesting that factors other than body size are responsible for the difference in food-niche breadth observed. Although we do not know the mechanism for broader food-niche breadth in males, we speculate that males acquire a broader array of search images from the greater time spent foraging during the breeding season, allowing them to key in on a greater variety of prey types year-round than females.

CONCLUSIONS

We suggest the reason for low rodent numbers and dominance of Orthoptera in the diet,

the primary difference between the diet of Burrowing Owls in the Imperial Valley and the diet at other sites in California (Rosenberg and Haley in press) and elsewhere (Haug et al. 1993), is low availability of rodents, rather than preference for Orthoptera. Orthoptera are abundant year-round in the Imperial Valley (K. Sturm personal observation) and may explain the high density of Burrowing Owls reported by Rosenberg and Haley (in press). This prey source may be sufficient to maintain a high density of Burrowing Owls, but insufficient in quality to permit high per capita reproductive success. In particular, clutch size may be limited by the per capita availability of energy or nutrients, such as protein (Williams 1996, Nager et al. 1997). A high density of owls may influence the per capita availability of these resources through competition. We suggest that per capita prey resources may be limiting the reproductive success of Burrowing Owls in the Imperial Valley. Research on the abundance, availability, and nutrient quality of prey would allow a more thorough understanding of the foraging ecology of Burrowing Owls and of the relationship between diet and demographic characteristics.

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THE SHORT SONG OF BREWER'S SPARROW: INDIVIDUAL AND GEOGRAPHIC VARIATION IN SOUTHERN IDAHO

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ABSTRACT.—Brewer's Sparrows (*Spizella breweri*) have two song types—a “short” song that has 1 to 3 trill types and a “long” song that has 5 to 10 or more trill types. I describe the short song and examine patterns of individual and geographic song variation from 15 sites on the Snake River Plain in southern Idaho. Territorial males sang the short song regularly during the breeding season. Two-trill song types comprised 72.9% of all song types, with 3-trill types (18.8%) and 1-trill types (8.2%) less frequent. Over 90% of the males sang their song type(s) essentially without variation. Many trill types appeared most often in only 1 of 3 possible song positions, i.e., 1st, 2nd, or 3rd trill. Trill types that occurred in different song positions differed in syllables per second, trill and syllable duration, and frequency variables. First trill types were more variable than 2nd or 3rd trill types. There was no evidence that birds at sites closer together shared more trill types or pairs of trill types than those farther apart. There was no tendency for territorial neighbors to sing similar song types. Brewer's Sparrows' small territories, dense populations, and apparently high rate of annual turnover may mediate against the evolution of song sharing or vocal dialects.

Key words: *Brewer's Sparrow*, *Spizella breweri*, song dialects, geographic variation, Idaho, individual variation, sagebrush, Snake River Plain.

Brewer's Sparrow (*Spizella breweri* Cassin) is a migratory species that is abundant during the breeding season over large expanses of sagebrush (*Artemisia* L. spp.) steppe in the western U.S. (Wiens and Rotenberry 1981, Rotenberry et al. 1999). Despite this abundance, Brewer's Sparrow song has not been described previously except in general terms (Bent 1968, Rising 1996, Doyle 1997, Rotenberry et al. 1999). Brewer's Sparrows have 2 song types—a “short” song that has 1 to 3 trill types and a “long” or “extended” (Doyle 1997) song that has 5 to 10 trill types, sometimes more. The long song is most often described, albeit inadequately, in field guides and other references.

My main purpose is to provide the first description of the “short” song of Brewer's Sparrow across a portion of the Snake River Plain in southern Idaho. The nature of song variation is of interest because Brewer's Sparrow is currently undergoing significant rangewide population declines (Saab and Rich 1997, Sauer et al. 1997) and is commonly detected and monitored by song during the breeding season. Changes in detectability over the breeding season have been described (Best and Petersen 1985). A more complete understanding of

its vocal behavior will help to ensure accurate monitoring.

I also examined patterns of geographic song variation, specifically testing the null hypotheses that there is no relationship between the geographic distance between males and the number of trill types or pairs of trill types shared. Geographic variation in song across multiple spatial scales provides insights into the behavior, social organization (Payne 1981, 1983), and ontogeny of song development (Kroodsma 1996). As I will show, there is no evidence for song sharing, song matching, or vocal dialects in this species within the study area. Small territory size, dense populations, and high turnover are consistent with the idea that Brewer's Sparrow is an r-selected species where simple songs emphasizing species identity prevail over a more complex social structure that might be enhanced by song sharing among neighbors (Payne 1981, 1983). This situation is contrasted with that of the broadly sympatric Sage Sparrow (*Amphispiza belli*), which exhibits vocal dialects in the same geographic area and habitats (Rich 1981) and in other parts of western North America (Wiens 1982).

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STUDY SITES

In May and June 1977, 1978, and 1979, I recorded songs of 284 Brewer's Sparrows from 15 sites on the Snake River Plain in southern Idaho (Fig. 1): BB, Bingham-Bonneville county line; BT, Kettle Butte; C, E, and SA, along U.S. Highway 26; CM, near Craters of the Moon along the road to Blizzard Mountain; DF, Deadman Flat; GR, Great Rift National Monument; HH, Huddles's Hole; JF, Juniper Flat; MB, 2 km north of Menan Buttes; MLF, Medicine Lodge Flats; PB, Pillar Butte; T, 1 km north of Atomic City; and VC, east slope of a prominent volcanic cone 2 km south of Atomic City. Songs of individual males are labeled by site name and a number, e.g., PB-2, BT-7. Site SA (Fig. 1) was sampled in all 3 years, and site CM was sampled in both 1978 and 1979. These resampled sites are treated separately and labeled SA7, SA8, SA9, CM8, and CM9, respectively, with numbers representing the year recorded.

METHODS

Songs were recorded between sunrise and about 1100 hours from 2 May to 19 June each year. At each site all males were recorded in one morning in an area of about 2 km² or less. I recorded as many neighboring birds as possible. Once I chose the next bird to record, I began counting the number of songs he sang as I approached him. I noted how many songs were sung with variation and the type of variation, e.g., truncation, extra trill, or 2nd song type. Due to Brewer's Sparrows' small territories, most males recorded at each site were within hearing distance of at least one, and usually several, neighbors. I noted all cases where territorial neighbors were recorded.

Most vocalizations were recorded with a Dan Gibson Electronic Parabolic Microphone and Audiotronics model 147A cassette recorder. Some songs were recorded on a Uher 4000 Report L recorder. I noted in the field which song was most typical for a given male and analyzed that song. Sound spectrograms were prepared on a Voice Identification, Inc. Series 700 sound spectrograph using the 300 kHz wide band and 80–20,000 frequency scale.

Spectrograms of short songs were randomized so their identities were not known. I then defined and cataloged syllable types. A syllable type was the largest unit of song that was

repeated to form a trill type. Each syllable type was identified by a letter and a number, e.g., A1, E12. Letters identify generally similar syllable types but are arbitrary and do not play a role in analysis. In defining syllable types, I considered their sound-spectrographic shapes but not their frequency. This approach emphasizes subtle similarities in shape in preference to time and frequency variables.

Although individual birds were not marked, inspection of the sonograms from SA7, SA8, and SA9 did not reveal any short songs that were the same between years. The same situation existed for sonograms from CM8 and CM9. Thus, I assumed that no individual male was re-recorded in successive years and that males do not change songs between years, and I treated these as independent samples. This clearly is a major assumption, but there is some evidence from the congeneric Clay-colored Sparrow, *S. pallida* (Knapp 1982, 1994), that this assumption is justified.

I analyzed similarities within and among sites in 3 ways. First, similarity values between pairs of sites were derived from Jaccard's coefficient (Southwood 1978) for trill types shared. Values range from 0.0 (no similarity) to 1.0 (perfect similarity) for each comparison. Second, the same analysis was conducted for pairs of trill types shared. For the latter, I compared how many consecutive pairs of trill types were shared between individuals. For example, song A1 B1 C1 has 3 trill types and 2 pairs of trill types (A1 B1 and B1 C1). Third, time and frequency variables were measured on the spectrograms: trill duration; syllable duration; syllables per second; minimum, maximum, and dominant frequency; and frequency range. Amplitude sections were used to determine dominant frequency. Durations were measured to the nearest 0.05 second, frequencies to the nearest 0.3 kHz, and syllables per second to the nearest 0.1. Syllables per second was chosen as a means of incorporating information on inter-syllable interval because the latter were often very brief and difficult to measure accurately. For all variables, the position of the trill in the song (1st, 2nd, 3rd) was also identified so that in a 3-trill song type there were 21 variables.

Univariate statistical analysis follows Zar (1974). Stepwise discriminant function analysis was performed with computer programs in the BMDP series (Dixon 1981). The null

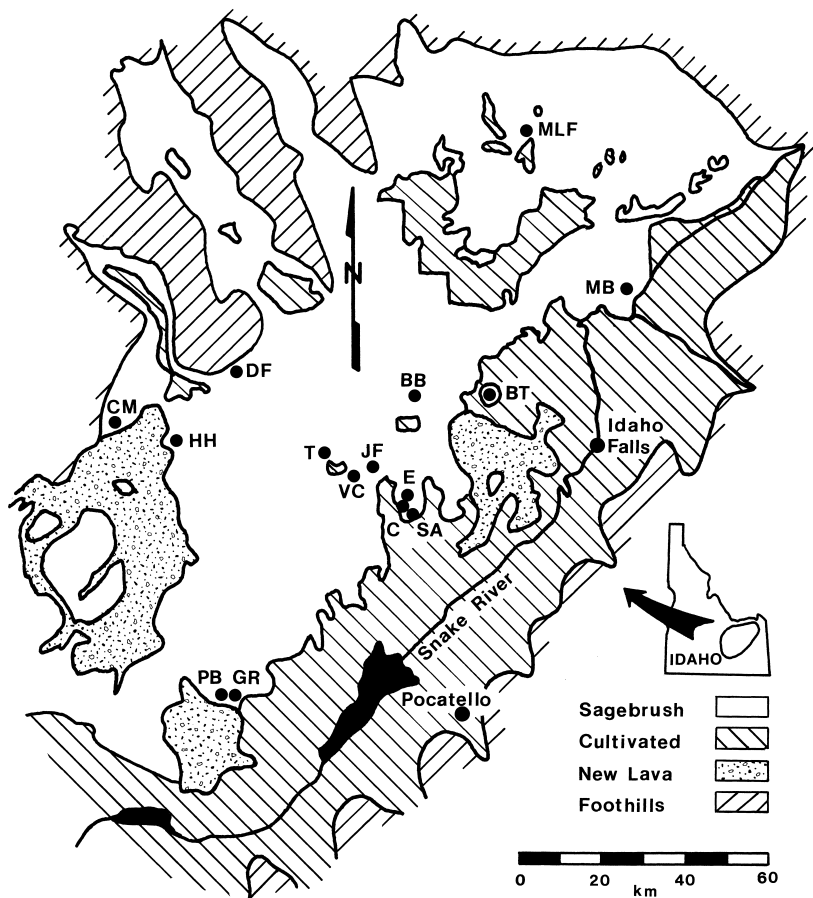


Fig. 1. Map of the upper Snake River Plain in Idaho composed from 1980 LANDSAT images. Lettered points are sites where Brewer's Sparrow songs were recorded.

hypotheses that there were no relationships between the matrix of distances among sites and the matrix of similarity values based on trill types shared or pairs of trill types shared were tested with Mantel's test (Schnell et al. 1985).

RESULTS

General Vocal Behavior

The Long Song

Brewer's Sparrows sang 2 types of songs—a "long" song (Doyle 1997) and a "short" song (Fig. 2). The long song (see sonograms in Kicka et al. 1999, Rotenberry et al. 1999) was sung much less frequently than the short song and appeared to be a vocalization stimulated by other males and/or females during the peak

of breeding activities (personal observation, Bent 1968, Willing 1970). Typically, a male began singing short songs and moved among perches while several of his neighbors were doing the same. Then as one male began singing the long song, many of his neighbors switched to their long songs. Often, some of the neighboring males, and possibly females, were rather close together, e.g., within 10 m, at the onset of the long-song singing. There was often considerable chasing involved as well. I also have elicited long songs from males by playing back recordings of their own short songs. A truncated long song could usually be distinguished from a short song because it began with a distinctive sequence. In particular, the long song is not simply the short song with additional trills appended.

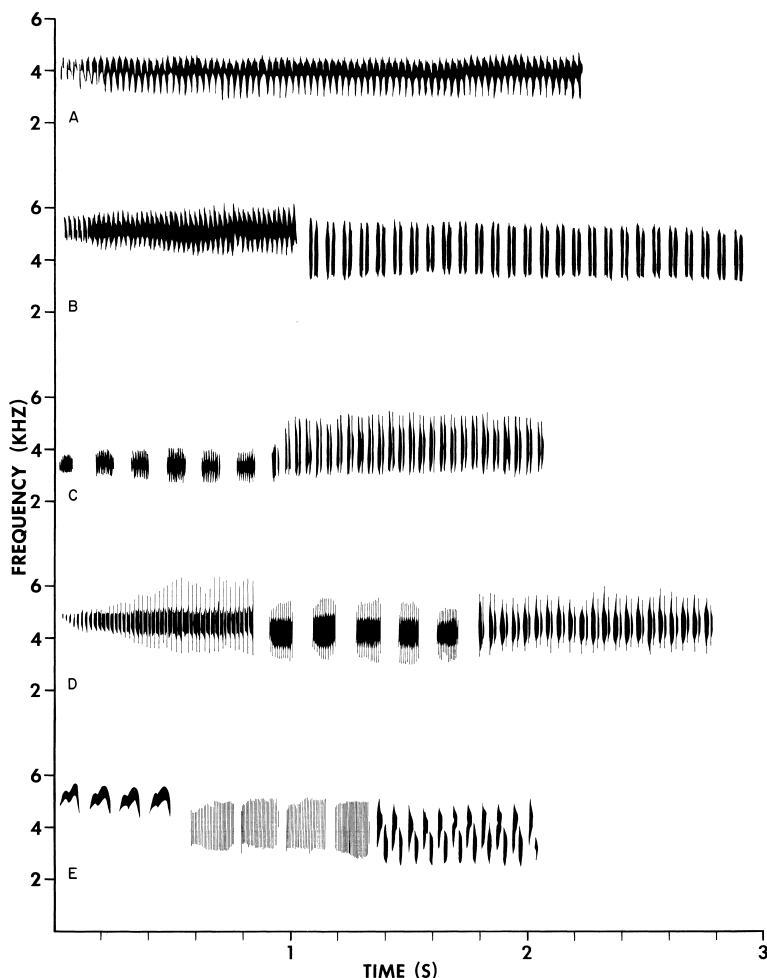


Fig. 2. Brewer's Sparrow short songs: A, a 1-trill song type composed of a single syllable type A6; B, a relatively typical song type composed of a higher-frequency, faster syllable type (A3) followed by a lower-frequency, slower syllable type (C8); C, another 2-trill song type E3 C6; D, a 3-trill song type A12 E3 C6; E, an uncommon 3-trill type, G E3 C5, showing a 1st trill type unique to 1 male.

The Short Song

NUMBER OF TRILLS PER SONG.—Territorial males sang the short song regularly during the breeding season. It consisted of 1 to 3 trills, depending on the bird (1 male sang 4 trills), and was sung with only minor variation (see below). Males sang in bouts that ranged from 4 to 143 songs, depending on the individual. Two-trill song types (Figs. 2B, C) comprised 72.9% of all song types, with 3-trill types (18.8%, Figs. 2D, E) and 1-trill types (8.2%, Fig. 2A) less frequent. In other parts of the Snake River Plain, in southern Oregon, northern Nevada, and southwestern North Dakota,

2-trill song types also were by far the most common type (personal observation).

VARIATION WITHIN INDIVIDUALS.—Of the 284 males recorded, I have data on song variation for 255 (Table 1). Of these, 190 (74.5%) sang song bouts with no variation aside from minor differences in trill duration. Another 33 males sang songs with substantial truncations, i.e., trills that had been sung completely were abruptly stopped before completion. In this group 18.8% of all songs heard were truncated. Six males (among the 33) truncated some songs after I recorded and then played back their own songs, and 3 others truncated songs after a neighboring male flew to a nearby perch and

TABLE 1. Nature and degree of song type variation within the short songs of individual Brewer's Sparrows on the Snake River Plain in southern Idaho.

No. males	% males	No. songs heard	Type of variation	Variable songs	
				No.	% ^a
190	74.5	3628	None	0	0.0
33	12.9	685	Truncated	129	18.8
10	3.9	170	Added 1 trill	48	28.2
8	3.1	174	Deleted 1 trill	31	17.8
6	2.4	232	2 song types	47	20.3
2	0.8	49	Punctuated 1st trill	20	40.8
2	0.8	35	Alternate 2nd trill	10	28.6
1	0.4	24	Replaced 2nd and 3rd trill type with 4th	6	25.0
1	0.4	33	3 song types	12	36.4
1	0.4	16	Combined 1st and 2nd trill types	2	12.5
1	0.4	35	Other	15	42.9

^aPercent of number of songs heard.

sang. Several other cases were undoubtedly caused by my presence, as males sang invariable songs at a steady rate while I approached them and then truncated some songs as I neared for recording. Therefore, I believe the truncated songs were caused by disturbances and were not meaningful variations. The 8 males who deleted 1 terminal trill should be considered similarly.

The remaining 24 males (9.5%) had song variations of consequence (Table 1). Ten males added a trill to an average of 28.2% of their songs. Six males had 2 different song types, and 1 had 3 types. Two males occasionally punctuated their 1st trill with a brief pause, and 2 others substituted a different 2nd trill in some songs. Three males with other variations were noted.

If the males who sang truncated songs and those who occasionally deleted a terminal trill are considered to have had invariable songs in the absence of disturbance, then 231 (90.6%) males sang without variation. Variation in the remaining 24 males affected 26.9% of their songs.

SYLLABLE TYPES AND TRILL TYPES.—Fifty-two syllable types were defined and cataloged from a total of 292 songs recorded from all males sampled (Fig. 3). The most common syllable type was A3, which occurred in 95 males (33.5%) and was the only type appearing at all 15 sites and in all years. The next most frequent type, B3, was sung by 59 males (20.8%). At the other extreme, 14 syllable types were unique to individual males. Unique types G

and H (Fig. 3) were particularly unusual for Brewer's Sparrows (personal observation).

PAIRS OF TRILL TYPES.—There were 323 pairs of trill types, i.e., combinations of consecutive trill types (excluding 24 one-trill songs) among all birds, and I classified 152 different pairs of types. Among those pairs, 105 (69%) were sung by only 1 male. The most common pair of trill types, A3 B3, was sung by 23 different males. The next most common, A3 C2, was sung by 11 different males.

The 24 one-trill song types were composed from only 10 different trill types, and 8 one-trill song types were unique. The most common syllable type, B3, was sung by 6 males. Thus, B3 appeared in the most common 1-trill and 2-trill song types. Among the 55 three-trill song types, only 5 were shared by 2 males.

POSITION OF TRILL TYPES.—Many trill types appeared mostly in only 1 of 3 possible song positions (Table 2, Fig. 3). The most striking example was syllable type A3, the most common type, that appeared 90 times as a 1st trill, 4 times as a 2nd trill, and only once as a 3rd trill. Types A6 and A9 occurred only in the 1st position. Other syllable types were most common in the 2nd position, e.g., B3, C2, C11, and E2. Only uncommon syllable types A5 and D5 occurred most often in the 3rd position. All other types that appeared in the 3rd position more than 2 times occurred most frequently in the 2nd position, e.g., B1, B3, C8, and C9.

DISCRIMINANT ANALYSIS OF SYLLABLE TYPES.—The syllable types that occurred in different positions within a song type had obvious

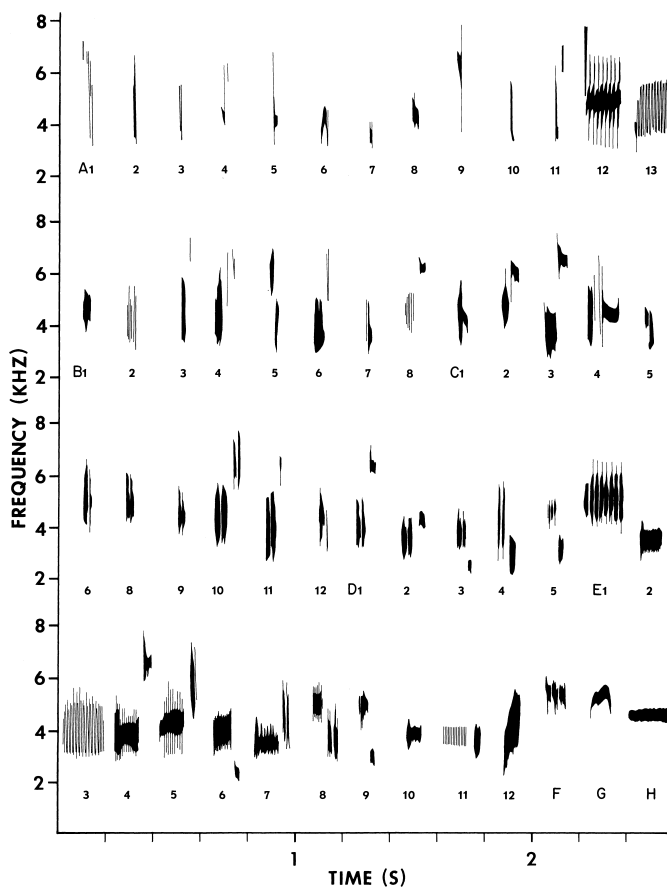


Fig. 3. Syllable type catalog for Brewer's Sparrow. For types A12 and A13, several repetitions of the type are shown.

differences, in many cases, in duration, trill rate, and frequency (Fig. 3). To further define these differences, I examined trill types by song position: the only trill in a 1-trill song (1-of-1), the 1st trill in a 2-trill song (1-of-2), and so on up to the 3rd trill in a 3-trill song (3-of-3).

Summary statistics for these data revealed several differences by position (Table 3). Song types with more trills had shorter trills. Syllable duration was more constant, except for the 2-of-3 position, which was longest. Syllables per second showed the greatest variation among positions and is one of the most obvious features differentiating syllable types (Fig. 3). In 2- and 3-trill song types, 1st trills were faster than later trills, whereas trill rate of 1-trill song types was slower. Maximum frequency also showed substantial differences, with 1st trills being higher than later trills. Minimum frequency and dominant frequency varied in proportion to maximum frequency. Frequency

range was greatest in trill types of 1-trill songs, with other positions only slightly less.

Discriminant analysis of the 6 trill-position groups revealed that syllables per second was the most important discriminating variable (Table 4). Trill duration was next, while syllable duration and minimum frequency, although also significant discriminators, did not greatly improve the *U*-statistic.

The classification matrix (Table 5) showed that most trill types were correctly classified by song position. One-of-one trill types were the most distinctive, with 91.7% correctly classified. In the 1-of-2 category, 55.9% were correctly placed, but 24.4% were classified in the 1-of-3 position. One-of-three category trills were also confused somewhat with the 1-of-2 category. The 2-of-2 category was distinguishable 60.6% of the time, but 21.1% were incorrectly classified into category 3-of-3. Similarly, 27.3% of the 3-of-3 trills were placed as 2-of-2

TABLE 2. Frequency of occurrence by song position, i.e., 1st, 2nd, or 3rd trill of song, for 52 syllable types in the short songs of 284 Brewer's Sparrows on the Snake River Plain in southern Idaho.

Syllable type	Frequency in position			Syllable type	Frequency in position		
	1	2	3		1	2	3
A1	4	2	0	C8	0	18	5
A2	2	0	0	C9	3	12	6
A3	90	4	1	C10	0	4	0
A4	2	0	0	C11	1	12	1
A5	1	1	2	C12	0	3	2
A6	48	0	0	D1	1	11	2
A7	19	2	0	D2	0	1	0
A8	14	0	0	D3	0	1	0
A9	28	0	0	D4	0	3	0
A10	1	0	0	D5	0	0	1
A11	2	0	0	E1	1	0	0
A12	0	1	0	E2	8	26	2
A13	1	0	0	E3	2	3	1
B1	2	12	5	E4	0	10	1
B2	5	5	2	E5	1	0	0
B3	12	42	4	E6	2	0	1
B4	1	7	2	E7	0	2	0
B5	0	15	1	E8	2	6	1
B6	0	5	0	E9	0	1	0
B7	14	4	2	E10	0	1	0
B8	0	2	0	E11	0	1	1
C1	0	2	1	E12	0	1	0
C2	9	24	1	F	1	0	0
C3	0	4	0	G	1	0	0
C4	1	2	0	H	1	0	0
C5	9	7	1				
C6	3	11	9				

trills. In short, there was similarity mainly between 1-of-2 and 1-of-3 categories, i.e., 1st trill types, and between 2-of-2 and 3-of-3 categories, i.e., last trill types.

Geographic Song Variation

SHARING OF TRILL TYPES AND PAIRS OF TRILL TYPES.—There was a weak inverse relationship between trill type sharing and geographic distance between pairs of sites (Fig. 4). A similar pattern resulted from plotting scores for the sharing of pairs of trill types (not shown). As these points are not independent, the "regression" lines have no statistical meaning. However, one can test the null hypotheses that there was no relationship between the matrix of distances among sites and the matrices of similarity values based on trill types shared and pairs of trill types shared. Neither null hypothesis was rejected: for trill types shared, $t = -0.06$, $P > 0.50$ and for pairs of trill types shared, $t = -0.69$, $P > 0.50$ (Mantel's Test; Schnell et al. 1985).

NEIGHBORS ON TERRITORIES.—There were 136 pairs of males that were neighbors on ter-

ritories. Among these pairs, 29% of trill types and 2% of pairs of trill types were shared (Table 6). The observed sharing of trill types was not different from the sharing exhibited by randomly selected pairs of males (Table 6). Thus, there was no tendency for neighbors to sing similar songs.

DISCUSSION

Evidence presented here suggests that there is 1 stereotyped short song for most male Brewer's Sparrows (Willing 1970). For those few males with more than 1 song type, the alternate types were sung in a regular manner, suggesting that one could expect to hear the entire repertoire in a few minutes. Three other *Spizella* sparrows also have 1 song type per male: Field Sparrow, *S. pusilla* (Heckenlively 1976); American Tree Sparrow, *S. arborea* (Weeden 1965); and Chipping Sparrow, *S. passerina* (Borror 1959, Marler and Isaac 1960, Albrecht and Oring 1995). The Clay-colored Sparrow (Knapton 1982, 1994), has 1–3 (usually 2) song types per male, and these are stable for at least

TABLE 3. Mean and standard deviation for 7 variables for 615 Brewer's Sparrow trill types by position in the short song. For example, "1 of 1" means that the trill is the only trill in a 1-trill song type and "2 of 3" means that the trill is the 2nd trill in a 3-trill song type.

Variable	Trill position					
	1 of 1	1 of 2	1 of 3	2 of 2	2 of 3	3 of 3
Trill duration (s)	2.21 (0.38)	1.04 (0.31)	0.82 (0.19)	1.37 (0.32)	0.94 (0.26)	1.17 (0.37)
Syllable duration (s)	0.03 (0.02)	0.02 (0.02)	0.02 (0.01)	0.03 (0.02)	0.06 (0.04)	0.03 (0.02)
Syllables/second	20.7 (10.8)	49.0 (19.9)	46.3 (13.6)	15.1 (6.1)	15.8 (17.9)	17.5 (8.3)
Maximum frequency (kHz)	6.4 (1.1)	6.3 (0.8)	6.2 (0.9)	5.8 (0.8)	5.6 (0.9)	5.9 (0.7)
Minimum frequency (kHz)	3.2 (0.7)	3.5 (0.7)	3.5 (0.7)	3.1 (0.5)	3.1 (0.5)	3.1 (0.4)
Dominant frequency (kHz)	4.6 (0.8)	4.9 (0.8)	4.9 (0.9)	4.2 (0.6)	4.2 (0.7)	4.3 (0.6)
Frequency range (kHz)	2.9 (1.0)	2.7 (0.9)	2.6 (0.9)	2.6 (0.6)	2.4 (0.7)	2.7 (0.6)

TABLE 4. Variables selected in discriminant analysis of Brewer's Sparrow short song trill types in 6 song positions.

Order	Variable entered	<i>U</i> -statistic	<i>F</i>	<i>P</i>
1	Syllables/second	0.438	157.16	0.001
2	Trill duration	0.252	121.3	0.001
3	Syllable duration	0.216	83.33	0.001
4	Minimum frequency	0.202	62.64	0.001

1 year. Thus, I assume that the short songs of Brewer's Sparrow are stable over time.

In addition to individual stereotypy is what might be called species stereotypy. Although 41.8% of all songs were unique by syllable type composition, results of the tabulation of syllable types by position and discriminant analysis of trill types by position revealed a considerable uniformity among individuals and sites in general song structure. The typical 2-trill song may be represented by a higher-frequency, faster trill followed by a lower-frequency, slower trill. This is exactly what Dawson (in Bent 1968) portrayed when he characterized Brewer's Sparrow song as "weeeezzz, tubitubitubitubitub." The discriminant analyses revealed that 1st trills were more variable than either 2nd or last trills, consistent with the prediction that the greatest complexity in broadcast song should occur near the beginning as an aid to individual recognition (Craig and Jenkins 1982).

Notable parallels in short song structure exist between Brewer's Sparrow and the Clay-colored Sparrow (Borror 1961, Willing 1970, Knapton 1982, 1994). Clay-colored Sparrows breed in brush habitat (*Symphoricarpos occidentalis*) that appears structurally similar (Knapton 1979) to the sagebrush of Brewer's Sparrow, and occasionally even hybridize with Brewer's (Rising 1996, N. Mahoney personal

communication). Syllable type A3 of Brewer's Sparrow, the most common type, is virtually identical to that shown in Knapton (1982:191) for the Clay-colored Sparrow. Maximum frequency in Clay-colored Sparrows is nearly the same (about 6.3 kHz) as that in 1st trills of Brewer's Sparrow, whereas minimum frequency in the Clay-colored Sparrow is lower (about 2.2 kHz vs. about 3.5 kHz in 1st trills of Brewer's Sparrow). Clay-colored Sparrows also sing more syllables per second (70) than Brewer's Sparrow (about 48 in 1st trills), although some syllable types, e.g., A3, sound much like the buzz of clay-colored (personal observation).

Knapton (1982) also made a distinction between long and short songs in the Clay-colored Sparrow, the former being sung near the incubating female/nest site and the latter being sung away from the nest site (Knapton personal communication). At least 4 other species—Five-striped Sparrow (*Aimophila quinquestriata*; Groschupf 1985), Cassin's Sparrow (*Aimophila cassinii*; Groschupf 1983), Great Reed Warbler (*Acrocephalus arundinaceus*; Catchpole 1983), and Redwing (*Turdus iliacus*; Lampe and Espmark 1987)—exhibit a similar use of simple and complex songs. This phenomenon also may occur in Brewer's Sparrow. In all these species, song behavior is consistent with the argument that long complex

TABLE 5. Classification matrix from discriminant analysis of Brewer's Sparrow short song trill types by position in song. For example, "1 of 1" means that the trill is the only trill in a 1-trill song type and "2 of 3" means that the trill is the 2nd trill in a 3-trill song type.

Group	Percent correct	Number of cases classified into group					
		1 of 1	1 of 2	1 of 3	2 of 2	2 of 3	3 of 3
1 of 1	91.7	22	0	0	2	0	0
1 of 2	55.9	5	119	52	14	13	10
1 of 3	52.7	0	15	29	0	2	9
2 of 2	60.6	19	2	1	129	17	45
2 of 3	54.5	0	3	3	4	30	15
3 of 3	63.6	1	0	1	15	3	35
TOTAL	59.2	47	139	86	164	65	114

TABLE 6. Sharing of trill types and pairs of trill types by Brewer's Sparrow neighbors on territories and by randomly selected pairs of males.

Types of pairs of males	Number of Pairs	Trill types shared	Pairs of trill types shared
Observed pairs of neighbors	136	39 (29%)	2 (2%)
Random pairs from within sites			
Sample 1	136	42 (31%)	10 (7%)
Sample 2	136	37 (27%)	8 (6%)
Sample 3	136	35 (26%)	4 (3%)
Random pairs from all sites	136	48 (35%)	0 (0%)

songs have evolved through intersexual selection, whereas short stereotyped songs repeated in bouts have evolved through intrasexual selection and are used mainly in territorial defense (Catchpole 1980, Catchpole and Slater 1995).

There also are similarities between Brewer's Sparrow and Chipping Sparrow song (Borror 1959, Marler and Isaac 1960, Willing 1970, personal observation). Whereas the Chipping Sparrow normally sings a single long trill (Borror 1959), Marler and Isaac (1960) and Bent (1968) report birds with 2-trill songs and 1 individual with a 6-trill song (B. Walker personal communication). Borror (1959) classified Chipping Sparrow song into 28 different patterns. Those I judged to be most like Brewer's Sparrow song, patterns 1-4 (Borror 1959:352), were classified by Borror as having a buzzy quality and either 1- or 2-part syllables.

I have 2 suggestions for those monitoring Brewer's Sparrow populations by song. First, the monitor should listen to a singing bird through several song renditions and listen for repeated song types in order to be certain (s)he is hearing a single bird. Because of the assumed stereotypy of the short song in most individuals, males can be readily identified and tallied.

If an individual has a 2nd or 3rd song type, it is likely that he will sing those much less often than his primary type. Even with more than 1 type, individual males can be readily identified and mentally tracked.

Second, a monitor must be able to distinguish long songs from short songs. One also must avoid tallying 2 birds when a single male switches from the long to the short song, or vice versa. The long song has a sequence of trills and a quality that I believe also is stereotyped among males. Although the syllable types may vary, the long song can be quickly recognized.

Analysis of geographic variation in Brewer's Sparrow song in this study revealed no patterns. The general nature of geographic variation is summarized by the scattergrams that show a weak inverse, nonsignificant relationship between sharing of trill types, or pairs of trill types, and geographic distance. Neighbors on territories shared no more trill types or pairs of trill types than did randomly paired males. Knapton (1982) also found that neighboring Clay-colored Sparrows did not tend to share song types. This was especially important for 12 pairs of males composed of returning adults and "new" males occupying adjacent territo-

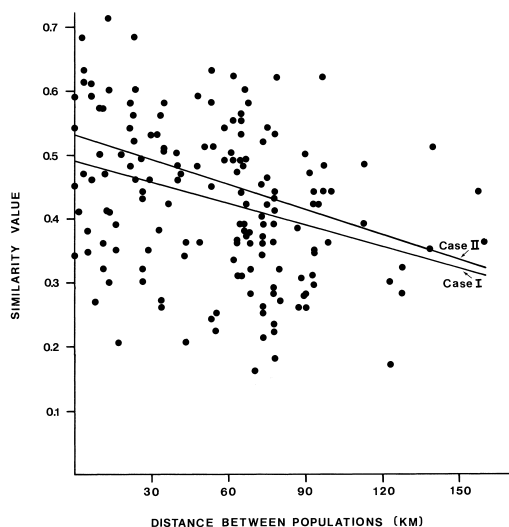


Fig. 4. Scattergram of song similarity values, based on trill types shared, and geographic distance between all pairs of Brewer's Sparrow populations. For the "regression" lines, Case I includes all points and Case II excludes the 4 self \times self points for populations sampled in the same site in different years. The relationships between song similarity and distance were not significant.

ries for the first time. He also concluded that young male Clay-colored Sparrows probably do not copy the songs of adults. The lack of song sharing between members of these pairs suggests that the social adaptation model of Payne (1981, 1982, 1983) may not apply to Clay-colored Sparrows or Brewer's Sparrows.

Among Clay-colored Sparrows, 63% of the adult males returned to the breeding area—many to the same territories—whereas only 18% of adult females and none of 146 nestlings returned (Knapton 1982). Although I did not have marked birds and I did not specifically attempt to evaluate this phenomenon, the fact that no sonograms from the same geographic site in subsequent years (SA7, SA8, SA9 and CM8, CM9) were the same suggests that there was considerable annual turnover in this species or that the same bird sang a different song each spring. Such turnover obviously would confound the establishment of dialects. Turnover was considered as a possible explanation for the lack of dialects in the White-throated Sparrow, *Zonotrichia albicollis* (Lemon and Harris 1974), and the Rock Wren, *Salpinctes obsoletus* (Kroodsma 1975).

Another factor that may indirectly work against song sharing in Brewer's Sparrow is the small territory size (0.65 ha per pair; Rich

unpublished) and high densities (Wiens and Rotenberry 1981). Even if a young male does learn his song from other males through social interaction (Payne 1981), he is presented with a large number of songs from which to learn. Not only the short songs but also the more complex long songs offer a variety of trill types to copy. This is further complicated by the great amount of social interaction, especially chasing, that occurs early in the breeding season. It seems possible that an individual's short song could be composed of trill types from more than 1 model and perhaps from long, as well as short, songs. On the other hand, Indigo Buntings (*Passerina cyanea*) also have closely packed territories with many neighbors, but a young male focuses on only a single model when it learns and copies a song (Payne 1996).

Because signals "must coevolve with other life history parameters" (Kroodsma 1996), several other potentially important factors affecting geographic song variation are suggested by contrasting Sage Sparrows (*Amphispiza belli*) and Brewer's Sparrows, a "key comparative situation" (Kroodsma 1996). Rich (1981) and Wiens (1982) both found a high degree of song sharing among neighboring Sage Sparrows, and Rich (1981) studied birds on some of the same sites as covered in this paper. This suggests that there were no habitat or landscape features that similarly affected dispersal and habitat selection by these broadly sympatric species, at least on the sites covered in this study. Baker (1983) came to a similar conclusion after finding no concordance between the spatial variation in songs of White-crowned Sparrows (*Zonotrichia leucophrys*) and Song Sparrows (*Melospiza melodia*) on the same sites.

Brewer's Sparrows are smaller (8.9–11.8 g) than Sage Sparrows (17.4–20.4g; Wiens and Rotenberry 1980) and have much wider niches (14.58 and 5.52, respectively; Rotenberry and Wiens 1980), based on habitat variables. The breeding density of Brewer's Sparrow also varies over a wider range (29–533 km⁻²) than that of the Sage Sparrow (16–172 km⁻²; Wiens and Rotenberry 1981).

Greater yearly variation in populations of Brewer's Sparrow also is strongly suggested by Breeding Bird Survey (BBS) data (Sauer et al. 1997). I calculated BBS count coefficients of variation (CV) over the period 1966 to 1996 for all routes that had been run for more than 9 years and for which Brewer's Sparrows,

Sage Sparrows, and Sage Thrashers (*Oreoscoptes montanus*) all were present. This screen helped ensure that I examined variation in core habitat for these sagebrush obligates. Among the 48 routes that met these criteria, Brewer's Sparrow count CVs exceeded Sage Sparrow count CVs on 40 routes.

This information suggests that Brewer's Sparrows are a relatively r-selected species, whereas Sage Sparrows are relatively K-selected. One might predict that Brewer's Sparrow life spans will be shorter, productivity will be more variable, and dispersal will be greater (Pianka 1983) than for Sage Sparrows. Under these conditions it may be more adaptive for breeding individuals to emphasize species identity over individual identity. The selective advantage of breeding within a short life span following greater dispersal might take precedence over the advantages of a more complex social structure mediated by vocal communication (Kroodsma 1974, 1979, Baker and Mewaldt 1978, Jenkins 1978, Baptista and Morton 1982, Payne 1982, 1983, 1996). Groschupf (1983) makes a similar argument for the lack of song sharing among Cassin's Sparrows. This species depends on spatially and temporally unpredictable rainfall and "must be ready to locate, advertise, and defend a territory, and successfully attract a female in a very short time."

Kroodsma (1996) urged the further study, specifically, of *Spizella* sparrows, including genetics, signal variation, and ontogeny. The study of Brewer's Sparrow offers several other research avenues. We do not fully understand the taxonomic status of *S. b. taverneri* (Swarth and Brooks 1925, American Ornithologists' Union 1957, Sibley and Monroe 1990, Rising 1996, Doyle 1997, Klicka et al. 1999), the functions of the long or the short song (Catchpole and Slater 1995), the individual and geographic variation in the long song, the ontogeny of any vocalization (Kroodsma 1996), or how the functions of these signals compare to those of Sage Sparrows (Rich 1981, Wiens 1982) and Sage Thrashers (Reynolds et al. 1999) sharing the same habitats and territories.

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SOIL DEPTH EFFECTS ON CHIHUAHUAN DESERT VEGETATION

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ABSTRACT.—We evaluated relationships between soil depth and vegetation standing crop components over a 3-year period on 3 adjoining pastures with similar size, vegetation, and soils on the Chihuahuan Desert Rangeland Research Center in south central New Mexico. Soils on our study pastures are primarily light sandy loams varying from a few centimeters to 1 m or more in depth underlain by a calcium carbonate layer. Study pastures were ungrazed in 1995 and 1996 and conservatively grazed in 1997. Linear regression equations using perennial grass standing crop (kg ha^{-1}) and honey mesquite (*Prosopis glandulosa* Torr.) cover (%) as dependent variables and soil depth as the independent variable were significant ($P < 0.05$) and similar for all 3 pastures. Deep soils had low perennial grass standing crop and high mesquite cover, while the opposite occurred for shallow soils. Within shallow soils, honey mesquite and perennial grass standing crop were not correlated ($P = 0.78$, $n = 18$), but a significant ($P = 0.01$) negative correlation occurred on deep soils ($r = -0.67$, $n = 15$). Perennial grass standing crop differed greatly among years when data were pooled across pastures, ranging from 64 kg ha^{-1} in 1995 to 248 kg ha^{-1} in 1997. Our study shows that soil depth has a major influence on Chihuahuan Desert vegetation. Perennial grasses are favored by shallow sandy soils while deep sandy soils favor honey mesquite.

Key words: rangeland, herbicides, brush control, cattle, grazing.

Site factors such as topography, soil depth, soil texture, and precipitation play a critical role in determining the type of vegetation and its potential productivity for any rangeland area (Holechek et al. 2001). Sound decisions on management practices such as brush control, seeding, and fertilization depend on understanding site potential.

Honey mesquite (*Prosopis glandulosa* Torr.) invasion has been considered a major range management problem in the Chihuahuan Desert of southwestern United States and northern Mexico (Buffington and Herbel 1965, Gibbens et al. 1992). However, long-term monitoring studies in southern New Mexico showed no change in mesquite cover during the period from 1952 to 1999 across 40 sites (McCormick and Galt 1993, Galt et al. 1999). Nearly all sites that were grasslands in the early 1950s still remain grasslands today (Galt et al. 1999). Grazing intensity levels on 80% of these sites were considered to have been light to moderate during most years (Galt et al. 1999).

Mesquite invasion in the Chihuahuan Desert may be closely related to site characteristics such as soil depth and texture. However, studies

evaluating how soil factors influence honey mesquite levels are lacking.

The objectives of our study were to evaluate the effects of soil depth on mesquite canopy cover, mesquite density, and perennial grass standing crop during 3 consecutive years in the Chihuahuan Desert of south central New Mexico. The primary null hypothesis tested was that soil depth has no effect on mesquite cover and perennial grass standing crop.

Study Area

The study was conducted during autumn 1995, 1996, and 1997 on the New Mexico State University Chihuahuan Desert Rangeland Research Center (CDRRC), 40 km north of Las Cruces, Doña Ana County, New Mexico. The CDRRC lies in the southern portion of the Jornada del Muerto Plain between the San Andres Mountains and the Rio Grande. The elevation of the study area is 1340 m. Topography is generally level with all slopes less than 5%. The area is arid, with no permanent water except the river and stock watering points supplied by wells and temporary earthen tanks. Annual precipitation during the study period

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varied from 180 to 298 mm. The 63-year average is 230 mm (Table 1). About half of the annual precipitation occurs between July and September, with highest precipitation in August. Wood (1969) described the climate of the area as semidesert, with annual temperatures varying from -23° to 42°C and daily fluctuations of up to 30°C . June is the warmest month and January the coldest.

Soils of the CDRRC study area are mainly light sandy loams varying in depth from a few centimeters to 1 m or more underlain by a calcium carbonate hardpan (caliche; SCS 1980). The soils are classified as fine loamy, mixed, thermic, Typic Haplargids and are in the Simona-Cruces associations (SCS 1980). In areas where groundcover is sparse, sand dunes have formed around mesquite plants (Wood 1969). Over most of the study area, the soil profile is relatively well preserved and stable.

Vegetation on the study area is characterized as Chihuahuan Desert grassland with shrubs scattered throughout the area. Large areas have varying cover of honey mesquite (*Prosopis glandulosa* Torr.). Understory vegetation consists largely of black grama (*Bouteloua eriopoda* Torr.), mesa dropseed (*Sporobolus flexuosus* [Thurb.] Rydb.), and spike dropseed (*S. contractus* A. Hitch). Broom snakeweed (*Gutierrezia sarothrae* Greene) dominates a few small areas.

METHODS

We conducted our study on 3 adjoining pastures on the CDRRC having similar soils, topography, and size. These pastures are 992, 1267, and 1219 hectares, respectively. Overall ecological condition of pastures 1 (west) and 2 (center) is late seral, while pasture 3 (east) is in

high mid-seral condition (Table 2). Honey mesquite cover and density within each of the 3 pastures show considerable variation. Large portions of each pasture received herbicidal control of brush in the early 1960s (McNeely 1983). Mesquite root kill levels were generally around 65%. Additional herbicidal control was applied in the mid 1980s, but mesquite kill levels were under 5%. Depending on year, these pastures were conservatively to moderately stocked from 1968 to 1994. All pastures were destocked in late July 1994 due to severe drought conditions and were restocked in late November 1996 following procedures of Holechek (1988). Forage use by cattle during 1997 was light to conservative (25–35% use of perennial grasses) in all pastures.

In the fall of 1995, range inventories in the 3 pastures established a baseline databank for intensive evaluation of long-term vegetation trends. We measured total herbage standing crop, forage production, and plant basal cover on all pastures in October 1995, 1996, and 1997. Ten permanent key areas were systematically established for monitoring each of the 3 pastures. We selected these key areas by dividing each pasture into 10 equal parts and then locating the key area near the center of each part. This resulted in key areas being evenly spaced within each pasture. In fall 1996 and 1997, we measured 3 more key areas in sites densely populated with mesquite. One key area was added in pasture 1 and 2 key areas in pasture 3. All key areas were in the center of discreet areas with uniform soils and vegetation. A point-intercept method was used to determine groundcover, plant composition, and trend on all key areas. A transect consisted of 61 m of line located by rebar stakes at each end and another in the center of the line.

TABLE 1. Annual and growing season¹ precipitation (mm) for pastures 1, 2, and 3 from 1995 through 1997 on the Chihuahuan Desert Rangeland Research Center².

Pastures	1995		1996		1997	
	Year total	Growing season total	Year total	Growing season total	Year total	Growing season total
----- mm -----						
1 – West	167	102	197	127	295	139
2 – Middle	175	112	187	120	327	159
3 – East	168	97	230	150	294	138

¹Growing season is from July through September.

²Long-term average precipitation (1930–1993) is 230 mm total and 127 mm during the growing season.

TABLE 2. Vegetation basal cover (%) pooled across years (1995, 1996, 1997) on pastures 1, 2, and 3 on the Chihuahuan Desert Rangeland Research Center in south central New Mexico.

	Pasture		
	1	2	3
	----- % cover -----		
Black grama (<i>Bouteloua eriopoda</i>)	1.4	1.1	0.1
Mesa dropseed (<i>Sporobolus flexuosus</i>)	0.8	0.1	0.4
Threeawn spp. (<i>Aristida</i> sp.)	0.2	1.2	0.2
Other grasses	0.4	0.1	0.3
Total perennial grasses	2.8	2.5	1.0
Forbs	0.7	0.7	0.7
Broom snakeweed (<i>Gutierrezia sarothrae</i>)	0.4	0.3	0.3
Honey mesquite (<i>Prosopis glandulosa</i>)	7.0 ^a	4.2 ^a	5.2 ^a
Other shrubs	0.1	0.1	0.1
Total shrubs	7.5	4.6	5.6
Total vegetation cover	11.0	7.8	7.3

^aCanopy cover

We measured plant basal cover at 0.61-m intervals using a pin along a tape stretched between the 2 permanent rebars. One hundred observations were taken per transect, and data were recorded by plant species (annual and perennial), litter, rock and gravel, and bare soil. For species composition information, we recorded the nearest plant species in the case of hits on bare ground.

Herbage production was evaluated by offsetting the 61-m line by 3.05 m and placing ten 0.5-m square quadrats parallel to the first line at 6.1-m intervals. All plant species were clipped on each plot to ground level, air-dried for 3 days, and then oven-dried for 24 hours at 55°C. In autumn 1997 we adjusted grazed plants to equivalent weight of ungrazed plants by clipping ungrazed plants of similar height and basal diameter outside of quadrats. These adjustments were minimal because very few plants within quadrats showed visible grazing use. Current year's growth was separated from old growth. Standing crop estimates in this study involved only current year's growth. Transects for herbage production were moved 3.0 m each year to avoid clipping in the same spot.

Mesquite canopy cover on key areas was evaluated along the transects previously described by using the line-intercept method (Canfield 1941). Honey mesquite densities on key areas were determined by establishing

belt transects. Three 40 × 2-m belt transects were laid out perpendicular to the 61-m line to estimate number of plants per hectare. The belt transects covered a measured area of 240 m² on each of the 33 key areas.

Soil depth was determined by digging pits at each of the 33 key areas. Two range sites were encountered (shallow sandy and deep sandy). We considered the shallow sandy range key areas to be those having soils ≤40 cm in depth, and deep sandy range key areas were those having soil depth >40 cm. All 3 pastures had shallow (10–40 cm) and deep soils (41–120 cm). Pasture 1 had 5 shallow and 6 deep key areas, pasture 2 had 8 shallow and 3 deep key areas, and pasture 3 had 5 shallow and 7 deep key areas. Soil depth on each key area was relatively uniform, based on data gathered by driving a steel measuring rod into the ground at various points and recording the depth to the caliche layer.

Statistical Analyses

Using regression and correlation analyses, we evaluated relationships between mesquite cover, mesquite density, soil texture, soil depth, year, and herbage production for individual pastures and across all pastures (Neter and Wasserman 1974). Regression analyses were performed using the Proc Reg Command in SAS. Relationships were evaluated using linear, quadratic, and cuboidal models (SAS 1986).

RESULTS

Mesquite cover and density both showed significant positive correlations ($P < 0.05$) with soil depth across the 3 study pastures (Table 3, Fig. 1). Because the effect of pasture was not significant ($P > 0.83$), data were pooled across pastures for all regression analyses. Results of regression analyses are shown in Tables 4 and 5. In brief, curvilinear regression equations better fit these data than a linear equation.

Black grama and perennial grass standing crops were negatively correlated with soil depth (Table 3, Fig. 2). Curvilinear regression equations appear to better describe the data than a linear equation (Table 4).

Mesquite canopy cover and density on the 33 transects had weak negative ($P < 0.05$) correlations with black grama and perennial grass standing crop (Table 3, Fig. 3). Regression equations fit with linear, quadratic, and cuboidal

TABLE 3. Significant ($P < 0.05$) simple correlation coefficients for associations between mesquite cover (%), mesquite density (kg ha^{-1}), soil depth (cm), black grama standing crop (kg ha^{-1}), and total grass standing crop (kg ha^{-1}) based on 33 transects in 3 pastures for data pooled across years (1995, 1996, 1997).

	<i>Prosopis glandulosa</i> cover		<i>Prosopis glandulosa</i> density		Soil depth	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
<i>Bouteloua eriopoda</i> standing crop	-0.336	0.05	-0.314	0.05	-0.492	0.04
Total	-0.471	0.02	-0.485	0.04	-0.670	0.01
<i>Prosopis glandulosa</i> cover			0.796	0.01	0.873	0.01
<i>Prosopis glandulosa</i> density					0.743	0.01
Soil depth						

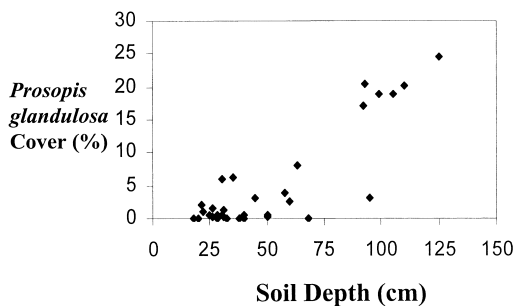


Fig. 1. Relationship between soil depth and mesquite canopy cover on the Chihuahuan Desert Rangeland Research Center in south central New Mexico using data pooled across years (1995, 1996, 1997).

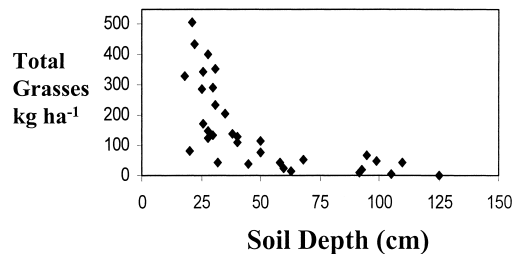


Fig. 2. Relationship between soil depth and total perennial grass production on the Chihuahuan Desert Rangeland Research Center in south central New Mexico using data pooled across years (1995, 1996, 1997).

models appeared to be similar for these relationships ($r^2 \cong 0.22$, Table 5). Although these results suggest that mesquite canopy cover influences grass production, it is important to recognize that high mesquite cover occurred only on deep soils unfavorable for perennial grasses (Fig. 2). No correlation ($P = 0.78$) between mesquite cover and total perennial grass standing crop occurred within shallow soils. However, mesquite cover was negatively correlated ($P = 0.01$) with total perennial grass standing crop within deep soils ($r = -0.67$, $n = 15$).

Perennial grass standing crops differed greatly among years. When data were pooled across the 33 key areas, total perennial grass production averaged 64 kg ha^{-1} in 1997, 116 kg ha^{-1} in 1998, and 248 kg ha^{-1} in 1999. Rainfall on the study area during the growing season (July through September) was 16% below average for 1995 but 1% and 16% above average for 1996 and 1997, respectively (Table 1). Perennial grass standing crop in 1997 showed substantial recovery from drought in 1994 and 1996.

We recognize that regression relationships of mesquite cover and soil depth to total grass standing crop could be influenced by year. Therefore, we conducted multiple regression analyses involving year or time in models using soil depth and mesquite cover to predict total grass standing crop. These analyses were conducted using the mixed model procedures of SAS where time was fit as a fixed regression variable and mesquite cover and soil depth were fit as random independent variables (SAS 1996). In these analyses, linear, quadratic, and cubic relationships were tested. The linear term of time and the quadratic term of time were found to be significant ($P < 0.05$) in the model using mesquite cover to predict total grass. However, the actual linear (mesquite cover*time) and quadratic terms (mesquite cover*time*time) were not significant ($P > 0.20$). The coefficient of determination for these models was very weak ($R^2 < 0.14$). Therefore, even though year was significant in the analyses, these regressions were not strong. We took the analyses one step further and analyzed each year independently with the Proc

TABLE 4. Linear, quadratic, and cubic regression equations for predicting grass standing crop (kg ha^{-1}) and mesquite cover (%) from soil depth (cm) based on 33 transects in 3 pastures for data pooled across years (1995, 1996, 1997).

Model type	Pasture	Dependent variable	Equation	<i>n</i>	<i>r</i> ²	<i>P</i>
Linear	All	<i>Prosopis glandulosa</i>	$y = 0.213x - 5.788$	33	0.75	0.01
Quadratic	All	<i>Prosopis glandulosa</i>	$y = 0.0026x^2 - 0.013x + 2.35$	33	0.82	0.01
Cubic	All	<i>Prosopis glandulosa</i>	$y = 0.00002x^3 + 0.0007x^2 - 0.035x + 6.1$	33	0.82	0.01
Linear	All	Grass standing crop	$y = -3.1x + 307.5$	33	0.45	0.01
Quadratic	All	Grass standing crop	$y = 0.07x^2 - 11.8x + 517.1$	33	0.58	0.01
Cubic	All	Grass standing crop	$y = 0.001x^3 + 0.26x^2 - 23.4x + 707$	33	0.61	0.01

TABLE 5. Linear, quadratic, and cubic regression equations for predicting grass standing crop (kg ha^{-1}) from honey mesquite cover (%) based on 33 transects in 3 pastures for data pooled across years (1995, 1996, 1997).

Model type	Pasture	Dependent variable	Equation	<i>n</i>	<i>r</i> ²	<i>P</i>
Linear	All	Grass standing crop	$y = -8.8x + 195.9$	33	0.22	0.01
Quadratic	All	Grass standing crop	$y = 0.78x^2 - 12.66x + 200.4$	33	0.22	0.03
Cubic	All	Grass standing crop	$y = 0.012x^3 - 0.209x^2 - 9.7x + 198.3$	33	0.22	0.05
Linear	1	Grass standing crop	$y = -10.8x + 237^a$	11	0.35	0.06
Linear	2	Grass standing crop	$y = -10.3x + 239^a$	10	0.20	0.09
Linear	3	Grass standing crop	$y = -5.7x + 126^a$	12	0.27	0.07

^aLinear regression equations for individual pastures did not differ ($P > 0.10$).

Reg procedures of SAS (SAS 2000) and found great similarity for each year analyzed. Therefore, based upon these analyses, we feel that pooling the data across years for the relationship of mesquite cover and total grass is an appropriate analysis and presentation of the data. In the multiple regression analyses using soil depth to predict total grasses, similar results to the relationship of mesquite cover and total grass were found (i.e., linear and quadratic terms of time were significant, but the terms involving soil depth were not). The coefficient of determination using soil depth to predict total grass was somewhat stronger across years (r^2 ranging from 0.3 to 0.4). However, these coefficients of determination are still modest for prediction equations, and the regression equations for each individual year are very similar for the 3 years studied. Results of these analyses indicate that the data are best described by curvilinear or quadratic equations, but the similarities found across years suggest that pooling of data across years is a justifiable presentation. Therefore, we believe that the data are best presented pooled across years.

DISCUSSION

It has been commonly postulated that deep, coarse-textured soils facilitate downward water infiltration and retain little moisture near the soil surface (Holechek et al. 2001). Theoretically, this benefits shrub species (such as honey mesquite) having extensive, coarse root systems. In contrast, most moisture is retained near the soil surface by clay soils and sandy soils having a shallow, restrictive (caliche) layer. This should favor grasses with dense, short, fibrous root systems such as black grama. Our data provide evidence supporting these statements. Furthermore, Buffington and Herbel (1965) found that honey mesquite abundance in the Chihuahuan Desert is greatest on deep sandy soils. Herbel and Gibbens (1996) found low black grama and perennial grass standing crops on deep sandy soils on the Jornada Experimental Range in south central New Mexico. The most productive black grama stands occurred on shallow loamy or shallow sandy soils.

On our 6 deep sandy sites where mesquite cover exceeded 15%, perennial grass standing

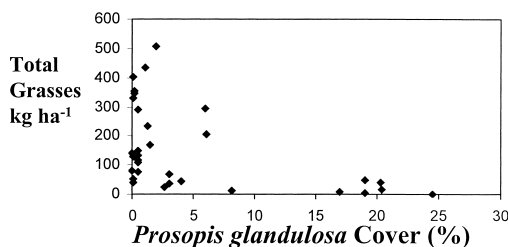


Fig. 3. Relationship between total perennial grass production and mesquite canopy cover on the Chihuahuan Desert Rangeland Research Center in south central New Mexico using data pooled across years (1995, 1996, 1997).

crops were low ($<50 \text{ kg ha}^{-1}$) in all 3 years of study (Fig. 3). Scifres and Polk (1974) found little to no increase in forage production on mesquite control areas where mesquite canopy cover had been less than 15–20%. However, there is evidence from Arizona (Glending 1952), Texas (McDaniel et al. 1982), and New Mexico (Warren et al. 1996) that when mesquite canopy cover exceeds 15–20%, it adversely impacts perennial grass production.

MANAGEMENT IMPLICATIONS

Our 3-year study on the Chihuahuan Desert Rangelands Research Center showed perennial grasses are favored by shallow sandy soils while honey mesquite is favored by deep sandy soils. A 47-year study involving 40 sites well distributed across the Chihuahuan Desert of southern New Mexico showed that conservatively to moderately grazed grassland areas had little invasion of honey mesquite from 1952 to 1999 (Galt et al. 1999). Soil depth appears to largely explain why some parts of the Chihuahuan Desert are now dominated by honey mesquite while other areas remain as grasslands. Deep sandy soils with good remaining perennial grass cover are the sites most vulnerable to honey mesquite invasion from drought and heavy livestock grazing. Care should be taken to ensure these sites receive light to conservative livestock grazing. Burning and/or herbicidal control of mesquite may be necessary to prevent its invasion on deep sandy sites after extended droughts such as occurred in the 1950s. However, these treatments are unlikely to be cost effective for ranchers at today's cattle prices because of the low forage production potential associated with deep sandy sites.

Mesquite invasion does not appear to be a threat on most shallow sandy sites if sound grazing practices are applied. Range improvements such as seeding and brush control will be much more cost effective on degraded sites with shallow soils than those characterized by deep sands.

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KANAB AMBERSNAIL AND OTHER TERRESTRIAL SNAILS IN SOUTH CENTRAL UTAH

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ABSTRACT.—Surveys for succineid snails were conducted to improve genetic and geographical information for the endangered Kanab ambersnail (*Oxyloma haydeni kanabensis* Pilsbry) and related taxa within the Succineidae. Surveys were carried out in the Bureau of Land Management Kanab District, at the Grand Staircase–Escalante National Monument, on 3 private holdings, and along Highways 89, 12, and 14, all in south central Utah. A population of Kanab ambersnails was known to exist in the region; other populations of *Oxyloma* were discovered in primarily seep-fed wetlands in Kanab Creek and in tributaries of and wetlands along the Virgin, Sevier, and Escalante rivers in Kane, Garfield, and Piute counties. None of the newly discovered populations was identified as Kanab ambersnail on the basis of anatomical evidence, although one was at the type locale for that species. We list other snail species encountered and discuss the status of the Kanab ambersnail in light of recent genetic research.

Key words: ambersnail, taxonomy, Colorado Plateau, *Oxyloma*, *Succineidae*.

In North America succineid snails (Mollusca: Stylommatophora: Succineidae) are often, but not invariably, terrestrial and are associated with a variety of wetland habitats. Although they have been widely collected and described, identification of succineid specimens can be difficult, and taxonomy within Succineidae is in flux, owing, in some cases, to anatomical similarity of species (e.g., Franzen 1981, 1985, Frest and Dickson 1986, Hoagland and Davis 1987, Miller et al. 2000, Stevens et al. 2001) and in other cases also to conflicting results from anatomical and genetic studies (Hoagland and Davis 1987, Miller et al. 2000, Stevens et al. 2001). New species descriptions and expansions of known ranges are ongoing in North America (Harris and Hubricht 1982, Franzen 1983, 1985, Frest and Dickson 1986, Spamer and Bogan 1993a, 1993b). Currently, 2 species in the family (Kanab ambersnail, *Oxyloma haydeni kanabensis* Pilsbry, and the Chittanooga ovate ambersnail, *Succinea chittanoogaensis* Pilsbry) are federally endangered.

In the southwestern U.S., succineid collections are patchy (e.g., Ferriss 1910, Chamberlin and Jones 1929, Baily and Baily 1952, Bequaert and Miller 1973, Hovingh 1993, Kerns 1993, Spamer and Bogan 1993a, 1993b). In 1992 the Kanab ambersnail was listed as federally endangered (U.S. Fish and Wildlife

Service 1992) after searches at the type locality in Kanab Canyon, near Kanab, Utah, located only 3 individuals (Clarke 1991) and the owner of the only other known site for the species (in Three Lakes Canyon also near Kanab) began plans to develop the property. During the listing process, a 3rd population was discovered in Grand Canyon, Arizona (Spamer and Bogan 1993a, 1993b); all 3 populations were included in the listing. Since listing, 2 additional populations of *Oxyloma* have been located in Grand Canyon (at Indian Gardens along South Bright Angel Trail, and at 9-Mile Marsh along the edge of the Colorado River); both were identified on the basis of anatomy as *O. h. haydeni* Binney (Stevens et al. 1997, Miller et al. 2000).

In his reclassification of *O. h. kanabensis* (originally *Succinea hawkinsi* Baird), Pilsbry (1948) indicated that the new subspecific status should be regarded as preliminary and that full species status might be warranted. No further work on taxonomy of southwestern succineids was undertaken until after listing of the Kanab ambersnail. Results of preliminary molecular taxonomic work with the Grand Canyon *O. h. haydeni* and *O. h. kanabensis* populations and the remaining *O. h. kanabensis* population on private land in southern Utah were inconsistent with anatomical results (Miller et al. 2000). Here we report on surveys

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undertaken to improve understanding of succineid distribution in south central Utah and to provide specimens for further taxonomic study.

MATERIALS AND METHODS

Surveys

We conducted surveys in the Bureau of Land Management's (BLM) Kanab District; in the Grand Staircase–Escalante National Monument (also BLM land); and on private land in Three Lakes Canyon, in Kanab Canyon, and on The Nature Conservancy's Autumn Buttercup Preserve in the Sevier drainage in Garfield County. Additional public rights-of-way, all in south central Utah (Fig. 1), were also surveyed, i.e., along Highway 89 in the Sevier and Virgin drainages, along Highway 12 near the northern boundary of the monument, and along the east end of Highway 14. In all cases we briefly described riparian and seep-fed wetlands and systematically searched them for live or recently dead snails. Succineids from several sites were collected for genetic analysis reported elsewhere (Stevens et al. 2001).

Survey of Kanab Canyon followed the August 1998 discovery of an *Oxyloma* population in the canyon containing the type locality of Kanab ambersnail (Meretsky and North 2000). Survey efforts extended from the dam at the Kanab City Reservoir north to the confluence with Red Canyon (a straight-line distance of 11.2 km) and included the area believed to be the type locality for *O. h. kanabensis*.

Following discussions with BLM personnel and helicopter surveys of potential habitats for succineid snails, we determined survey locations in Grand Staircase–Escalante National Monument. Ground surveys were conducted primarily from Skutumpah Road, Highway 12, and Cottonwood Canyon Road. The monument contains many small patches (< 100 m in any dimension) of potential habitat and considerable fenced land; not all potential habitat was visited. *Oxyloma* specimens from one site in Upper Valley died before being preserved but we did not re-collect from the site as a sample was collected and successfully preserved from a nearby site along the same drainage.

The Nature Conservancy's Autumn Buttercup Preserve, north of Panguitch in Garfield County, was surveyed in response to reports of

Oxyloma there (Lunceford personal communication). Surveys along Highways 89 and 14 were conducted where wetland vegetation could be reached in the public rights-of-way.

In 1996 and 1998 we conducted surveys of Three Lakes; surveys in the remainder of Kane County and in Garfield County were conducted in 1999. Two sites, one in Piute County and the other in Garfield County (below the Burr Trail), were visited in 2000; Burr Trail specimens, which were collected after anatomical identifications had been completed, are identified only to genus. All other *Oxyloma* were identified to species by Shi-Kuei Wu of University of Colorado (no geographical information was supplied so that identifications were purely on the basis of anatomy); *Catinella* were not identified with certainty and are recorded only at the genus level; other snails were identified by Eric North. Specimens were archived at Northern Arizona University's Laboratory of Quaternary Paleontology and at the Museum of Northern Arizona, both in Flagstaff.

Population Estimation

Population estimation was undertaken at Three Lakes, where the Kanab ambersnail was known to be present, and in Kanab Canyon, the type locality for the Kanab ambersnail (although snails there were later identified by anatomy as belonging to other taxa). Snails were counted in haphazardly placed 20-cm-diameter circles in appropriate habitat; we dispersed samples throughout the habitat but did not grid the sites to allow true random sampling.

Habitat in Kanab Creek was too extensive to sample every patch; an initial estimate of snail density was constructed by sampling in several different wetland patches, stratified by habitat type (e.g., wet meadow, cattail stand). Using GPS equipment, we measured or surveyed areas of habitat patches, categorized them by habitat type, and calculated population estimates from the median densities of the initial sample of similar wetlands. Final estimates considered only snails ≥ 4 mm in length, as these were considered to be equally observable by all surveyors and in all habitats and to be somewhat more likely to survive to adulthood (7 mm; Wu personal communication) than smaller snails. Snails in streamside vegetation along Kanab Creek were not included

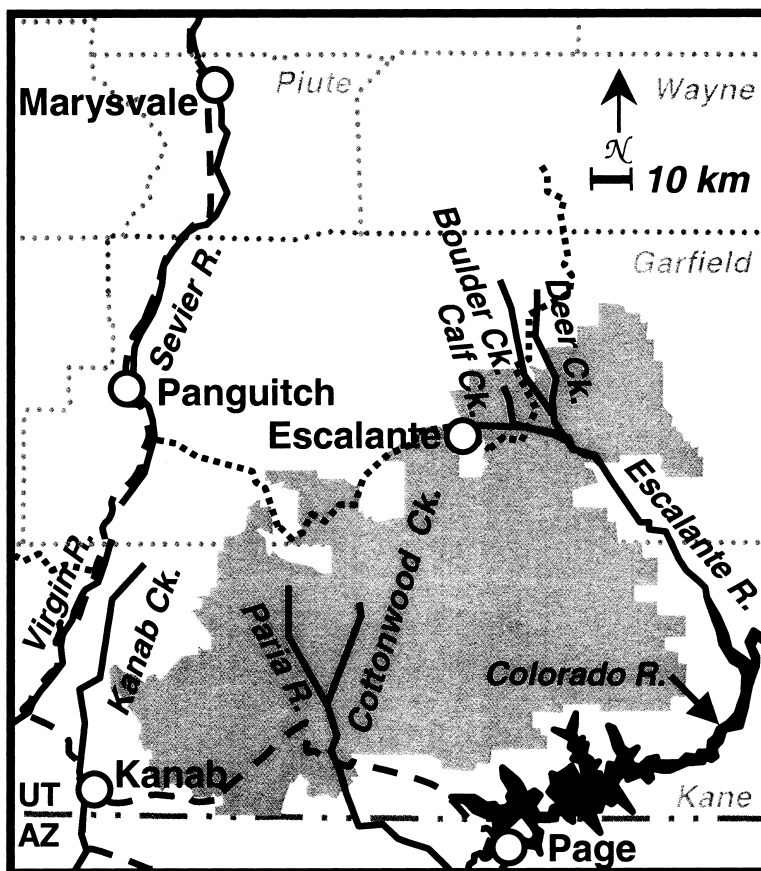


Fig. 1. Study area in south central Utah. Black dashed lines represent Highway 89 (long dashes), Highway 14 (short dashes west of Highway 89), and Highway 12 (short dashes east of Highway 89). Shaded area is Grand Staircase-Escalante National Monument.

in the population estimates because the creek undergoes major flooding during monsoon rains. We expected mortality rates to be high in these habitats and excluded snails there (which were present only in comparatively very low densities) to provide more conservative estimates of population size. Additional details on estimation techniques are given in Meretsky and North (2000). We surveyed habitat area in Three Lakes and used 30 samples from each of 3 habitat types to extrapolate total population size.

RESULTS

Surveys

Succineids were found, primarily in spring- or seep-fed habitats, along the Virgin, Sevier, and Escalante rivers and their tributaries, in

Kanab Creek (but not in its surveyed tributaries), in isolated wetlands near Henrieville Creek (along Highway 12), in Harris Flats (along Highway 14), and at a pond north of Calf Pasture Point (Table 1). At least 4 succineid taxa from 2 genera (*O. h. haydeni*, *O. h. kanabensis*, *O. retusa*, *Catinella* spp.) and 14 other species from 12 genera were found alive or recently dead: *Cochlicopa lubrica* (Müller), *Discus cronkhitei* (Newcomb), *Euconulus fulvus* (Pilsbry), *Gyraulus circumstriatus* (Tryon), *Hawaiiia minuscula* (Binney), *Nesovitrea electrina* (Gould), *Pupilla muscorum* (Linnaeus), *P. sonorana* (Sterki), *Sonorella* sp., *Vallonia cyclophorella* (Sterki), *Vertigo ovata* (Say), *Vitrina limpida alaskana* (Dall), *Zonitoides arboreus* (Say), and *Z. nitidus* (Müller). Some sites supported only succineids, and no site that contained other snails lacked succineids.

TABLE 1. Locations of snail surveys in south central Utah, with snail species located and habitats present. Agency designations for public lands indicate Grand Staircase–Escalante National Monument (GSENM), non-monument Bureau of Land Management lands (BLM), Dixie National Forest (DNF), and State of Utah (UT). Species designations within *Oxyloma* are based on anatomy. Habitat in rights-of-way (RoW) was not measured. Locations are based on the WGS84 datum.

County	Agency	Description	Lat	Long	Species and habitat
Kanab Creek and tributaries					
Kane		Kanab Canyon, upper bench near road	37° 08.58′	112° 32.46′	<i>Oxyloma retusa</i> , marsh and wet meadow, grazed.
Kane		Kanab Canyon, Big Lake (upper bench)	37 09.47	112 32.70	<i>O. retusa</i> , marsh and wet meadow, grazed.
Kane	part BLM	Kanab Creek near dam, S end of survey of lower bench	37 04.63	112 32.41	(next line)
Kane	part BLM	Kanab Creek S of Red Cyn, N end of lower bench survey	37 10.05	112 32.21	<i>O. h. haydeni</i> , <i>Vertigo ovata</i> , <i>Euconulus fulvus</i> , <i>Z. arboreus</i> , <i>Nesovitrea electrina</i> . Willow, marsh, wet meadow, wetland forb vegetation, some grazing. Total surveyed Kanab Canyon habitat approx 67,000 m ² .
Kane		Three Lakes, north lake in Three Lakes Canyon	37 08.26	112 34.01	<i>O. h. kanabensis</i> , <i>Discus cronkhitei</i> , <i>Vertigo ovata</i> , <i>N. electrina</i> , <i>Gyraulus circumstriatus</i> , <i>E. fulvus</i> . Marsh, wet meadow, and wetland forb vegetation, some grazing. Total habitat at north lake approximately 1200 m ² .
Kane	BLM	Hog Cyn (to 3 hr up from Kanab Ck)	37 05.33	112 30.86	No snails, less than 1500 m ² of wet meadow habitat.
Kane	BLM	Trail Cyn (coordinates are confluence)	37 04.10	112 32.37	No snails, no wetland habitat.
Kane	BLM	Red Cyn (coordinates are confluence)	37 10.61	112 32.22	No snails, no wetland habitat.
Kane	UT/BLM	Water Cyn (coordinates are confluence with Cottonwood Ck)	37 04.19	112 36.96	No snails, no wetland habitat.
Virgin River and tributaries					
Kane		Below KOA campground N of Glendale	37 22.94	112 34.62	<i>O. retusa</i> , willow, wet meadow in RoW.
Kane		Hidden Lake outflow	37 20.71	112 36.09	<i>O. h. haydeni</i> , marsh, wet meadow in RoW.
Kane		Virgin River N of Glendale	37 20.06	112 36.13	<i>O. h. haydeni</i> , wet meadow in RoW.
Other Kane County sites					
Kane		1 km W of Long Valley Jn on Hwy 14	37 29.44	112 31.31	No snails, no wetland habitat.
Kane	DNF	S of Hwy 14, 6 km W Long Valley Jn	37 29.29	112 33.69	No snails, water present.
Kane	DNF	Harris Flats on Hwy 14	37 29.51	112 34.33	<i>Catinella</i> sp., water present.
Kane	DNF	Harris Flats on Hwy 14	37 29.67	112 34.72	<i>Catinella</i> sp., water present.

Oxyloma h. haydeni and *O. retusa*, but not *O. h. kanabensis*, were found in Kanab Creek (Table 1). *Oxyloma h. haydeni* was identified from 2 collecting sites on the lower bench, which ranges from less than a meter to somewhat over a meter above Kanab Creek at base flow. We identified *Oxyloma retusa* from 2 sites on the upper bench, approximately 30 m above Kanab Creek. *Oxyloma h. haydeni* and *O. retusa* were also found in the Virgin River drainage, and *O. retusa* was found in the Sevier and Escalante watersheds. *Catinella* occurred along the Sevier and Escalante rivers

and their tributaries, at isolated springs within Grand Staircase–Escalante National Monument, and along Highway 14.

Of 26 sites from which snails were absent, 10 supported no wetland habitat. Grazing occurred at several sites without snails; however, grazing also occurred at sites that supported diverse snail assemblages, although these tended to be larger sites or complexes of sites. Wetland vegetation types containing snails included willow stands (*Salix* spp.), marsh vegetation (generally cattails and bulrushes: *Typha* spp., *Scirpus* spp., and *Schoenoplectus* spp.),

TABLE 1. Continued.

County	Agency	Description	Lat	Long	Species and habitat
Sevier River and tributaries					
Garfield	TNC	Sevier River Preserve, Utah Nature Conservancy	37 57.22	112 24.93	<i>O. retusa</i> , <i>Hawaia minuscula</i> , <i>E. fulvus</i> found in wet meadow that extends beyond the property. No grazing, but fire recently used for management.
Garfield		Sevier River near mile marker 121.3 on Hwy 89	37 57.30	112 24.71	<i>Catinella</i> sp. in wet meadow in RoW.
Garfield		Mammoth Creek, near mile marker 114.5 on Hwy 89	37 42.59	112 23.50	<i>Catinella</i> sp. in wet meadow in RoW and adjacent unfenced property.
Garfield		Asay Creek, at Hwy 89	37 35.05	112 28.59	<i>Catinella</i> sp., <i>Vertigo ovata</i> , <i>Pupilla sonorana</i> in wet meadow in RoW.
Piute		6.4 km N of Marysville on Highway 89, Sevier backwater	38 29.54	112 14.84	<i>O. haydeni</i> found in sparse marsh vegetation in RoW.
Grand Staircase–Escalante National Monument and vicinity					
Escalante River and tributaries					
Garfield	GSENM	Lower Calf Creek Falls to campground	37 49.72	111 25.17	<i>O. retusa</i> , <i>Catinella</i> sp., <i>Cochlicopa lubrica</i> , <i>P. muscorum</i> , <i>Zonitoides nitidus</i> , <i>Sonorella</i> sp. found near falls. Willow, wet meadow, and wetland forbs.
Garfield	GSENM	Escalante River from Hwy 12, surveyed to 4 km west of hwy	37 46.53	111 25.41	<i>O. retusa</i> , <i>Catinella</i> sp. found in wetland near confluence with Calf Creek in <1000 m ² of wet meadow.
Garfield	GSENM	Dry Hollow Ck to Boulder Ck near Escalante, N end of survey	37 50.44	111 25.05	<i>Catinella</i> sp., <i>Vitrina limpida alaskana</i> , <i>P. sonorana</i> , <i>Vallonia cyclophorella</i> , <i>Z. arboreus</i> found in sparse, fringing wet meadow.
Garfield	GSENM	Dry Hollow Ck to Boulder Ck near Escalante, S end of survey	37 48.56	111 23.10	(previous line)
Garfield	GSENM	Escalante River east of Boulder Creek	37 45.58	111 20.38	No snails, small, flood-prone tributary.
Garfield	GSENM	Deer Ck, S of Burr Trail	37 51.15	111 21.32	<i>Oxyloma</i> sp. in approx. 10,000 m ² of wet meadow.
Garfield		Allen Ck/Upper Valley	37 43.04	111 47.05	<i>O. retusa</i> in sparse wet meadow in RoW.
Garfield		South Hollow/Upper Valley	37 41.12	111 48.66	<i>Catinella</i> sp. in RoW.
Garfield	GSENM ¹	Birch Ck/Upper Valley	37 45.71	111 41.47	<i>Oxyloma</i> sp., <i>Catinella</i> sp. in wet meadow in RoW.
Garfield	DNF	Garden Spring	37 42.13	111 50.55	<i>Catinella</i> sp., water present.

wet meadow vegetation (generally rushes and sedges: *Juncus* spp. and *Carex* spp.), and wetland forbs (generally watercress and cutleaf water-parsnip: *Nasturtium officinale* and *Berula erecta*).

Population Estimates

The populations of *Oxyloma* in Kanab Canyon were concentrated in the habitat between approximately 2 km north of Highway 89 bridge and 1 km below Red Canyon. In sum-

mer 1999 the Kanab Canyon *Oxyloma* population was estimated at 1.52 million snails ≥ 4 mm, with approximately 1.35 million on the lower bench and 170,000 on the upper bench. Although the upper and lower bench collections each contained only a single species, one upper bench site known to contain *O. h. retusa* flows down to the lower bench, and wetland vegetation occurs along much of the short connecting stream. Given the area of habitat involved (over 52,000 m² on the lower and

TABLE 1. Continued.

County	Agency	Description	Lat	Long	Species and habitat
<i>Paria River and tributaries</i>					
Garfield		Paria River E of Cannonville	37 33.68	112 02.67	No snails, dry meadow.
Garfield	GSENM	NE of Henrieville Springs	37 36.27	111 54.61	<i>O. retusa</i> , wet meadow in RoW.
Garfield	GSENM	Unnamed spring NE of Henrieville	37 35.83	111 58.71	No snails, 75 m ² of wet meadow.
Garfield	GSENM	Unnamed spring NE of Henrieville	37 35.88	111 57.06	No snails, wet meadow in RoW.
Kane	GSENM	Unnamed spring in Cottonwood Cyn, near campground	37 19.45	111 53.01	No snails, 150 m ² of marsh. Flood prone.
Kane	GSENM	Unnamed spring in Cottonwood Cyn, approx 7 km N of Hackberry Cyn	37 19.81	111 53.02	No snails. 400 m ² of marsh and willow, very flood prone.
Kane	GSENM	Lower 3 km of Hackberry Cyn (lat-long is confluence with Cottonwood Cyn)	37 15.42	111 54.60	No snails, willow and <i>Tamarisk</i> habitat, but very flood prone.
Kane	GSENM	Pump Canyon Spring	37 20.73	111 52.47	No snails, no wetland habitats, grazed.
<i>Other springs in or near GSENM</i>					
Kane	GSENM	Unnamed spring below Harry Colwes Spring, S end of 50-Mile Mountain	37 14.86	111 08.33	No snails, <500 m ² of wet meadow, grazed.
Kane	GSENM	Lake Pasture in Lake Draw, 50-Mile Mountain	38 17.46	111 08.49	No snails, approx. 5000 m ² of wet meadow and wetland forbs, grazed.
Kane	BLM	Slide Canyon, 3 km outside GSENM	37 20.77	112 16.26	No snails, <3000 m ² of wet meadow, grazed.
Kane	GSENM	Pond N of Corral Canyon, N of Calf Pasture Point	37 22.64	112 10.21	<i>Catinella</i> sp. near pond in marsh, wet meadow. Incompletely surveyed due to nesting raptors.
Kane	GSENM	Adam Springs	37 22.05	112 09.68	No snails, no wetland habitats seen.
Kane	GSENM	First Point Spring	37 15.61	112 19.99	No snails, 5 m ² of wet meadow, grazed.
Kane	GSENM	Old Corral Spring	37 16.09	112 19.73	No snails, 150 m ² of wet meadow, grazed.
Kane	GSENM	Unnamed water reserve	37 17.02	112 18.47	No snails, no wetland habitat.
Kane	GSENM	Unnamed spring along Red Breaks	37 16.45	112 18.34	No snails, no wetland habitat.
Kane	GSENM	Seaman Spring	37 07.14	112 14.69	No snails, 2800 m ² of willow, marsh, and wet meadow.
Kane	GSENM	Unnamed spring; BLM calls "Brown"	37 12.47	112 10.29	No snails, 100 m ² of wet meadow, grazed.
Kane	GSENM	Unnamed spring	37 12.08	112 12.09	No snails, wet meadow, grazed.
Kane	UT	Cottonwood Spring	37 15.08	112 18.95	No snails, no wetland habitat.

¹On monument border.

over 15,000 m² on the upper bench), the likelihood of more than one taxon on at least the lower bench was too large to ignore. Thus, we do not specify population size at the species level. Snails were found primarily in seep-watered willow, marsh, wet meadow, and herbaceous wetland vegetation on the lower bench and in seep-watered marshes and wet meadows on the upper bench.

The upper lake in Three Lakes Canyon contained the most extensive and accessible habitat for Kanab ambersnails on that property. The population of *O. h. kanabensis* there was estimated to include approximately 180,000 snails >1 mm in length in June 1998, before

the major reproductive period. Additional habitat (less, in total, than the approximately 1220 m² at the upper lake) was available at and between the other lakes. Ambersnails were observed in cattails and wet meadow vegetation, as well as in stands of buckbean (*Menyanthes trifoliata*).

DISCUSSION

Our results indicate that succineid snails are more common in south central Utah than previously reported, although Chamberlin and Jones (1929) list many locations for succineids farther north. Even small (<600 m²) wetland

habitat patches can harbor these snails. Although vegetation differed among the various wetlands that contained succineids, occupied areas consistently provided unusually stable hydrologic conditions in this desert region. Sandstone aquifers and their associated seeps and springs were often key to this stability.

Although several streams in the area are permanent (e.g., the Virgin and Escalante rivers, Calf, Boulder and Kanab creeks) and might be expected to support snail populations in their riparian zones, occasionally they are subject to large floods, particularly during monsoon rains. Periodic floods generally scour vegetation, rework streambeds, and move considerable sediment (e.g., Webb et al. 1992), actions likely to eliminate all snails in strictly riparian vegetation; we found no snails in flood-prone areas that lacked refugia (e.g., backwaters or seep-fed vegetation out of the flood zone). Stevens and Meretsky (1997) reported that all *O. h. kanabensis* inundated by floodwaters at Vasey's Paradise in Grand Canyon in 1996 were swept away by water or knocked from vegetation by floating debris. In addition, several local streams are at least 1 m below their banks at base flow, so that only xeroriparian vegetation and woody riparian vegetation occur along the banks. Utah biologists searched the East Fork of the Virgin River and reported only xeric and flood-prone habitats there and no succineids (Webb and Fridell 2000).

Kanab Ambersnail

The current understanding of succineid taxonomy is incomplete. Pilsbry (1948) and Franzen (1963, 1964) suggested that anatomy of the genus *Oxyloma* could be quite variable; and yet anatomy has, until recently, been the only taxonomic tool available, and published species descriptions are based on anatomy. Preliminary genetic studies of *Oxyloma* have revealed apparent discrepancies between anatomical and genetic information (Miller et al. 2000, Stevens et al. 2001). Specifically, individuals from the 2 populations identified as *O. haydeni kanabensis* appear, on the basis of genetic data, to belong to different taxa. Thus, this endangered taxon, as it is presently legally understood (on the basis of peer-reviewed taxonomy), is composed of 2 populations that are not closely related (Miller et al. 2000). Endangered status cannot be reviewed until new peer-reviewed taxonomic classifications are

published; however, studies to support reclassification have yet to be undertaken. Taxonomic discrepancies also may exist within *Catinella* (Stevens et al. 2001).

The location of the type locale for the Kanab ambersnail is not entirely clear from written records. Ferriss described the location simply as "The Greens, 6 m[iles] above Kanab on Kanab Wash," and added that snails were "found on a wet ledge among the moss and moccasin (*cypripedium*) flowers" (personal communication to Pilsbry, 1910).

Prior to the 1880s, Kanab Creek in Kanab Canyon was a small stream running through a large, wet meadow with a high water table (Webb et al. 1992). During the 1880s a series of catastrophic floods, probably aided by overgrazing, cut the streambed down 20–30 m, leaving a series of separate wet meadows watered by springs along an upper bench and exposing a lower series of springs just above the current level of Kanab Creek. This double-benched landscape with an entrenched stream has remained relatively unchanged since approximately the time that Ferriss made his original collection. The development of wetland vegetation at that time is unclear, but grazing was almost certainly widespread; the present major landowner in the snail-inhabited reach does not permit grazing in most of the wetlands, and so lower-bench habitat is likely more extensive now. However, water is currently withdrawn by pipe directly out of the rock at several locations at the back of the upper bench, reducing and/or eliminating the wet meadows that would have been present there in Ferris' time.

One person who grew up in the area recalled that the name "The Greens" was used for the entire seep-fed section of the canyon. Others identified this as a more specific area of wet meadow or meadows on the west side of Kanab Creek, on the upper bench. A member of a family that owned a portion of the canyon indicated the name applied most specifically to a particular upper-bench meadow that still contains *Oxyloma retusa*. This location is approximately 6 miles (9.6 km) above the town of Kanab in Kanab Canyon. Ladyslipper orchids (*Cypripedium* sp.) mentioned by Ferriss do not currently grow there, and none have ever been reported in Kane County (Welsh et al. 1993). However, the helleborine orchid (*Epipactis gigantea*), which has a somewhat similar

flower, is relatively common in Kanab Canyon. Local movie filming in the 1960s further disturbed this particular canyon (N. Cram personal communication), and a cattle tank and diversion pipes have been added more recently.

The meadow specifically identified as "The Greens" is approximately 350 m from the site Clarke (1991) searched when the Kanab amber-snail population in Kanab Canyon was reported as consisting of only a few individuals; it is 200 m from a lower-bench site from which *O. h. haydeni* was collected in 1998 and 1999 from a population estimated at over a million, and 350 m from the nearest upper-bench site containing *O. retusa*. Of snails collected in the region in the past 10 years and identified on the basis of anatomy, only snails from Three Lakes have been identified as *O. h. kanabensis* (Wu personal communication). Three Lakes is approximately 2 km from Kanab Canyon, and outflow from Three Lakes and nearby springs formed a tributary to Kanab Creek until the tributary was piped for the town of Kanab in the early 1900s (Robinson 1970).

When Clarke surveyed Kanab Canyon for *O. h. kanabensis*, he was apparently unaware that Pilsbry and Ferriss (1911) reported not only *Succinea hawkinsi* (reclassified in 1948 by Pilsbry as *O. h. kanabensis*), but also *Succinea retusa* (later *O. retusa*) from "The Greens." Thus, it is not clear which taxon Clarke found in small numbers in 1991; the specimens were not subject to anatomical evaluation. Spamer and Bogan (2002) suggested that this 2nd taxon, *O. retusa*, was recorded in error, but the confirmation of *O. retusa* in the present day suggests otherwise.

Unfortunately, the anatomical identification of *O. retusa* was made after the genetic studies reported in Stevens et al. (2001) were completed. No individuals of Kanab Canyon populations identified as *O. retusa* were included in that study, although individuals identified anatomically as *O. retusa* from other sites were included, as were individuals from the lower bench of Kanab Canyon (identified as *O. h. haydeni*) and from Three Lakes (identified as *O. h. kanabensis*). These specimens, apparently from 3 species, all appeared to cluster as a single genetic group that is distinct from the Grand Canyon population identified as *O. h. kanabensis* (Stevens et al. 2001). The confusion of geographical, historical, anatomical, and genetic information leaves us with little

certainty on any front. The justification for an endangered *Oxyloma* subspecies in south central Utah, or even for a distinct *Oxyloma* taxon there, has been called into question. Additional genetic research may, in time, clarify first the taxonomic and then the legal standing of this perplexing group.

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GENETIC DIFFERENTIATION OF RARE AND COMMON VARIETIES OF *ERIOGONUM SHOCKLEYI* (POLYGONACEAE) IN IDAHO USING ISSR VARIABILITY

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ABSTRACT.—Idaho populations of *Eriogonum shockleyi* are divided taxonomically into 2 varieties: *E. shockleyi* var. *packardae*, which is endemic to Idaho, and the typical variety, which is widespread in the western United States. Recent morphological investigations of *E. shockleyi* in Idaho have identified potentially reliable morphological characters for field identification of the subspecific taxa. This paper investigates the genetic basis for the separation of the 2 varieties of *E. shockleyi* using inter simple-sequence repeats (ISSR) markers. Although we found some morphological differences between the populations that correlated with the 2 varieties, we identified no molecular markers in this study to distinguish between them. Morphological measurements obtained in the field indicate that although a population may have an overall average morphology that defines the variety, some individuals in nearly all populations have putative diagnostic characters that define the other variety. The morphological characters used to distinguish the 2 varieties are most likely the result of environmental variability and could result from differences in precipitation and soil water retention. Alternatively, high levels of outcrossing through pollen flow could be obscuring selection for morphological characters at particular sites.

Key words: *Eriogonum shockleyi*, ISSR, variety, rare plants, Polygonaceae, populations.

Increasing pressures on natural resources have raised questions and concern regarding the status and management of rare populations and species of plants. Of critical concern regarding the status of rare plants is whether they are genetically distinct from more common and widespread congeners and conspecifics (Falk and Holsinger 1991). Genetic variation and the distribution of this variation in rare plant populations provide information for understanding the origin and evolution of rare plants as well as management considerations.

One plant species that merits further study is *Eriogonum shockleyi* S. Wats (Polygonaceae). *Eriogonum shockleyi* is a widespread species in the western United States, known from California to Colorado, south to Arizona and New Mexico, and north to Idaho. This species commonly occurs on barren rocky, clay, or sandy substrates in shrubland or pinyon-juniper communities (Reveal 1985). The species has been separated into 2 varieties, *E. shockleyi* var. *shockleyi* S. Wats and *E. shockleyi* var. *packardae* Reveal. *Eriogonum shockleyi* var. *packardae* is a rare Idaho endemic found from the Halverson Lakes region of Ada County along the

Snake River to the Bruneau River drainage of Owyhee County (Fig. 1, Table 1).

The 2 varieties have a history of being difficult to distinguish (DeBolt and Rosentreter 1988). Both are mound-forming perennials with densely compact rosettes. Recent morphometric analysis of these 2 varieties has identified 4 morphological characters that readily delimit them (Moseley and Reveal 1996). These 4 characters are peduncle length, leaf blade width, leaf blade length, and petiole length. In general, *E. shockleyi* var. *shockleyi* has longer peduncles and larger leaves than does *E. shockleyi* var. *packardae* (Moseley and Reveal 1996). These 4 characters readily separated all Idaho populations of *E. shockleyi* into the 2 varieties, with the exception of a single population from Upper Sugar Valley, Owyhee County (Fig. 1). This last population was identified as an intermediate between the 2 varieties during morphometric analyses of herbarium material, although morphologically the individuals were readily identified as one or the other in the field (Moseley and Reveal 1996).

The morphological distinctiveness and geographic disjunction of the 2 varieties of *E. shockleyi* raise the possibility that these represent a

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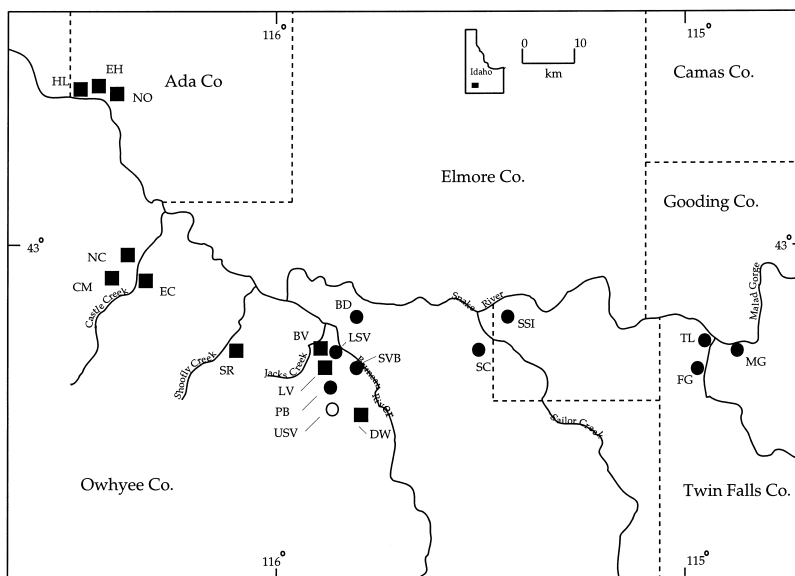


Fig. 1. Map of southern Idaho showing localities for all *Eriogonum shockleyi* var. *packardae* (shown with squares) and *E. shockleyi* var. *shockleyi* (shown with circles) populations sampled as part of this study. The population represented by a mixture of the 2 varieties is shown with an open circle (USV). Abbreviations for populations follow Table 1.

progenitor-derivative pair (Gottlieb 1973a, 1973b, 1974). In progenitor-derivative pairs, the rare taxon is generally thought to have evolved from an isolated population of its more common and widespread relative. Isolation may have occurred as the result of climate changes (Smith and Pham 1996), substrate differences (Gottlieb 1973b), polyploidy (Ownbey 1950, Soltis and Soltis 1991), chromosome rearrangements (Gottlieb 1974), or long-distance dispersal into new habitats (Kliman and Hey 1993). If this progenitor-derivative hypothesis is correct, the genetic variation found in populations of *E. shockleyi* var. *packardae* is expected to be a subset of that found in *E. shockleyi* var. *shockleyi* (Gottlieb 1973a, 1974).

The best means of assessing genetic variation of rare plants is to examine directly the level and structure of genetic diversity of several populations of both varieties. Molecular methods have provided many insights into the genetic diversity of rare plants (Waller et al. 1987, Lesica et al. 1988, Hickey et al. 1991, van Buren et al. 1994, Smith and Pham 1996, Hickerson and Wolf 1998, Archibald et al. 2001). In this paper we make use of inter simple-sequence repeats (ISSRs). These markers provide considerable amounts of variability within populations and have gained a reputa-

tion for their repeatability. The markers utilize regions of DNA that are segments of short repetitive sequences. For example, a segment of DNA may have a sequence of GGA repeated any number of times. This variability in the size of these segments (number of times the sequence is repeated) is often used as a population level marker (microsatellite; Sunnucks 2000). ISSR variability instead makes use of the spaces between these repeats. The primers for ISSR markers incorporate simple-sequence repeats and are anchored on one end with a random tag from outside the repeating region (Zietkiewicz et al. 1994). Amplified products are the areas between the primer binding sites, and the data used in the analysis are whether 2 repeat sites are in close enough proximity to produce a band of DNA during the amplification procedure. Sites that differ in the length of DNA between them will be scored as different loci.

ISSRs have not had the breadth of use that RAPDs have, but studies utilizing these data report a high degree of resolution among populations and individuals (Charters et al. 1996, de la Hoz et al. 1996, Tsumura et al. 1996, Yang et al. 1996, Nagaoka and Ogihara 1997, Wolfe et al. 1998). In their study of diploid hybrid speciation in *Penstemon*, Wolfe et al.

TABLE 1. Sampled populations of *Eriogonum shockleyi*. Taxonomic classification follows that of Moseley and Reveal (1996) with the exception of OR that was classified by the first author based on population averages of morphological measurements. Full descriptions and coordinates of localities are available in Moseley and Reveal (1996) with the exception of OR, which was found at 41°37.111'N, 114°49.631'W, 1713 m elevation.

Variety	Abbreviation	Idaho county	Site
<i>E. shockleyi</i> var. <i>packardae</i>	EH	Ada	East of Halverson Lakes
	HL	Ada	Halverson Lakes
	NP	Ada	North of Priest Ranch
	BV	Owyhee	Bruneau Valley Rim
	CM	Owyhee	Castle Creek Mines
	DW	Owyhee	Deer Water
	EC	Owyhee	East of Castle Creek
	LV	Owyhee	Little Valley
	NC	Owyhee	North of Castle Creek
	SR	Owyhee	Shoofly Road
	USV	Owyhee	Upper Sugar Valley
	OR	Elko, NV	O'Neill Basin Road
<i>E. shockleyi</i> var. <i>shockleyi</i>	SSI	Elmore	South of Schoff's Island
	MG	Gooding	Malad Gorge
	BD	Owyhee	Bruneau Dunes
	LSV	Owyhee	Lower Sugar Valley
	PB	Owyhee	Prominent Buttes
	SC	Owyhee	Lower Sailor Creek
	SVB	Owyhee	Sugar Valley Badlands
	FG	Twin Falls	Fossil Gulch
	TL	Twin Falls	Lower Salmon Falls Dam Transmission Line

(1998) scored 270 bands across 5 taxa, of which 4 were fixed across all populations of all taxa. Other bands provided sufficient variation such that individual DNA accessions could be genotyped with 1 to 3 ISSR primers, and markers for all species were found with these data. Likewise, 41 ISSR markers from 3 primers successfully distinguished among 34 lines of Chinese sorghum (Yang et al. 1996), and either of 2 primers successfully distinguished 16 of 20 cultivars of *Brassica napus* ssp. *oleifera* (Charters et al. 1996). Thus, the variability detected in ISSR markers has utility to recognize different lineages, cultivars, species, and groups of closely related species (Wolfe et al. 1998).

This paper specifically seeks to determine (1) the genetic variability in the rare variety *E. shockleyi* var. *packardae* using ISSR markers, (2) degree of genetic distinctiveness between *E. shockleyi* var. *packardae* and its more common conspecific, *E. shockleyi* var. *shockleyi*, and (3) degree of morphological distinctiveness between the 2 aforementioned varieties.

METHODS

Material Acquisition

All known populations that were located in a 1995 survey of *Eriogonum shockleyi* var.

packardae (Moseley and Reveal 1996) from Idaho were sampled (Fig. 1, Table 1), with the exception of 1 population near Perjue Canyon, Owyhee County. This population is located near the Shoofly Road; therefore, its omission from the analysis is not likely to seriously bias the conclusions. An additional population from Nevada that fit the description of *E. shockleyi* var. *packardae* (R. Moseley personal communication) also was sampled, although the variety was not known previously to occur outside of Idaho. Twelve populations were assigned to *E. shockleyi* var. *packardae* (Table 1).

We also sampled 9 of 11 known populations of *E. shockleyi* var. *shockleyi* in Idaho (Moseley and Reveal 1996, Fig. 1, Table 1). Two populations near Horse Hill, Owyhee County, were omitted (Moseley and Reveal 1996, Narad et al. 1997). Their omission is unlikely to affect the results, however, as other populations near the Horse Hill population were sampled. From each of the 21 populations, we randomly selected 28 individuals.

DNA Analysis

DNA was extracted from all individuals using Qiagen DNeasy plant miniprep kits following the manufacturer's instructions. All amplifications used 1 µL of template DNA in

25 μ L reactions. Eight primers were used in all reactions: (1) (CT)₈TG, (2) (CT)₈RG, (3) (CA)₆RY, (4) (GT)₆RG, (5) (GT)₆AY, (6) CAA(GA)₆, (7) (GT)₆ YR, and (8) (CA)₆RG. Reaction conditions were 1X magnesium-free buffer provided by manufacturer, 3 mM MgCl₂, 0.16 mM each of dCTP, dATP, dGTP, and dTTP, 0.1 mg mL⁻¹ BSA, 0.4 pmol primer, and 0.5 μ L Taq polymerase (Promega). Amplification profiles varied in annealing temperature, depending on the primer, and were optimized for each of the primers to produce clear and repeatable amplifications. They otherwise consisted of 1.5 minutes at 94°C, followed by 35 cycles of 40 seconds at 94°C, 45 seconds at 44°C, 1.5 minutes at 72°C followed by 45 seconds at 94°C, 45 seconds at 44°C, and 5 minutes at 72°C. Ultimately, we used 3 different annealing temperatures for the different primers: 44°C was used for primers 1, 3, 5, and 7; 42°C for primers 2, 6, and 8; and 48°C for primer 4.

Total amplified reaction mixes were run on 1.4% agarose gels for 5 hours at 35 volts. After electrophoresis, gels were stained with ethidium bromide and photographed. Standard markers were included in the first and last lane of each gel. Initial surveys of each ISSR primer, using a subset of the individuals in the analysis, indicated that bands were fully repeatable in duplicate gels.

Data Scoring

Gels were scored by first determining the size of the amplified fragment and then scoring each individual for presence or absence of each band. Primer 2 never successfully amplified population MG (Table 1) despite several attempts at altering reaction conditions and annealing temperatures. Likewise, primer 6 did not amplify populations SSI and LSV (Table 1). When we obtained no amplification products from individuals, these individuals were considered to be missing data and were not scored as homozygous recessives for the absence of the amplified bands.

Molecular Data Analysis

Each amplified fragment of a particular size was scored as a distinct locus. Because ISSR markers act as dominants, heterozygous individuals all will be counted as dominants with the marker present. We converted presence of each locus into a population percentage based

on the number of individuals with the marker in each population for all populations. These data were then analyzed in BIOSYS-1 (Swofford and Selander 1981) to determine gene diversity statistics (Nei 1973) and genetic relatedness. Since primers 2 and 6 had missing data for entire populations, these data were removed from the analysis. Percent loci polymorphic was calculated with and without the data from primers 2 and 6.

Gene diversity statistics (Nei 1973) were calculated for each ISSR marker scored using the WRIGHT78 program of BIOSYS-1 (Swofford and Selander 1981). Because of limitations in using amplified gene regions to assess genetic diversity (heterozygotes remain undetected due to inheritance of markers as dominants), we expected assessments of diversity using these markers to be lower than when compared to studies with codominant loci such as isozymes (Novak et al. 1996, Smith and Pham 1996). In addition, markers with high frequencies (1-3/N, 0.995 in this study) were omitted from the analysis, as recommended by Lynch and Milligan (1994), based on theoretical examination of the use of dominant markers in estimating genetic diversity.

Genetic relatedness for all populations was analyzed using the CLUSTER program of BIOSYS-1 (Swofford and Selander 1981).

Morphological Characters

Four morphological characters have been identified as readily separating *Eriogonum shockleyi* var. *shockleyi* from *E. shockleyi* var. *packardae* in Idaho (Moseley and Reveal 1996): peduncle length, leaf width, leaf length, and petiole length. These 4 morphological characters were measured for each individual on fresh plant material. We averaged these morphological data for each of the characters for each population and calculated a standard deviation for each mean. Significant differences between means were determined using a *t* test (Snedecor and Cochran 1980).

Analysis of variance (ANOVA) was used to determine if each of the morphological variables differed between varietal designation. Regression analysis was used to determine if morphological variables depended on longitude of the populations or precipitation received by the population. Since the goal was to determine a correspondence to longitude and precipitation for the entire species, all

TABLE 2. Summary of morphological data gathered for all populations of *Eriogonum shockleyi* sampled from Idaho. Populations are listed in order of increasing peduncle length. Classification to variety follows Moseley and Reveal (1996). Superscript letters denote groups of means that are not significantly different from each other at the $P = 0.05$ level using a t test.

Variety	Population	Peduncle length (cm) mean \pm s	Leaf length (mm) mean \pm s	Leaf blade width (mm) mean \pm s	Petiole length (mm) mean \pm s
<i>packardae</i>	NC	4.5 ^a \pm 2.0	6.2 ^b \pm 1.1	1.9 ^{bcd} \pm 0.5	1.7 ^{abc} \pm 0.6
<i>packardae</i>	SR	4.9 ^a \pm 3.1	6.5 ^{bcd} \pm 1.8	1.7 ^{ab} \pm 0.5	1.9 ^{bcd} \pm 1.0
<i>packardae</i>	NP	5.0 ^a \pm 2.3	6.8 ^{bcd} \pm 1.1	1.8 ^{abc} \pm 0.4	2.4 ^{efg} \pm 0.6
<i>packardae</i>	BV	5.5 ^{ab} \pm 2.4	6.5 ^{bcd} \pm 1.4	1.9 ^{bcd} \pm 0.5	1.6 ^{ab} \pm 0.6
<i>shockleyi</i>	SSI	5.5 ^{ab} \pm 3.3	6.4 ^{bc} \pm 1.2	2.2 ^{de} \pm 0.6	1.7 ^{abc} \pm 0.7
<i>packardae</i>	EH	5.6 ^{ab} \pm 2.6	5.1 ^a \pm 1.1	1.5 ^a \pm 0.4	1.3 ^a \pm 0.5
<i>packardae</i>	DW	5.7 ^{ab} \pm 2.4	7.0 ^{bcd} \pm 1.5	2.1 ^{cde} \pm 0.6	2.0 ^{bcd} \pm 0.7
<i>packardae</i>	CM	5.7 ^{ab} \pm 3.3	6.8 ^{bcd} \pm 1.3	2.1 ^{cde} \pm 0.6	1.8 ^{bcd} \pm 0.6
<i>shockleyi</i>	LSV	5.8 ^{ab} \pm 2.9	7.4 ^{ef} \pm 1.7	2.1 ^{cde} \pm 0.5	2.3 ^{defg} \pm 0.8
<i>packardae</i>	USV	5.9 ^{ab} \pm 3.2	6.8 ^{bcd} \pm 1.6	1.9 ^{bcd} \pm 0.6	1.9 ^{bcd} \pm 1.1
<i>packardae</i>	OR	6.0 ^{ab} \pm 5.5	6.2 ^b \pm 1.3	1.8 ^{abc} \pm 0.4	1.8 ^{bcd} \pm 0.7
<i>shockleyi</i>	SVB	6.3 ^{abc} \pm 2.9	7.3 ^{def} \pm 1.3	2.3 ^e \pm 0.7	2.1 ^{cde} \pm 0.6
<i>packardae</i>	HL	7.1 ^{bcd} \pm 2.4	7.2 ^{cde} \pm 1.6	1.9 ^{bcd} \pm 0.7	2.6 ^g \pm 1.2
<i>packardae</i>	EC	7.5 ^{bcd} \pm 2.8	7.1 ^{cde} \pm 1.1	2.2 ^{de} \pm 0.4	2.0 ^{bcd} \pm 0.6
<i>shockleyi</i>	PB	7.5 ^{bcd} \pm 3.3	7.8 ^{fg} \pm 1.2	2.5 ^{fg} \pm 0.6	2.5 ^{fg} \pm 0.6
<i>packardae</i>	LV	8.1 ^{cd} \pm 3.3	7.8 ^{fg} \pm 1.5	2.4 ^e \pm 0.6	2.7 ^g \pm 0.9
<i>shockleyi</i>	BD	8.4 ^d \pm 3.6	7.4 ^{ef} \pm 1.4	2.4 ^e \pm 0.5	2.1 ^{cde} \pm 0.7
<i>shockleyi</i>	SC	10.6 ^e \pm 3.6	7.1 ^{cde} \pm 1.1	2.3 ^e \pm 0.7	2.0 ^{bcd} \pm 0.6
<i>shockleyi</i>	FG	12.7 ^f \pm 4.3	8.4 ^{gh} \pm 1.7	2.5 ^{fg} \pm 0.6	2.3 ^{defg} \pm 1.7
<i>shockleyi</i>	MG	15.1 ^g \pm 5.9	9.2 ^{hi} \pm 2.0	3.0 ^g \pm 0.6	2.5 ^{fg} \pm 1.0
<i>shockleyi</i>	TL	15.9 ^g \pm 5.6	9.5 ⁱ \pm 2.2	2.9 ^{fg} \pm 0.8	2.5 ^{fg} \pm 1.0

populations were considered together in these analyses. Additionally, a minimum of longitude data for each variety precluded a separate analysis for each variety separately. Precipitation data were determined from a precipitation map for the region (Fig. 3). All analyses were done using SAS (Version 8) and were conducted using the population means (Table 2) of the morphological variables.

RESULTS

Six to 12 different bands were amplified for each of the primers, with an average of 8 bands per primer (including data for primers 2 and 6) and a total of 64 loci from all 8 primers. Due to the lack of amplification for entire populations with primers 2 and 6, and limitations to the number of loci that can be analyzed using BIOSYS-1, we excluded the data from primers 2 and 6 from the analysis for a total of 51 bands examined. None of the amplified products were monomorphic across all populations examined. The least polymorphic locus had a frequency of 98.3%. Eight bands were found within a single population and are rare within each population, occurring in only 4–13 individuals from each population.

The proportion of ISSR loci polymorphic per population ranged from 25.5% (population SSI, Table 1) to 66.7% (population PB, Table 1) with the bands from primers 2 and 6 excluded, both from *Eriogonum shockleyi* var. *shockleyi*. When the data from primers 2 and 6 were added separately or combined, proportions differed only slightly and ranking was altered in terms of the highest proportion of loci polymorphic in only a few cases. With all data included, the proportion of loci polymorphic ranged from 20.3% (SSI) to 62.5% (PB and CM, the latter population *E. shockleyi* var. *packardae*).

None of the markers sampled in this analysis occurred at a frequency higher than the 0.995 recommended cutoff value of Lynch and Milligan (1994). Total genetic diversity (H_T) ranged from 0.003 to 0.499 for all 21 populations, with a mean of 0.263. Within (H_S)- and among (D_{ST})-population diversity components ranged from 0.003 to 0.391 and 0.000 to 0.381, respectively. Means for within- and among-population diversity were 0.163 and 0.100, respectively. Gene differentiation relative to total population (G_{ST}) ranged from 0.016 to 0.954, with a mean of 0.299. Means for the varieties did not differ greatly from each other

or from the overall mean for the species: $H_T = 0.268$ and 0.261 ; $H_S = 0.162$ and 0.173 ; $D_{ST} = 0.096$ and 0.089 ; $G_{ST} = 0.270$ and 0.279 for *E. shockleyi* var. *shockleyi* and *E. shockleyi* var. *packardae*, respectively.

There was little correspondence between assignment of taxonomic rank based on morphology and groupings based on ISSR data (Fig. 2). Populations from both varieties were scattered throughout the tree. There was also very little correspondence to the groupings based on UPGMA and any morphological features measured in this analysis. Genetic identity values ranged from 82.1% (FG to the remaining populations, Fig. 2) to 96.5% (MG to TL) and are within the range expected between varieties of a single species (Crawford 1983).

Populations can be segregated readily into one or the other variety on the basis of averages for morphological data (Table 2), but they do not correspond to previous classifications of these populations (Moseley and Reveal 1996). Peduncle length has been used as a key character to distinguish the 2 varieties (Reveal 1985, Moseley and Reveal 1996). Plants are assigned to *Eriogonum shockleyi* var. *shockleyi* if their peduncle length is >1 cm and to *E. shockleyi* var. *packardae* if the peduncle length is <1 cm. Populations traditionally assigned to *E.*

shockleyi var. *packardae* based on morphology (Moseley and Reveal 1996) do have a population average peduncle length <1 cm, but so do 5 other populations traditionally assigned to *E. shockleyi* var. *shockleyi* (SVB, LSV, PB, BD, and SSI; Table 2). Only 4 of the easternmost populations remain in *E. shockleyi* var. *shockleyi* based on average peduncle length alone (SC, MG, TL, and FG; Table 2, Fig. 1).

The morphological data are complex, with much of the information obscured among the averages. When the raw data are examined, it is clear that within each of these populations are individuals with characteristics of both varieties. In all but a single population of *E. shockleyi* var. *packardae* that was sampled (NC), at least 1 individual had a peduncle length that was equal to or exceeded the 1-cm boundary between the 2 varieties. Likewise, all populations of *E. shockleyi* var. *shockleyi* had a minimum of 3 individuals with a peduncle length <1 cm. Only 1 population (NC) entirely comprised individuals with a peduncle length <1 cm.

Although means for each of the morphological characters fell into distinct classes that were statistically different from each other, there were few classes that did not have one or more populations that bridged the gap (Table 2).

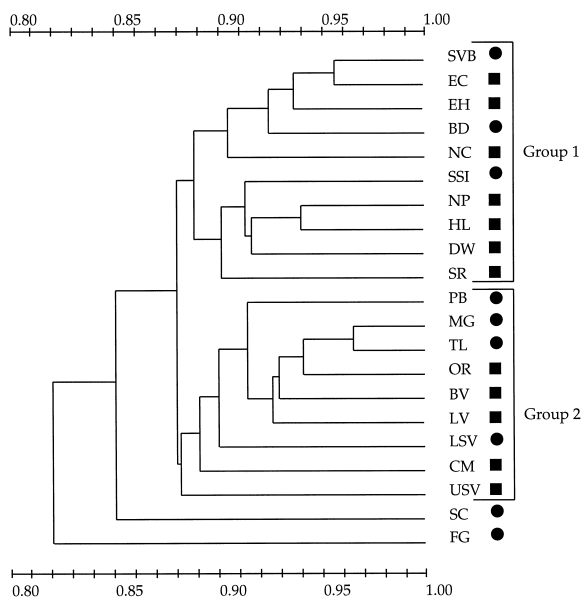


Fig. 2. UPGMA tree based on data used to calculate gene diversity statistics. Abbreviations for populations follow Table 1. *Eriogonum shockleyi* var. *packardae* are represented with squares and *E. shockleyi* var. *shockleyi* with circles.

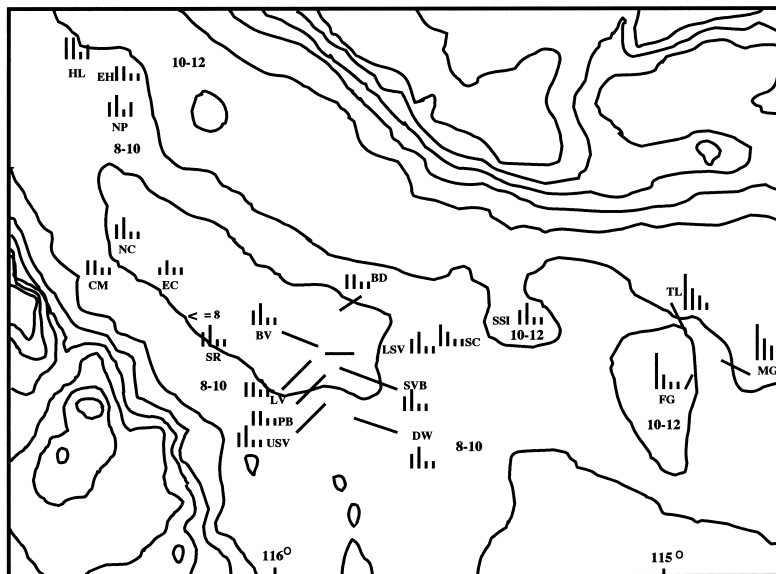


Fig. 3. Map of populations of *Eriogonum shockleyi* sampled in this study with the population average for peduncle length, leaf length, leaf width, and petiole length (Table 2) represented by bars of proportional length for each character. Isobars represent precipitation levels (inches per year), which are labeled for appropriate regions. Map is approximately the same area presented in Figure 1, although county boundaries and rivers have been removed for clarity. Population abbreviations follow Table 1.

Results of the ANOVA and regression analyses indicated that peduncle length, leaf length, and leaf width each differed significantly between the varietal designations of Moseley and Reveal (1996); $P < 0.01$ in each case. All 3 measures were larger in *E. shockleyi* var. *shockleyi* (Table 2). Petiole length did not differ significantly between varieties ($P = 0.13$). Likewise, peduncle length, leaf length, and leaf width each significantly varied with longitude ($P < 0.01$, $r^2 = 0.47$; $P < 0.01$, $r^2 = 0.33$; and $P < 0.01$, $r^2 = 0.39$, respectively), with larger measures tending to be in the more easterly populations. Petiole length did not vary significantly with longitude ($P = 0.36$). Varietal designations differed significantly in their longitude ($P < 0.01$), with *E. shockleyi* var. *packardae* being the more westerly. However, there was no significant relationship between variety and precipitation ($P = 0.20$). A significant positive relationship exists between peduncle length and precipitation ($P = 0.027$, $r^2 = 0.24$), but not for any of the leaf measurements ($P = 0.23$, 0.21 , and 0.77 , respectively).

Eriogonum shockleyi grows in areas receiving the least precipitation in Idaho. Populations

sampled in this study are found in areas receiving <8 inches per year, 8–10 inches per year, or 10–12 inches per year. Morphological characters, expressed as averages for each population, are positioned onto a map for south-western Idaho showing annual precipitation zones (Fig. 3).

DISCUSSION

The molecular markers sampled in this analysis do not support the taxonomic distinction of *Eriogonum shockleyi* populations into 2 varieties in Idaho (Fig. 2). The UPGMA analysis of markers from 6 ISSR primers does not group populations in accordance with previous taxonomic classifications of Moseley and Reveal (1996).

Similarly, the morphological data do not show any statistically significant gaps that separate the populations based on the characters sampled here (Table 2). However, peduncle length, leaf width, and leaf length each differed significantly between varieties based on a regression analysis, indicating that a gradient in morphology exists. While this is in agreement with the data from Moseley and Reveal (1996),

petiole length did not show a significant difference. Although this seems to provide evidence for a morphological distinctiveness between the 2 varieties, each of the characters that showed a significant difference between varietal designation also had a significant relationship with longitude. Therefore, it is not possible to state whether the morphological differences seen among these populations are related to taxonomic varieties or to longitudinal position.

A minimum of 2 groups were delimited in this analysis based on ISSR variability (Fig. 2); however, these groups do not correspond well to any morphological feature that may separate them. There is a loose correlation with peduncle length, although this mostly corresponds with the statistically significant difference between (1) SC and all other populations; (2) FG and all other populations; and (3) MG and TL together, but distinct from all other populations (Table 2, Fig. 2). Otherwise, there is only a loose correlation, as populations in group 1 (Fig. 2) have a tendency toward shorter peduncles and those in group 2 (Fig. 2) have longer peduncles (Table 2, Fig. 2). However, there is complete statistical overlap of all 4 morphological characters between all populations in these 2 groups (Table 2).

There is also little correspondence between groupings based on ISSR markers and geographic location of populations. As with the morphological data, there is a slight longitudinal trend with the westernmost populations in group 1 and the easternmost populations in group 2 (Fig. 2). However, the ISSR data do not separate the populations based on their taxonomic designations as there are populations from both varieties in both groups; most notably, FG, which is closest in proximity to MG and TL (Fig. 1), is distinct from all other populations in the analysis (Fig. 2). Likewise, SC, which is closest geographically to SSI (Fig. 1), is clearly genetically distinct from its nearest population (Fig. 2).

Although the data presented here do not demonstrate a distinct difference between the 2 varieties, based either on molecular or morphological evidence, it should be noted that *Eriogonum shockleyi* has a much broader distribution with considerable morphological variation that was not sampled as part of this study. It is possible that the lack of distinctiveness

among the Idaho populations is due to the fact that all may be members of *E. shockleyi* var. *packardae* and all may be genetically and morphologically distinct from the remainder of the species throughout its range.

Correlation with Environmental Variation

As others have noted (e.g., Moseley and Reveal 1996), there is a general trend in *Eriogonum shockleyi* toward smaller plants in the West and larger plants in the East. This same trend was also observed in this study (Fig. 3, Table 2). Thus, there is a geographic correlation with morphological variation. Statistically significant relationships between peduncle length, leaf width, leaf length, and longitude all were observed in this study, although no significant relationship between petiole length and longitude was observed. The correlation between geography and morphology and the lack of correlation between genetic markers and either of these 2 parameters imply that the differences between populations may be the result of environmental differences. Mapping the sampled populations and population averages for the 4 morphological measurements made in this study onto a map showing precipitation data gives us a rough correspondence between precipitation, geography, and morphology (Fig. 3). Populations from western Idaho comprise the smallest plants and receive the smallest amounts of precipitation. Both plant size and precipitation increase eastward across the state. Westernmost populations are found in either the <8 inch or the 10–12 inch rainfall zone. In contrast, the easternmost populations are found mostly in the 12–14 inch zone or, if in the 10–12 inch zone (SC), are close to the 12–14 inch zone boundary (Fig. 3). Thus, the easternmost populations are receiving more precipitation than those in the West.

A significant relationship between peduncle length and precipitation was detected in this analysis, although no other significant relationship between morphological characters and precipitation was observed. The relationship between morphology and precipitation is not perfect, and in a few cases smaller plants occupy sites with greater amounts of rainfall than a corresponding population with larger plants (SSI and SC). Such discrepancies may be the result of microclimatic or edaphic differences

between sites. Alternatively, seasonal differences in precipitation may result in morphological variability at different sites. Although the data provide a rough correspondence between precipitation and morphological variation in this species, further work is clearly needed to test whether this is the case. Seeds from different populations should be grown in a common garden environment and the morphological characters measured in these individuals to further verify the differences seen here.

Although the climatic data imply that morphological differences seen in *Eriogonum shockleyi* are environmental, it is possible that the 2 varieties are either in the process of becoming distinct or were formerly distinct, with gene flow now carrying both molecular markers and morphological characters across populations. This possibility also is supported by a significant relationship between longitude and varietal designation, but no significant relationship between longitude and precipitation. If the morphological variability seen among these populations could be attributed entirely to precipitation, then there should be a corresponding relationship between precipitation and longitude as there is with morphology and longitude. Although precipitation sampling areas are few and approximate, the lack of relationship between longitude and precipitation implies that the relationship between morphology and longitude could be due to isolation by distance, or it could be related to other environmental conditions that do have a significant relationship with longitude that were not sampled here.

Although peduncle length served to classify correctly only a single population (NC), there are significant trends in the morphological data. Lack of any distinctness may be the result of incomplete selection against the respective traits in the different populations. Alternatively, it could be the result of gene flow through pollen transfer. The distinctive mixture of individuals of different size classes in the different populations does imply that there may be some selection for certain sizes at different sites, but extensive gene flow from other populations continuously carries alleles with a lesser fitness into the population. To test this, further studies examining the relative fitness of plants of different size categories would be needed on plants in situ at different sites.

Progenitor-derivative Hypothesis

ISSR data do not provide evidence for a progenitor-derivative relationship (Gottlieb 1973a, 1973b, 1974) between the 2 varieties of *Eriogonum shockleyi*. If such a relationship existed, we would expect levels of genetic variation in *E. shockleyi* var. *packardae* to comprise a subset of the variation found in *E. shockleyi* var. *shockleyi*. Instead, variation was found to be approximately equal and mixed across all populations sampled in this analysis. There was only a single locus that was present in *E. shockleyi* var. *shockleyi* that was absent in *E. shockleyi* var. *packardae*. In contrast, 6 loci were unique to *E. shockleyi* var. *packardae*; however, these were restricted to single populations and were present in only 1–6 individuals within those populations. Four of the 6 loci were found within 1 population (SR). The rare alleles found in this study are most likely the result of limited sample size. Greater sampling would likely find these loci in additional populations.

Genetic Diversity Among Populations

Levels of genetic variation within rare or geographically restricted plant species are typically low (Ledig and Conkle 1983, Waller et al. 1987, Lesica et al. 1988, Hickey et al. 1991), although several recent studies have indicated high levels of genetic variability in some rare species (Gottlieb et al. 1985, Karron 1987, Ranker 1994, Lewis and Crawford 1995, Smith and Pham 1996, Hickerson and Wolf 1998, Archibald et al. 2001). Within this study, the level of variation as estimated by proportion of ISSR loci polymorphic is approximately equal for populations of both *Eriogonum shockleyi* vars. *shockleyi* and *packardae*. Populations of *E. shockleyi* var. *shockleyi* have both the highest (PB) and lowest (SSI) levels. Because of this, the 2 varieties cannot be separated based on their levels of ISSR loci polymorphic per population.

Conservation Implications

Results of this study indicate that the varieties of *Eriogonum shockleyi* in Idaho are not distinct from each other based on genetic or morphological data. Morphological variation that exists may be the result of environmental

differences or, potentially, could be selection in process. Prior to any changes in conservation status of these populations, important information needs to be gathered. First, it is imperative that these populations be compared to others of *E. shockleyi* from throughout the range of the species. It may be that although all Idaho populations are similar, they are distinct from the remainder of the species, and these limited populations in Idaho merit attention. Likewise, even if the Idaho populations do not merit any taxonomic status, their geographic location at the northern limits of the species' range implies that unique loci or alleles may be present and should be accounted for in conservation programs. Second, common garden experiments should be performed on the Idaho populations to determine if, and which, environmental parameters may be affecting morphological variability. If populations remain distinct under common environmental conditions, then it is clear that there is selection occurring among these populations and that they merit conservation status.

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ARBUSCULAR MYCORRHIZAE OF MOJAVE DESERT PLANTS

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ABSTRACT.—Roots of 15 Mojave Desert plant species were assessed for arbuscular mycorrhizal (AM) colonization in spring and autumn 1999. Another 19 species were assessed in autumn only. Perennial species were AM colonized, whereas annual species contained very low levels of AM hyphae or were nonmycorrhizal. The nonnative tree *Tamarix ramosissima* was also nonmycorrhizal. Levels of hyphae changed over the season in 2 species, arbuscle levels increased in 1 species, and vesicles decreased in 7 species. Mycorrhizal inoculum potential (MIP) was assessed in the soils associated with spring-collected plants. All soils were found to contain MIP. MIP values were not correlated with AM root colonization.

Key words: arbuscular mycorrhizae, Mojave Desert, seasonality, burrows, Nevada Test Site, River Mountains, mycorrhizal inoculum potential.

Arbuscular mycorrhizae (AM) are important components of virtually all terrestrial ecosystems. Over 90% of all higher plants are estimated to be mycorrhizal, and >80% of these form AM relationships (Brundrett 1991). Plant growth is often enhanced by this association, mainly due to an increased ability to take up nutrients, principally phosphorus (Mullen and Schmidt 1993, Smith and Read 1997) and nitrogen (Tobar et al. 1994). This mutualism also enhances plant host drought resistance (Davies et al. 1992), competitive ability (West 1997a, Titus and del Moral 1998), and resistance to fungal pathogens (West 1997b) and insect herbivores (Gange and Bower 1997).

Many studies have found that seasonal factors, which are directly related to the stage of development or physiological state of the host plant, play a major role in AM colonization levels (e.g., Sanders and Fitter 1992a, Mullen and Schmidt 1993, Sanders 1993, Titus and Lepš 2000). For example, AM root colonization is often lowest in early summer because rapid root growth outstrips the spread of AM colonization (Douds and Chaney 1982, Warner and Mosse 1982, Dickman et al. 1984, Ebberts et al. 1987). In addition, temporal factors play a major role in host benefit from AM colonization. For example, AM may benefit plants only during the brief periods when phosphorus

demand is high during fruit production (Fitter 1989, Sanders and Fitter 1992b).

Arbuscular mycorrhizal mutualism is considered to be critical to the survival of most plants in arid environments. Perennial plants in undisturbed arid environments have generally been found to be mycorrhizal (e.g., Trappe 1981, Bloss 1985, Siguenza et al. 1996, Carrillo-Garcia et al. 1999, Stutz et al. 1999). However, the mycorrhizal status of most desert species and the shift in level of colonization over the seasons remain little known. It has been found that mycorrhizal colonization in a semiarid system is higher toward the end of summer than in midwinter (Requena et al. 1996).

This study was conducted to characterize AM colonization of common Mojave Desert plants. First, plants were collected over 2 seasons at the Mojave Global Change Facility (MGCF) located on the Nevada Test Site (NTS). The MGCF is a large-scale experiment being developed to test desert ecosystem responses to 3 global change scenarios: increased summer precipitation, increased nitrogen deposition, and biological soil crust removal. We collected plant roots and soil samples in spring and autumn to examine seasonal changes in AM colonization levels. Second, we examined AM colonization levels of common plants of the River Mountains located southeast of Las Vegas.

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METHODS

The MGCF site is located in the northern Mojave Desert in Nye County, Nevada, USA (36°49'N, 115°55'W), 90 km northwest of Las Vegas at an elevation of 960–975 m. The NTS, a U.S. Department of Energy facility, experiences minimal disturbance. Unlike much of the Mojave Desert, the NTS has not been grazed by cattle or utilized by off-road vehicles for at least 50 years. The area has a largely intact biological soil crust that covers ~20% of the soil surface (J. Titus unpublished data). The River Mountains site is located 15 km southeast of Las Vegas (36°03'N, 114°55'W) at an elevation of 700–800 m. Due to the rugged rocky substrate, much of the area is largely undisturbed even though biological soil crusts are not common.

Vegetation at both sites is a *Larrea tridentata*–*Ambrosia dumosa* plant community (Ostler et al. 1999, taxonomy based on Hickman 1993). Common shrubs include the evergreen *Larrea tridentata*; the deciduous *Ambrosia dumosa*, *Lycium pallidum*, *L. andersonii*, *Krascheninikovia lanata*, *Acamptopappus shockleyi*; and the evergreen gymnosperm *Ephedra nevadensis*. A common subshrub is *Polygala subspinoso*. Common perennial forbs include *Sphaeralcea ambigua* and *Baileya multiradiata*. Abundant native grasses are *Pleuraphis rigida* (C₄), *Achnatherum hymenoides* (C₃), and the short-lived *Erionueron pulchellum* (C₄). The non-native annual grass *Bromus madritensis* ssp. *rubens* is common in shrub understories. Vegetation at the NTS is further described in Beatley (1967, 1976) and Jordan et al. (1999).

The Mojave Desert experiences sporadic, low annual precipitation, with annual rainfall of <200 mm. Winter rains are widespread and may last several days. Summer storms generally occur in July and August and are usually local, intense, and unpredictable. Relative humidity is low (<20% is common), resulting in very high potential evaporation. Moisture is the primary limitation to plant growth in the Mojave Desert (Turner and Randall 1989, Smith et al. 1997). Temperatures are extreme, with a mean minimum winter temperature of –10°C and maximum summer temperature >47°C. A large diurnal temperature fluctuation occurs throughout the year (Bowers 1987). Soils are aridisols and are characterized by spatial heterogeneity in nutrients, infiltration,

and texture (Romney et al. 1973, 1980). Nitrate, ammonium, and phosphorus levels vary from 50, 4, and 20 ppm, respectively, in areas beneath larger shrubs to 3, 1, and 9 ppm in areas between shrubs (J. Titus unpublished data). Soils are basic with a mean pH of 8.2. Mounds and burrows created by the activities of small mammals, particularly kangaroo rats (*Dipodomys* spp.) and desert tortoises (*Gopherus agassizii*), are common and frequently located at the base of shrubs.

Plant Collection

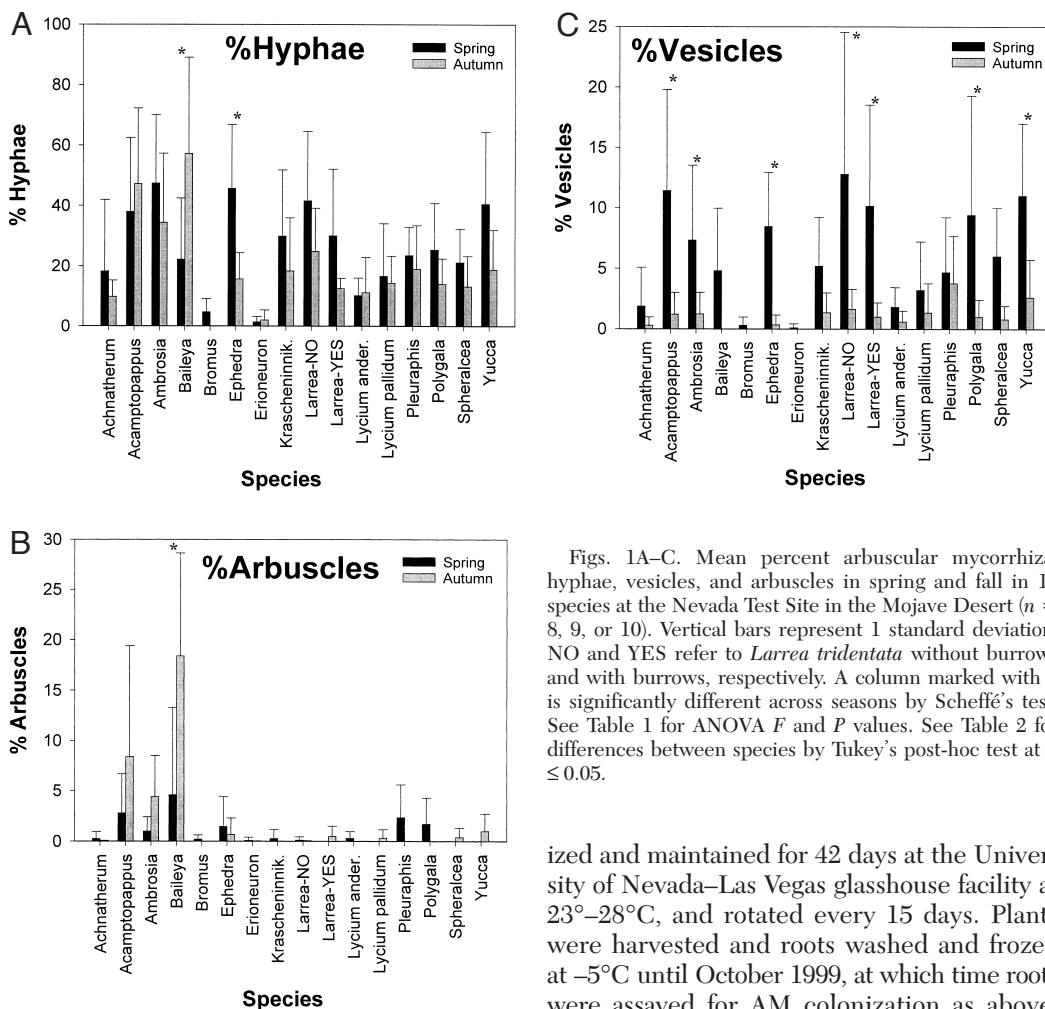
We collected roots from common LDER species in spring (May–June) and autumn (September–November) 1999 for assessment of AM colonization ($n = 10$ for each species in each sampling period). Spring is usually the period of growth and reproduction for most species collected in this study, but 1999 was a dry spring with an annual precipitation of 94 mm (S. Zitzer unpublished data). Thus, plant activity was strongly reduced. Autumn, generally a dry season in the Mojave, was dry in 1999. Roots were collected from *Larrea tridentata* plants both with and without small mammal burrows. Roots of plants common in the River Mountains were collected in autumn 1999 ($n = 5$) and stored in a freezer.

Staining

Roots were separated, washed, cleared, and stained with trypan blue (Brundrett et al. 1994). Using a dissecting microscope, we estimated percent AM colonization of fine roots (<1 mm in diameter). A grid of 1-cm squares was placed below a petri plate that contained the root sample. One hundred locations in which a root crossed a line on the grid were scored for hyphae, arbuscles, and vesicles. We examined many samples under higher power to ascertain that the structures were indeed AM. The number of mycorrhizal “hits” is used as an estimate of percent root colonized by the 3 AM structures (Brundrett et al. 1994).

Mycorrhizal Inoculum Potential

Mycorrhizal inoculum potential (MIP) is an index of the quantity of inoculum in the soil as measured by the percent AM fungal colonization of corn roots (Moorman and Reeves 1979, Titus et al. 1998). MIP was assessed only for the species collected at the NTS. Ten soil



Figs. 1A–C. Mean percent arbuscular mycorrhizal hyphae, vesicles, and arbuscules in spring and fall in 15 species at the Nevada Test Site in the Mojave Desert ($n = 8, 9,$ or 10). Vertical bars represent 1 standard deviation. NO and YES refer to *Larrea tridentata* without burrows and with burrows, respectively. A column marked with * is significantly different across seasons by Scheffé's test. See Table 1 for ANOVA F and P values. See Table 2 for differences between species by Tukey's post-hoc test at $P \leq 0.05$.

samples per species were collected in the spring at the same time that plants were harvested. For each soil sample, 600 g of soil was amended with 20% sterile perlite to increase porosity, split in half, and each half placed into 10 × 10-cm freely draining plastic pots. Bioassays were conducted with nonfungicide-treated *Zea mays* seeds. All pots were watered daily with tap water. Fertilizer was applied in 50-mL aliquots per pot of 10% Hoagland's solution minus phosphorus at planting and at weekly intervals throughout the experiment. The control consisted of 10 pots of sterile soil placed randomly among the treatment pots and planted with corn to determine if contamination by glasshouse AM propagules occurred. Previous work showed that AM propagules, if present, rapidly colonize corn in the glasshouse (Titus et al. 1998). Pots were random-

ized and maintained for 42 days at the University of Nevada–Las Vegas glasshouse facility at 23°–28°C, and rotated every 15 days. Plants were harvested and roots washed and frozen at –5°C until October 1999, at which time roots were assayed for AM colonization as above. For each sample, we averaged the percent colonization of the 2 corn plants to achieve MIP.

Data Analysis

AM colonization levels for species collected in spring and autumn at the NTS were arcsine transformed and compared by 2-way ANOVA at $\alpha = 0.05$. Due to poor sample quality, the sample size for a few of the species was $n = 8$ or $n = 9$. Post-hoc tests were conducted by Tukey's honestly significant difference test. Spring versus autumn AM colonization levels for **each** species were compared by Scheffé's test at $\alpha = 0.05$ (Zar 1984). Scheffé's test was used instead of 48 t tests to avoid type II error. Species collected at the River Mountains were not compared statistically due to small sample size. The nonparametric Spearman's rank correlation test (Zar 1984) was conducted between MIP and percent hyphae to

TABLE 1. Two-way ANOVA F and P values for arbuscular mycorrhizae structures from 14 species at the Nevada Test Site in the Mojave Desert in spring and autumn 1999 ($n = 8, 9$, or 10 , $P \leq 0.05$ for significance, data arc-sine transformed). See Figures 1A–C for results and Table 2 for results of Tukey's post-hoc tests for species.

AM structure	Variable	F	P
Hyphae (%)	Species	6.840	0.000
	Season	7.474	0.007
	Interaction	2.606	0.002
Arbuscles (%)	Species	12.223	0.000
	Season	7.513	0.007
	Interaction	5.047	0.000
Vesicles (%)	Species	2.720	0.001
	Season	60.631	0.000
	Interaction	2.059	0.015

assess whether these 2 AM components were correlated.

RESULTS

NTS species differed in their levels of AM colonization in all 3 AM structures in both spring and autumn (Figs. 1A–C, Tables 1, 2). Roots of shrubs and perennial herbs generally contained more hyphae and vesicles than the short-lived herbaceous species such as *Bromus* and *Erioneuron* (Figs. 1A, 1C). A similar pattern occurred with the River Mountain species (Table 3), with the annuals having little or no AM colonization. Only a single perennial, the invasive riparian species *Tamarix*, was nonmycorrhizal. Due to the very dry spring and summer, few native annual species were available. *Larrea* without mammal burrows had higher values for AM structures, except for fall arbuscles, than did *Larrea* with mammal burrows; however, differences were not significant. Although *Grayia spinosa* was collected at the NTS, it is included in Table 3 because it was collected only in autumn ($n = 5$). The nonnative annual grass *Bromus madri-tensis* ssp. *rubens* was not present in autumn.

For all species combined hyphae and vesicles decreased from spring to fall and arbuscles increased (Table 1). Only 2 species showed a significant seasonal change in hyphae, and 1 species in arbuscles, but a decrease in vesicles occurred in 7 of the species (Figs. 1A–C). *Baileya* and *Ephedra* showed a seasonal shift in 2 AM structures: increased hyphae and arbuscles for *Baileya* and decreased hyphae and vesicles for *Ephedra*.

Mycorrhizal inoculum potential was significantly different across species ($F = 8.063$, $P =$

0.000), but post-hoc tests found the only significant difference was with the high MIP of *Yucca schidigera* soil (Fig. 2). Large standard deviations prevented other differences from occurring. MIP and percent hyphae were not correlated by Spearman's rank correlation ($P = 0.076$). Control corn plants were nonmycorrhizal.

DISCUSSION

All native perennial species of the Nevada Test Site and River Mountains were found to be mycorrhizal. Short-lived species, particularly nonnative weeds, contained few hyphae, as has been found elsewhere (e.g., Berch et al. 1988, Boerner 1992a, Peat and Fitter 1993, Titus et al. 1998). However, a range of native annuals could not be tested because drought conditions did not allow germination and establishment. An invasive, nonnative tree (*Tamarix*) was found to be nonmycorrhizal. *Tamarix* is an aggressive invader of southwestern U.S. riparian zones (Smith et al. 1998), and nonmycorrhizal status is common in both invasive (Pendleton and Smith 1983, Boerner 1992b, Titus et al. 1998) and wetland species (Peat and Fitter 1993).

Studies of AM colonization for the species tested here are infrequent in the literature. Bethlenfalvay and Dakeasian (1984) found that AM colonization levels in *Achnatherum hymenoides* from Reno, Nevada, were 86% in ungrazed plots and 40% in grazed plots, both values much higher than in this study. Cui and Nobel (1992) assessed *Ferocactus cylindraceous* (*F. acanthodes* in their study) and found it to have AM colonization levels very similar to this study (Table 3). The nonnative annual *Salsola kali* has been reported to be nonmycorrhizal (Khan 1974, Miller 1979, Reeves et al. 1979). Although AM colonization of *Salsola* occurred in our study, levels were very low and consisted of hyphae only. It is probable that plant-mycorrhizae mutualism is not functional in this species (Allen et al. 1989).

The presence of an animal burrow near a shrub may have a significant influence on soil nutrients and a wide array of other soil parameters (reviewed in Whitford and Kay 1999). Although animal burrows did not influence AM colonization or MIP values in our study, during more mesic years burrows may cause differences to emerge because of greater

TABLE 2. Growth form characteristics of 14 species collected in the Mojave Desert at the Nevada Test Site in spring and autumn 1999. "Burrows" refer to small mammal burrows at the base of shrubs. Within each column, species with different letters are significantly different in percent AM hyphae, arbuscles, and vesicles by Tukey's post-hoc test results at $P < 0.05$ ($n = 8, 9$, or 10). See Figures 1A–C for results and Table 1 for 2-way ANOVA F and P values. *Bromus madritensis* is not included here because the species was not present in autumn.

Species	Growth form	Hyphae	Arbuscles	Vesicles
----- % -----				
<i>Achnatherum hymenoides</i>	perennial C ₃ grass	abc	a	ab
<i>Acamptopappus shockleyi</i>	deciduous shrub	d	b	c
<i>Ambrosia dumosa</i>	drought deciduous shrub	d	ab	abc
<i>Baileya multiradiata</i>	short-lived perennial herb	cd	c	abc
<i>Ephedra nevadensis</i>	evergreen gymnosperm shrub	cd	ab	abc
<i>Erioneuron pulchellum</i>	short-lived perennial C ₄ grass	a	a	a
<i>Krascheninnikovia lanata</i>	deciduous shrub	bcd	a	abc
<i>Larrea tridentata</i> (no burrows)	evergreen shrub	cd	a	c
<i>Larrea tridentata</i> (with burrows)	evergreen shrub	abcd	a	bc
<i>Lycium andersonii</i>	drought deciduous shrub	ab	a	ab
<i>Lycium pallidum</i>	drought deciduous shrub	abc	a	abc
<i>Pleuraphis rigida</i>	perennial C ₄ grass	abcd	ab	abc
<i>Polygala subspinoso</i>	deciduous subshrub	abcd	ab	bc
<i>Sphaeracephala ambigua</i>	perennial herb	abc	a	abc
<i>Yucca schidigera</i>	treelike rosette	bcd	a	bc

TABLE 3. Percent arbuscular mycorrhizal colonization and growth form of plants collected in autumn 1999 in the River Mountains, 15 km southeast of Las Vegas, Nevada, in the Mojave Desert at an elevation of 700–800 m (mean \pm standard deviation, $n = 5$).

Species	Growth form	Hyphae	Arbuscles	Vesicles
<i>Acacia greggi</i>	drought deciduous tree	24 \pm 16	0.02 \pm 0.04	2.4 \pm 2.6
<i>Amaranthus fimbriatus</i>	perennial herb	1.6 \pm 3.6	0	0
<i>Opuntia basilaris</i>	cactus	13 \pm 9	0.7 \pm 1	0.3 \pm 0.8
<i>Boerhavia intermedia</i> var. <i>erecta</i>	perennial herb	1.2 \pm 2.6	0	0
<i>Chamaesyce setiloba</i>	prostrate annual	4.0 \pm 5.6	0	0
<i>Hymenoclea salsola</i>	subshrub or shrub	30 \pm 24	0.8 \pm 1.8	0.8 \pm 1.8
<i>Opuntia acanthocarpa</i>	cactus	18 \pm 6	0	2.0 \pm 2.4
<i>Dalea mollis</i>	mat-forming annual	0	0	0
<i>Eriogonum deflexum</i>	erect annual	0	0	0
<i>Eriogonum inflatum</i>	perennial herb	7.0 \pm 10	1.0 \pm 2.4	0.03 \pm 0.05
<i>Grayia spinosa</i> ¹	deciduous shrub	24 \pm 23	0	3.0 \pm 1.4
<i>Mammillaria tetrancistra</i>	cactus	13 \pm 7	0	0
<i>Pectis papposa</i>	erect annual	14 \pm 8	0.4 \pm 0.9	0.8 \pm 1.1
<i>Opuntia ramosissima</i>	cholla cactus	10 \pm 10	2.0 \pm 4.5	2.4 \pm 3.3
<i>Physalis crassifolia</i>	subshrub	7.2 \pm 2.6	0.4 \pm 0.9	1.2 \pm 1.8
<i>Ferocactus cylindraceous</i>	cactus	6.0 \pm 5.1	0	0
<i>Salsola kali</i>	nonnative annual	1.2 \pm 2.7	0	0
<i>Sphaeracephala ambigua</i>	perennial herb	10 \pm 8	0.5 \pm 1.0	0.5 \pm 1.0
<i>Tamarix ramosissima</i>	non-native tree	0	0	0
<i>Tridens muticus</i>	tufted perennial grass	1.6 \pm 3.6	0	0.4 \pm 0.9

¹Collected at the Nevada Test Site in autumn 1999, $n = 5$.

resource demand by vegetation and greater resource availability in burrow soil.

The decrease in hyphae and vesicles over the seasons is not surprising because plant phosphorus demand and soil moisture levels change over the season, and rates of root growth and turnover vary. For example, Cui and Nobel (1992) found AM colonization to increase in 3 Mojave Desert species from

March to May, perhaps representing fungal colonization of the season's new roots. Arbuscles are sites for the exchange of materials between the plant and fungus and are the best indicators of the quantity of material flow and therefore the intensity of the mutualism. Significant overall increase in arbuscles may be attributable to the marked increase that occurred in just 3 of the species (a significant

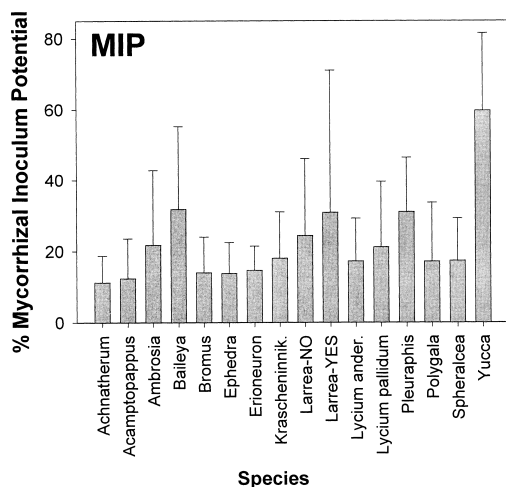


Fig. 2. Mean percent mycorrhizal inoculum potential (MIP) for soil collected from the base of 15 species at the Nevada Test Site in the Mojave Desert ($n = 10$). Vertical bars represent 1 standard deviation. NO and YES refer to *Larrea tridentata* without burrows and with burrows, respectively. Based on Tukey's post-hoc test at $P \leq 0.05$, *Yucca* MIP is significantly greater than that of all the other species; the other MIP values do not differ from each other. See Table 1 for ANOVA F and P values.

increase in *Baileya*). The fact that most of the species showed small increases or decreases in arbuscular levels suggests that for these species the intensity of the mutualism changed little from spring to autumn. This may be due to the fact that 1999 was a drought year and the rate of exchange of materials varied little from spring to autumn. *Baileya* was actively flowering at both collection times, and a heavy phosphorus demand might account for the increase in both arbuscles and hyphae. Because of reduced activity by most plant species in the fall, the other increases in arbuscles that occurred were unexpected. Vesicles indicate carbon storage, and their reduction may indicate a reduced reliance by the plant on the fungus, and hence a reduction in carbon translocation to the fungus. This would be an expected occurrence in autumn, even in a drought year.

Because most perennial arid zone plants in undisturbed environments are mycorrhizal, positive MIP values at the NTS would be expected. Although few studies have been done on arid zone MIPs, they appear to vary seasonally, spatially, and in relation to environmental variables (Al-Agely and Reeves 1995,

Requena et al. 1996), as in more mesic environments (Johnson, Zak et al. 1991, Brundrett et al. 1996). Similar MIP values were found in a related study at the NTS for several of the species (*Ambrosia*, *Pleuraphis*, *Lycium pallidum*, and *Larrea*; Titus et al. in preparation).

AM root colonization and MIP from adjacent soil were not correlated. Many studies have found AM parameters not to be correlated (e.g., Ebberts et al. 1987, Scheltma et al. 1987, Johnson, Pflieger et al. 1991). This may reflect patchiness in the distribution of AM propagules around a plant (Smith and Read 1997); and host species, surrounding vegetation, soil, and climatic and temporal factors are likely to influence AM root colonization levels (Johnson et al. 1992, Sanders and Fitter 1992c, Blaszkowski 1994, Titus and del Moral 1998). Thus, because of the large number of variables that influence AM parameters, a lack of correlation is not surprising.

This study increases our understanding of AM colonization levels of some Mojave Desert plants and illustrates that hyphal and vesicle levels decrease in these species from spring to autumn in a drought year, while arbuscles increase in a few species. This study also demonstrates that MIP levels present in soil adjacent to these species are similar, except for soil surrounding *Yucca*, which has higher MIP levels. Mycorrhizae are critical to the procurement of essential nutrients for desert plants for at least part of their life cycle. Because of this, mycorrhizae play a vital role in competitive outcomes and successional pathways in harsh arid environments where plant community development is very slow.

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AUTUMNAL MIGRATION OF EARED GREBES (*PODICEPS NIGRICOLLIS*) THROUGH SOUTHWESTERN WYOMING:
A KEY TO ASSESSING THE SIZE OF THE
NORTH AMERICAN POPULATION

Joseph R. Jehl, Jr.,¹ and Carl Johansson²

ABSTRACT.—In autumn the vast majority of the North American population of Eared Grebes (*Podiceps nigricollis*) congregates for several months at Great Salt Lake, Utah, and Mono Lake, California. Because the lakes are so large, it has not been possible to monitor grebe migration with sufficient accuracy to determine when peak numbers are reached. To clarify migration phenology, we analyzed data from 2 isolated wetland areas in southwestern Wyoming where grebes land en route between breeding areas in the interior and Great Salt Lake. Occasional birds, probably non-breeders or failed breeders, begin moving southward as early as mid-June. Migration of postbreeding birds starts in late July, peaks in late August and September, and is largely completed by the end of October, with very small numbers arriving into November. The pattern of migration and number of birds encountered varied annually, but 95% of the migration was usually completed by 15 October. As a result, censuses at the major staging lake made on or after 15 October but before the grebes depart for wintering areas can be used to study trends in size of the North American population.

Key words: Eared Grebe, *Podiceps nigricollis*, Great Salt Lake, Mono Lake, migration, population, monitoring.

The Eared Grebe (*Podiceps nigricollis*) is by far the most common grebe in North America (O'Donnel and Fjeldså 1997, Jehl et al. 1999, Jehl unpublished). In autumn nearly the entire population concentrates for several months at hypersaline lakes in the Great Basin to exploit the abundant invertebrate prey. Great Salt Lake, Utah, and Mono Lake, California, are the major staging areas (Jehl 1988, Jehl et al. 1999). The influx begins in late July and continues for an unknown period into late fall. Grebes remain at staging lakes continuously until food becomes unavailable and then, sometime between late November and early January in most years, continue southward to their main wintering area in the Gulf of California, Mexico. The return migration northward may begin as early as January in some years and extends into May. During that time hundreds of thousands gather at the Salton Sea, California, with peak numbers occurring in March (Jehl and McKernan 2002). Most then move through the interior of the continent, including Great Salt Lake, to arrive on their breeding grounds in the north central

U.S. and southwestern Canada from mid-April onward.

Major aspects of these annual movements have been well documented (Jehl 1988, 1993, 1994, 1997, Jehl and Yochem 1986, Cullen et al. 1999, Jehl et al. 1999, Jehl and McKernan 2002). Lacking from this picture is precise information on timing and intensity of the autumnal migration. Obtaining such information has been difficult because staging lakes are so large and numbers of birds are so enormous that it has not been possible to measure population size with sufficient frequency or precision to determine phenology in detail. During the fall arrival period at Mono Lake, for example ($\approx 180 \text{ km}^2$; peak grebe population > 1.5 million), an average of $> 20,000$ grebes arrives nightly (revised from Jehl 1988). However impressive that may seem, the influx is not measurable because the birds land before dawn and become indistinguishable among the thousands already present. Great Salt Lake ($\approx 2160 \text{ km}^2$; peak > 1.0 million) is even less amenable to quantitative studies because of its enormity (Boyd and Jehl 1998, Jehl et al. 1999).

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In this paper we show that census data from migrating Eared Grebes that stop briefly when flying between breeding areas in the interior and major fall staging areas provide an exceptional opportunity to study the timing and intensity of migration, and that these data can be applied to the broader question of determining and monitoring the size of the North American population.

STUDY AREAS AND METHODS

We analyzed data on migrating Eared Grebes gathered over the entire fall migration period in 4 years at 2 isolated wetland areas in arid southwestern Wyoming (Fig. 1). The migrants involved were en route to Great Salt Lake, 150 and 225 km westward, but interrupted their migration to seek safe havens at dawn, as is characteristic of the species. One location, near Kemmerer, consisted of 11 ponds ranging in size from 10.3 to 33 ha spread over 3.9 km²; the total surface area was 120 ha. The second, near Green River, consisted of a single 400-ha pond. Ponds at both locations were constructed to hold industrial waste water. Counts were made because of the actual or perceived risks to grebes and other migrating waterbirds due to poor water quality.

At Kemmerer fall observations were made by CJ and associates daily between 4 August and 22 November, and on 10 dates between 16 July and 3 August 1994. Counts were made between 0700 and 1000 hours, and barometric pressure was taken at dusk. The ponds' small size, configuration, and lack of screening vegetation made it possible to detect all birds. Spring counts at the same ponds were made at 3-day intervals between 22 March and 25 May 1994. At Green River the FMC company's waterfowl recovery and rehabilitation team gathered data on the following schedule: 1992, daily from 27 July through 3 December; 1993, on 7 dates between 9 and 29 July, and on all but 9 days (8 in August) between 2 August and 15 December; 1994, 6 days between 13 and 28 June, and daily from 1 July through 12 December; 1995, 5 days between 20 and 30 June, 7 days between 3 and 15 July, and daily from 17 July to 21 December. At least once each morning, all birds landing on the pond were counted from a small boat and the entire shoreline was surveyed for evidence of mortality. Given the size of the lakes, the open topog-

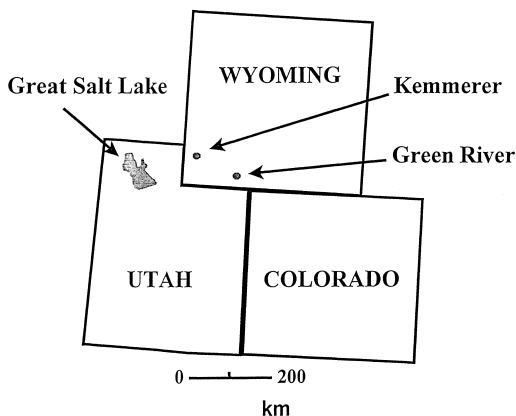


Fig. 1. The study sites lie 150 and 225 km east-north-eastward of Great Salt Lake.

raphy of the shoreline, and the diligence of the team (J. Jehl personal observation), we estimated the effectiveness of this technique in detecting grebes at >95%.

Daily numbers recorded at each locality can be considered to represent incursions of the previous night. Such conclusion is almost inevitable because grebes avoid migrating by day, and observations in Wyoming (R. McNalley personal communication, C. Johansson personal observation) and many other areas (J. Jehl personal observation) show that nearly all migrants arrive in the predawn hours and depart about dusk. Protracted stays of healthy birds at these ponds would not have been possible because all ponds were sterile and held no food suitable for any aquatic birds. Furthermore, at both sites, ponds contained high concentrations of several sodium salts (mainly sodium decahydrate), which might be considered toxic and would, under certain conditions, precipitate on feathers, thereby causing mortality through hypothermia and reduced buoyancy. Thus, at either location migrants that might attempt to remain through the day could become imperiled and quickly succumb.

RESULTS

GREEN RIVER.—The data set from Green River spans the entire autumnal migration period from 1992 through 1995. It indicates that a few grebes, almost certainly failed breeders or nonbreeders (Jehl 1988), begin moving toward staging lakes as early as late June. The regular and continuous migration of

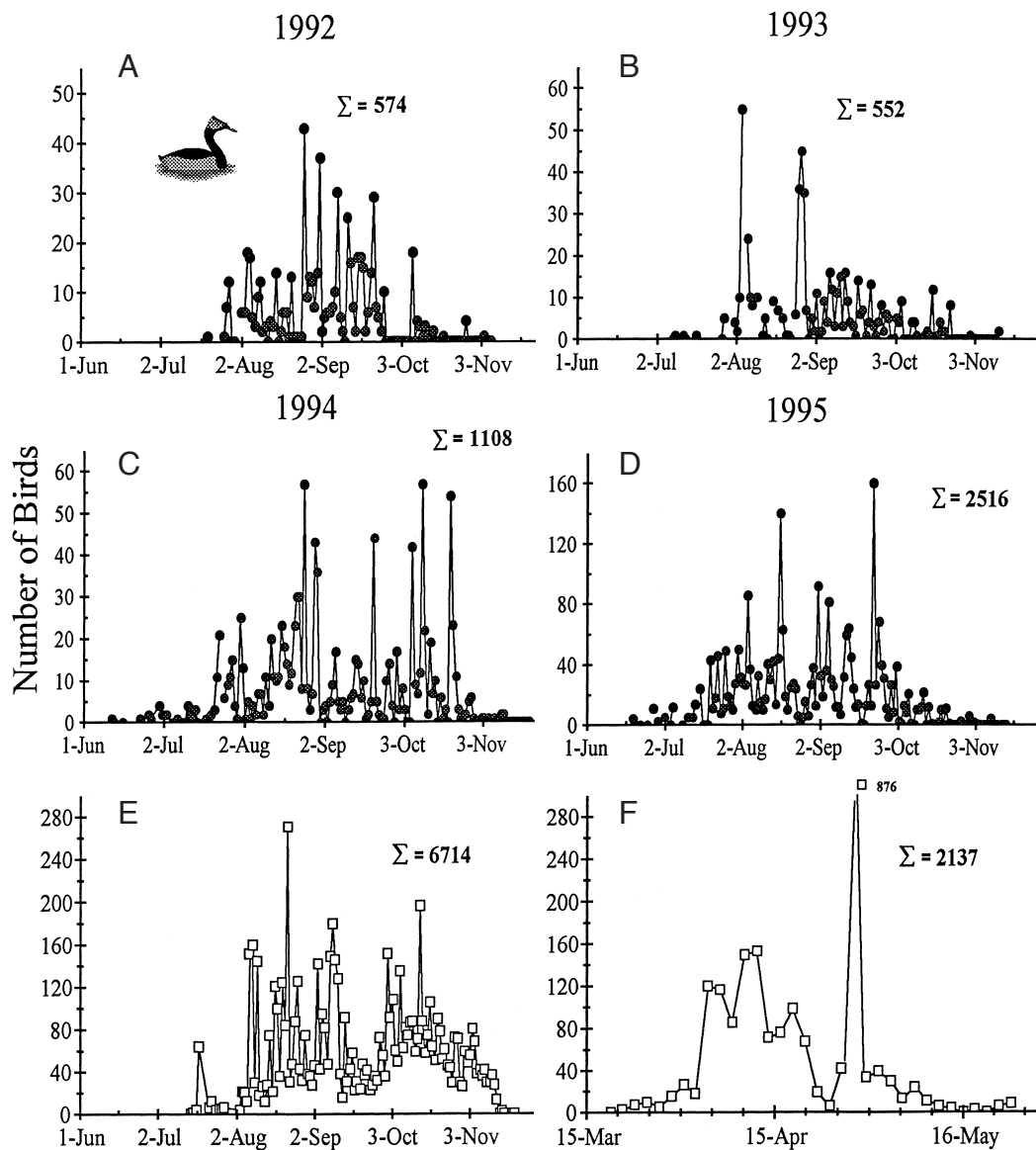


Fig. 2. Timing and pattern of Eared Grebe migration at Green River, Wyoming, in (A–D) autumn 1992–1995, and at Kemmerer, Wyoming, in (E) autumn 1994 and (F) spring 1994.

postbreeding birds and young begins in the last week of July and continues into early November. The pattern and number of birds encountered varied from year to year (Figs. 2 A–D). In some years major influxes were concentrated early in the season (1993), whereas in others they were concentrated in mid-period (1992, 1995) or skewed toward the latter half (1994). Phenology, however, was essentially constant. Migration was essentially

over by 15 October, by which time 95% of the migrants had usually passed through (Fig. 3A); 1992, 98.9%; 1993, 95.6%; 1994, 89.3%; 1995, 98.0%.

As soon as the main migration began, migrants were encountered almost daily. In 1992 between 27 July and 27 September (63 days), grebes were seen on 55 of 61 (90%) days for which we have data; in 1993 between 27 July and 25 October (84 days), on 66 of 78

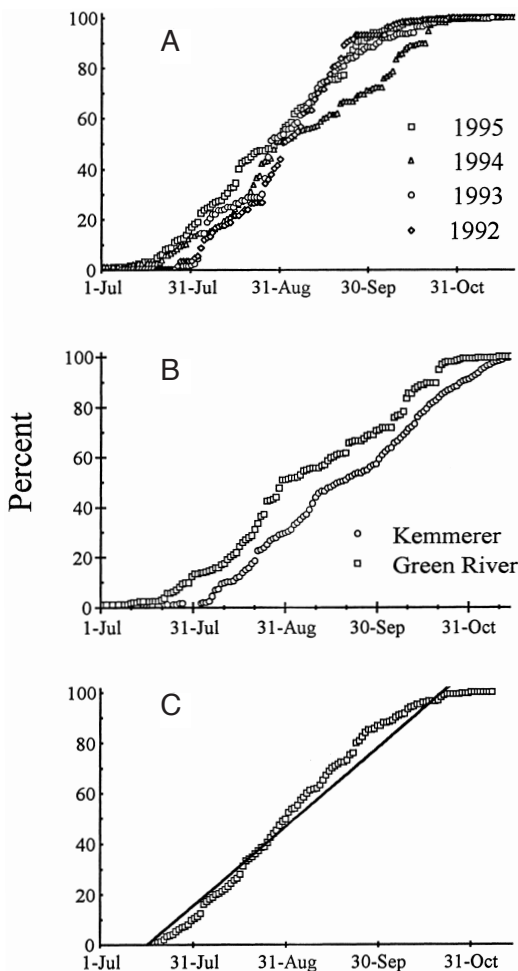


Fig. 3. (A) Cumulative percentage of Eared Grebes migrating through Green River, Wyoming, in 1992–1995 and (B) at Green River and Kemmerer in 1994. (C) The mean pattern at Green River (1992–1995), assuming 20 July as day 1 of the migration. Earlier migrants (assumed to be nonbreeders) were ignored.

days (85%); in 1994 between 1 July and 30 October (122 days), on 106 of 121 days (88%); and in 1995 on all 89 days (100%) between 21 July and 17 October.

KEMMERER.—Fall counts on 119 of 129 days from 16 July through 22 November 1994 showed that grebes arrived daily from 17 July through 17 November, except on 16 November; 97.5 % had passed through by 15 October (Fig. 2E). We recorded 6714 birds, with daily counts averaging 56.4 (range 1–270). Relatively large flights (>100) were spread out over 17 days between 8 August and 19 October.

On 34 spring counts between 22 March and 25 May, observers recorded 2137 migrants, with daily counts (excepting 29 April, see below) averaging 38 (range 0 [3 days] to 153). Peak migration (2023 birds, 94.5%) extended over 35 days from 1 April to 5 May. The pattern (Fig. 2F) approximated a slightly skewed, bell-shaped curve except for 29 April, when 876 birds (40%) arrived. That extreme concentration was associated with severe weather. Evidently, birds left Great Salt Lake on the evening of 28 April shortly after the eastward passage of a frontal system, but they reencountered the front and its associated freezing rain and snow along a line stretching from Pocatello, Idaho, to Kemmerer, to Grand Junction, Colorado, causing them to abort their flight at the first available open water (cf. Jehl 1993, 1994, Jehl et al. 1999).

METEOROLOGY.—Observations at Kemmerer indicated that fall flights might be associated with periods of relatively low barometric pressure. This was supported by a significant correlation between the number of birds recorded each morning and the local pressure measured the previous evening (Spearman rank order correlation, $N = 111$, Spearman $t = -0.205$, $P = 0.031$).

DISCUSSION

Comprehensive censuses in southwestern Wyoming provide unique insights into the migratory patterns of Eared Grebes away from the Great Salt Lake staging area in spring and toward the lake in fall. Spring migration through Kemmerer was relatively brief and concentrated in the first 3 weeks of April. Total number of birds observed (about half that detected in fall, when adjusted for observational effort and discounting the one exceptional flight) is surprisingly large because any grebes leaving Great Salt Lake around sunset should have been well past Kemmerer by dawn (a 2.5-hr flight at 60 km hr⁻¹; Cullen et al. 1999). It seems unlikely that spring migrants would fly only a few hours each night, in view of their need to cross large spans of inhospitable habitat to find safe landing sites, and because their extensive premigration reorganization of body composition (Jehl 1997) is suggestive of preparation for a long flight. The only apparent alternative is that some spring migrants transiting southern Wyoming do not

originate at Great Salt Lake but depart from farther south or east.

The autumn movement toward Great Salt Lake extends from late July into mid-November, with a broad peak stretching from early August through September. This pattern contrasts with that of most Northern Hemisphere migrants, in which the southward flight is concentrated over several weeks. A more concentrated period seems likely for local populations of Eared Grebes as well, but that is not detectable in Wyoming because transients to Great Salt Lake are derived from a source area that may involve most of the species' broad North American range (Jehl and Yochem 1986, Cullen et al. 1999), over which nesting can occur from early May to early August. Also, autumn migration from any area is protracted because of differential migration, with adults emigrating a week or two earlier than juveniles on average (Jehl 1988, Cullen et al. 1999).

We suspect that differences in breeding success account for much of the annual variation. In 1993, for example, when total numbers were low, there were no strong peaks after early September. Such a pattern would be consistent with poor production because juveniles migrate later on average. On the other hand, 1994 might have been a very successful year because total numbers were relatively high and flights persisted into late October. This relationship is hard to verify because of the grebes' widespread distribution and because we lack information on the age composition of migrants and their precise areas of origin. We simply note that in one major grebe breeding area, the Prairie Potholes, duckling production was poor in 1993 but good in 1994 (Caithamer et al. 1993, 1994, Krapu 2000).

Since the pattern of migration in all 4 years at Green River was similar to that recorded at Kemmerer in 1994, even though 6 times as many birds were recorded at the latter site (Figs. 2C–E, 3B), observations at either locality would provide a reasonable index to migration phenology and population composition through southwestern Wyoming in a particular year.

The influence of weather requires further study. Grebes arrive almost daily in both spring and fall. This suggests that migrants are not strongly affected by weather conditions. Yet, fall flights tend to be larger after periods of low pressure. Because the points of takeoff

of migrants moving toward Great Salt Lake probably extend over hundreds of miles of longitude, we cannot assert whether synoptic low pressure stimulates migration or whether local low pressure causes grebes to drop out short of their destination.

APPLICATIONS.—The majority of the North American population of Eared Grebes congregates at Mono Lake and Great Salt Lake in fall and remains at those lakes until forced to depart by food shortages in early winter (Jehl 1988, Cullen et al. 1999). The size of these staging masses has been determined by aerial photography in mid-October (Boyd and Jehl 1998, J. Jehl, S. Boyd, D. Paul unpublished). Because photo-censuses later in the season are often precluded by adverse weather, studies at the staging areas had not definitively established when the migration period is over and peak numbers are achieved. Wyoming data resolve that issue by showing that the pattern of migration is broadly consistent from year to year and that >95% of the population has usually passed through by 15 October (Fig. 3C). Accordingly, censuses at the major staging areas on or after 15 October and before grebes leave for wintering areas should encounter virtually all of the population. Furthermore, because nearly all grebes migrate within an 80-day period (21 July–15 October) and the cumulative increase in the percentage of grebes passing through southwestern Wyoming is essentially linear (the cumulative increase is 1.2% day⁻¹ through mid-October), it should be possible to extrapolate ultimate numbers from census data obtained earlier in autumn, so long as they were obtained sufficiently late in the season (say, after 25 September) to allow for the migration of young.

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ABUNDANCE AND CONDITION INDICES OF COYOTES ON HART MOUNTAIN NATIONAL ANTELOPE REFUGE, OREGON

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ABSTRACT.—U.S. Fish and Wildlife Service staff at Hart Mountain National Antelope Refuge (HMNAR), southeastern Oregon, documented high pronghorn (*Antilocapra americana*) fawn mortality, subsequent low fawn recruitment, and declining pronghorn numbers from 1996 to 1999. Coyote (*Canis latrans*) predation was the primary cause, accounting for 60–85% of fawn mortalities each year, and fawns were not physiologically predisposed to predation. Therefore, we investigated certain coyote population parameters (age structure, survival, density, physiology) to evaluate how or if these factors influence coyote predation rates on pronghorn fawns. We captured 11 coyotes (5 male and 6 female) in December 1998. Age of captured animals ranged from 1.7 to 10.7 yrs (\bar{x} = 5.0 years), and all coyotes appeared healthy upon capture. There were no known mortalities through December 1999. We estimated pre-whelping (December through February 1997–1999) density from howling surveys conducted within HMNAR to be 0.40–0.53 km⁻². Compared to other published studies, we found significant ($P \leq 0.05$) differences in selected blood parameters (e.g., blood urea nitrogen, total protein, white blood cell counts), indicating coyote nutrition may be marginal to deficient during winter at HMNAR. A high percentage of coyotes (91%) tested positive for serum-neutralizing antibodies to canine parvovirus. We judged that parasite (*Toxascaris* spp., *Alaria* spp., *Sarcocystis* spp., and *Isospora* spp.) prevalence and intensity were not high enough to influence coyote condition. Based on our data, the coyote population at HMNAR is old aged, at a relatively high density, and stable, but their nutrition may be marginal to deficient during winter. Presently, we are unable to draw direct conclusions relating the parameters we sampled with predation rates by this unexploited coyote population.

Key words: *Canis latrans*, coyote, health, hematology, howling survey, Oregon, physiology.

From 1996 to 1999, the U.S. Fish and Wildlife Service conducted a study on Hart Mountain National Antelope Refuge (HMNAR) in southeastern Oregon to investigate causes of poor pronghorn (*Antilocapra americana*) fawn recruitment and the subsequent decline of the pronghorn herd. During this period it was determined that fawns were not physiologically predisposed to predation, and yet coyote (*Canis latrans*) predation accounted for 60–85% of fawn mortalities and was limiting the pronghorn population (Dunbar et al. 1999, Dunbar 1999a, 1999b, Dunbar unpublished data).

These findings led us to consider other factors that may affect predation rates. Our first objective was to examine age structure, survival, and density of the HMNAR coyote population, and to analyze blood samples to assess health and exposure to disease. Our second objective was to explore relationships between these parameters and coyote predation rates on pronghorn fawns. We suspected HMNAR coyotes would be old aged, as has been reported from other unexploited populations (Gese et al.

1989, Windberg 1995). Older animals may be more efficient predators than younger animals (Pyrah 1984, Gese et al. 1996). Based on observations over the past several years, we believe coyote density on HMNAR is high, and this may also explain, at least partially, predation rates observed over the past 4 years. Physiological data may indicate whether HMNAR coyote nutrition is adequate. Inadequate nutrition at certain times of the year may also influence predation. Disease agents, particularly canine parvovirus (CPV), can impact coyote health, population dynamics, and population size, and therefore may affect predation rates as well.

This information will be useful in evaluating impacts of possible future management actions (coyote control, habitat alterations) on the coyote population.

MATERIALS AND METHODS

During December 1998 we captured 11 (5 male and 6 female) free-ranging coyotes on

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HMNAR. Coyotes were captured either by use of a net gun (Coda Enterprises, Incorporated, Mesa, AZ) fired from a helicopter ($n = 5$) or hand-caught using a pole snare after being located from a helicopter ($n = 6$). Captured animals were restrained with a pole snare fitted loosely around the neck and a leg snare placed around both hind legs. They were also blindfolded to reduce stress from handling.

The upper first premolar was extracted from each captured coyote for age estimation. Each animal was given an injection of approximately 0.1 mL lidocaine hydrochloride around the base of the tooth to alleviate pain before extraction using a tooth elevator and dental forceps. Teeth were air-dried and age was estimated by counting cementum annuli (Matson's Laboratory, Milltown, MT).

A radio transmitter with a 2-hour mortality sensor (Advanced Telemetry Systems, Incorporated, Isanti, MN) was fitted around each animal's neck. All coyotes were located at least twice a month from January through September 1999, and then once a month from October to December 1999. If a mortality signal was detected, the transmitter was located so that the cause of the signal (e.g., death, dropped transmitter) could be determined. Survival was estimated as a simple percentage because all animals were captured during the same time period and no monitoring was conducted until after all animals were captured (Heisey and Fuller 1985).

Coyote density (coyotes \cdot km⁻²) was estimated from data collected during coyote howling surveys (Wenger and Cringan 1978) conducted from 1997 through 1999. These surveys were conducted along a road in the study area seldom used by vehicles. Surveys began at approximately 2100 hours on nights when wind speed was ≤ 16 km \cdot hr⁻¹ (Wenger and Cringan 1978). Taped coyote howls were played through a loudspeaker (Johnny Stewart Wildlife Calls, Waco, TX) at each survey station ($n = 8$) to stimulate coyote response. Taped howls were played for approximately 1 minute, followed by a 3-minute listening period. If no coyotes responded, the tape was played again for 30 seconds, followed by another 3-minute listening period before moving to the next station.

Wenger and Cringan (1978) suggested that 1.6 km was the maximum radius coyote responses could be heard from a sampling sta-

tion. Our stations were approximately 4.8 km apart, which should have decreased the likelihood that we resampled the same coyote(s) at successive stations. We adopted the 1.6-km survey radius from Wenger and Cringan (1978) as our maximum to calculate minimum coyote density. Monthly coyote density along the survey route was estimated by dividing the maximum number of coyotes responding across all surveys conducted in a month by total area surveyed (64.32 km²).

Approximately 10 mL of blood was taken from each animal by venipuncture of the femoral vein. Blood samples were collected in EDTA tubes for a complete blood cell count (CBC) and in serum separator tubes for serology and serum chemistry analysis. Complete blood cell counts and serum chemistries were performed at Lake District Hospital, Lakeview, Oregon, on automated analyzers (Coulter T 660, Coulter Electronics, Incorporated, Hialeah, FL; opeRA Analyzer, Medium Systems, Bayer Diagnostic, Larrytown, NY).

We compared animals in our sample to animals >1 year old from other studies because we captured no animals <1 year old. We tested for differences in blood parameters due to sex in our sample using analysis of variance (Statistical Analysis System, Version 8.0, Cary, NC). We compared our results with those from Gates and Goering (1976), Rich and Gates (1979), and Smith and Rongstad (1980) using 2-tailed t tests in Corel QuattroPro 8.0 (Corel Corporation, Ottawa, ON). Analysis of variance and t -test results were considered significant at $P < 0.05$.

Because there were no between-sex differences ($P > 0.05$) in our sample for any blood parameter we examined, males and females were combined for analysis. Rich and Gates (1979) and Gates and Goering (1976) also reported means for both sexes combined. Smith and Rongstad (1980), however, reported means for both adult males and females, but there were no differences between sexes except for white blood cell count (WBC) and albumin. Therefore, we compared combined (male and female) values from our sample to male values from Smith and Rongstad (1980), except for WBC and albumin, for which we compared our combined sample to both males and females.

Serological analysis for selected infectious microorganisms was performed at Washington

Animal Disease Diagnostic Laboratory (WADDL), Washington State University, Pullman, Washington. Serum samples were tested for prevalence of disease agents using methods described by Silverstein and Greene (1998). Blood samples were tested for both canine distemper virus (CDV) and CPV using the immunofluorescent antibody/serum immunoglobulin G method. Threshold titer levels were 1:50 and 1:25 for CDV and CPV, respectively. The microagglutination test was used to test for *Leptospira interrogans* serovars: *canicola*, *grippotyphosa*, *hardjo*, *icterohemorrhagiae*, *pomona*, and *bratislava*. Threshold titer was 1:100. The rapid slide agglutination test was used to detect prevalence of *Brucella canis*. Threshold titer is qualitative (positive or negative) for this test. The virus neutralization test was used to detect canine adenovirus (CAV) at a threshold titer of 1:4.

To simplify comparisons of disease agent prevalence between HMNAR animals and those from other studies, we classified the 1.7-year-old animals from our study as yearlings, and animals >1.7 years as adults. We used this age classification only for comparisons of disease agents to other studies that classed yearlings as animals between 1 and 2 years old and adults as animals older than 2.

We collected fecal samples from 5 coyotes at time of capture. Samples were examined for parasites at WADDL, where eggs or oocytes per gram (EPG and OPG, respectively) of feces were determined by fecal flotation (Thienpont et al. 1979).

RESULTS

All coyotes captured appeared thin but otherwise in good condition. Age of coyotes ranged from 1.7 to 10.7 years ($\bar{x} = 5.0$). We captured no animals <1.7 years old, and only 36% ($n = 4$) of the sample was ≤ 2.7 years old. We found 1 radio-transmitter from a female coyote on 3 December 1999. No carcass or other evidence was found to suggest this animal died, but we censured her from survival estimates because it had been 2 months since she was last located. Survival of the 10 remaining HMNAR coyotes from 19 December 1998 to 19 December 1999 was 100%.

Coyote density during February 1997 was estimated at 0.50 km⁻². We estimated similar

densities from January and December 1998 (0.42 and 0.53 km⁻², respectively) and from December 1999 (0.40 km⁻²).

Tables 1 and 2 list mean hematologic and serum biochemical values, respectively, with standard deviations and *P*-values from *t* tests comparing HMNAR coyotes to other populations. Results and comparisons of tests of disease prevalence are presented in Table 3. No coyotes tested positive for *Leptospira interrogans* or any of its serovars or *Brucella canis*.

Eggs or oocytes from 4 different parasites were found in coyotes: *Toxascaris* spp., *Alaria* spp., *Isospora* spp., and *Sarcocystis* spp. All 5 coyotes tested were positive for *Toxascaris* spp., with EPG ranging from 94 to 610. The oldest coyote, a 10.7-year-old female, had the highest *Toxascaris* spp. count (610 EPG) and the highest *Alaria* spp. count (22 EPG). Three of 5 coyotes were positive for *Alaria* spp. (2–22 EPG), 2 for *Isospora* spp. (54 and 84 OPG), and 1 for *Sarcocystis* spp. (85 OPG).

DISCUSSION

We have assumed that the age structure of our sample is representative of the population at HMNAR, even though our sample size is small. Our results suggest the coyote population on HMNAR is old aged and may have experienced little recruitment in 1999, unless immigration occurred. If the older animals in our sample exhibit predation patterns as predicted in other studies (Gese et al. 1996), then age structure could be influencing predation rates on HMNAR pronghorn fawns. For example, older animals, through learned behavior, may be more efficient at locating and killing pronghorn fawns than younger, less experienced animals (Pyrarh 1984, Gese et al. 1996).

Annual survival of the radio-tagged sample at HMNAR was high (100%). Gese et al. (1989) found that adult survival in a lightly exploited population in Colorado was 87%. Windberg (1995) found adult survival rates in a lightly exploited population to be 64–73%. Nellis and Keith (1976) and Andrews and Boggess (1978) found survival rates of 60% and 60.9%, respectively, in moderately to heavily exploited populations. While other factors such as habitat, season, and prey availability influence these parameters (Parker 1995), human-caused mortality can have a large impact, as comparisons

TABLE 1. Hematologic values from free-ranging adult coyotes captured on Hart Mountain National Antelope Refuge, Oregon, December 1998, and *P*-values from *t* tests comparing values from reference populations to those from this study.

Parameter (units)	<i>n</i>	Mean \pm <i>s</i>	<i>P</i> -value		
			Gates and Goering (1976) ^a	Rich and Gates (1979) ^b	Smith and Rongstad (1980) ^c
Red blood cells ($\times 10^6/\mu\text{L}$)	9	7.9 \pm 0.4	0.17	0.001 (–) ^d	
Hematocrit (%)	9	57.8 \pm 3.3	≤ 0.001 (–)	≤ 0.001 (–)	≤ 0.001 (–)
Hemoglobin (g/dL)	9	19.7 \pm 1.3	≤ 0.001 (–)	≤ 0.001 (–)	≤ 0.001 (–)
MCV ^e (fL)	9	73.3 \pm 1.2	≤ 0.001 (–)	≤ 0.001 (–)	
White blood cells ($\times 10^3/\mu\text{L}$)	9	7.1 \pm 2.4	0.06	0.04 (+)	≤ 0.001 (+)
Lymphocytes	11	2.2 \pm 1.1	0.44	0.79	0.49, 0.002 (+)
Monocytes	11	0.1 \pm 0.1	≤ 0.001 (+)	≤ 0.001 (+)	≤ 0.001 (+)
Segmented neutrophils	11	3.7 \pm 1.0	≤ 0.001 (+)	≤ 0.001 (+)	≤ 0.001 (+)
Eosinophils	11	0.9 \pm 0.7	0.13	0.23	0.68, –
Basophils	11	0.82 ^f			
Platelets ($\times 10^3/\mu\text{L}$)	9	299.0 \pm 124.2			

^aData from wild-born, captive coyotes.

^bData from 18-month-old, wild-born, captive coyotes.

^cData from wild, free-ranging adult male coyotes, except WBC parameters, for which significance levels from comparisons of both males and females are reported as "males, females," unless significance level for both sexes was equal. See Methods for further explanation.

^d(+) = significantly greater than sample from this study; (–) = significantly less than sample from this study; no sign = no difference between samples.

^eMCV = mean corpuscular volume.

^fOnly mean is reported because standard deviation included negative values.

between our study and others indicate. High survival of adult coyotes could mean that a high density of coyotes could be maintained for a relatively long period of time even with little recruitment (Knowlton and Gese 1995), possibly maintaining higher-than-average predation rates.

Coyote density is difficult to calculate accurately due largely to the elusive nature of the animal and to biases of current survey techniques (Knowlton 1984). Density estimates from howling surveys are probably biased on the low side because not all coyotes within the survey area respond on each occasion (Wenger and Cringan 1978, Okeniewski and Chambers 1984, Gese and Ruff 1998). Response rates also vary by season, and transients and non-breeders typically do not respond (Gese and Ruff 1998). In addition, howling surveys have been criticized in the literature for being too variable and not sensitive enough to detect small to moderate changes in coyote densities (Wenger and Cringan 1978, Andelt and Andelt 1984, Fuller and Sampson 1988). We believe, however, that they do allow us to follow trends from year to year, as did Harrington and Mech (1982), and can be used to estimate densities on small study areas (Pyrah 1984), including HMNAR.

Knowlton (1972) suggested coyote densities in the U.S. could reach as high as 2.3 km^{–2} (6.0

mi^{–2}), but that density was most likely 0.19–0.38 km^{–2} (0.5–1.0 mi^{–2}) over most of the coyote's range. Parker (1995) reviewed many studies from across the U.S. and reported that pre-breeding and winter density estimates ranged from 0.01 to 3.0 km^{–2}, with the majority of estimates falling between 0.20 and 0.57 km^{–2}. Our minimum density estimates were near the middle to high end of what were common pre-whelping density estimates from across the U.S., suggesting a high density for HMNAR. Also, based on 3 years of data, it appears the coyote population in our study area has remained relatively stable. Because our density estimates are a minimum, it is possible the HMNAR coyote population is at saturation density and cannot absorb any new recruits. Recent high predation levels at HMNAR, then, may be influenced by high coyote density and population stability.

We obtained blood samples from coyotes subjected to the stress of capture and handling. Some blood values, including total protein (TP), blood urea nitrogen (BUN), and hemoglobin, are relatively unaffected by the capture techniques we employed, while others, including glucose and occasionally neutrophils, are strongly influenced. Therefore, interpretation of our blood data must take this into account even though we emphasized parameters that are relatively unaffected by

TABLE 2. Serum biochemical values from 11 free-ranging adult coyotes from Hart Mountain National Antelope Refuge, Oregon, December 1998, and *P*-values from *t* tests comparing values from reference populations to those from this study.

Parameter (units)	Mean \pm s	<i>P</i> -value	
		Rich and Gates (1979) ^a	Smith and Rongstad (1980) ^b
Sodium (meq/L)	143.0 \pm 2.6	0.03 (+) ^c	
Potassium (meq/L)	4.9 \pm 0.4	1.00	
Chloride (meq/L)	113.0 \pm 2.3		
Calcium (mg/dL)	7.9 \pm 0.6	≤ 0.001 (+)	0.003 (+)
Phosphorus (mg/dL)	3.5 \pm 1.5	0.52	0.83
Total protein (g/dL)	5.7 \pm 0.6	0.001 (+)	0.002 (+)
Albumin (g/dL)	3.3 \pm 0.4	0.001 (–)	0.008 (–), 0.13
Uric acid (mg/dL)	0.9 \pm 0.8	0.07	
Alkaline phosphatase (U/L)	10.5 \pm 10.2	≤ 0.001 (+)	
Alanine aminotransferase (U/L)	62.0 \pm 20.6		
Aspartate aminotransferase (U/L)	109.0 \pm 39.0		
Lactate dehydrogenase (U/L)	468 ^d		
Blood urea nitrogen (mg/dL)	39.0 \pm 15.3	0.02 (–)	0.02 (–)
Glucose (mg/dL)	159.0 \pm 59.4	0.09	0.92
Creatinine (mg/dL)	1.1 \pm 0.3	0.03 (+)	
Total bilirubin (mg/dL)	0.02 ^d		
Cholesterol (mg/dL)	148.0 \pm 25.95		0.54

^aData from 18-month-old, wild-born, captive coyotes.

^bData from wild, free-ranging adult male coyotes except albumin, for which significance levels from comparisons of both males and females are reported as "males, females."

^c(+) = significantly greater than sample from this study; (–) = significantly less than sample from this study; no sign = no difference between samples.

^dOnly mean is reported because standard deviation included negative values.

TABLE 3. Comparison of prevalence of antibody titers to canine distemper virus (CDV), canine parvovirus (CPV), and canine adenovirus (CAV) between coyotes at Hart Mountain National Antelope Refuge (HMNAR) and coyotes from studies in California (CA; Cypher et al. 1998) and Yellowstone National Park (YNP; Gese et al. 1997).

	% positive, yearlings			% positive, adults		
	HMNAR (2) ^a	CA (37)	YNP (11)	HMNAR (9)	CA (67)	YNP (33)
CDV	100	36 ^b	54	22	54	88
CPV	100	89	100	89	73	100
CAV	0	54	82	89	90	97

^aNumber tested.

^bOnly 36 coyotes were tested for antibodies to CDV.

capture and handling. Different laboratory methods used in different studies may also have some effect on values.

Red blood cell counts (RBC) were higher (Table 1) in our study compared with values of captive coyotes from Rich and Gates (1979), but they did not differ from those in a study of captive coyotes by Gates and Goering (1976). Hematocrit and hemoglobin values in our study were also higher when compared with values from 3 other studies (Gates and Goering 1976, Rich and Gates 1979, Smith and Rongstad 1980). The higher values we found could indicate that coyotes at HMNAR were in better

condition than those from other studies (Gates and Goering 1976, Rich and Gates 1979, Smith and Rongstad 1980). Seal and Mech (1983), however, found higher RBC, hemoglobin, and hematocrit values in gray wolves (*Canis lupus*) during winter compared to other seasons and determined seasonal variation was responsible. Because we collected blood samples during winter, we believe this may be the cause of the difference between HMNAR studies and the others.

Because neutrophilia can result from the stress of capture and handling, it is somewhat surprising that total WBC counts of HMNAR

coyotes were lower compared with 2 other studies (Rich and Gates 1979, Smith and Rongstad 1980), and neutrophils were lower in HMNAR coyotes than in coyotes from 3 studies (Table 2). We suspect that lower WBC counts in our study may be related to poor nutrition compared to coyotes in the aforementioned studies. Any differences in the other parameters presented in Table 1 are probably due to capture stress and likely would not influence the long-term condition of the coyotes.

Blood urea nitrogen values in our study (Table 2) were higher than values from Rich and Gates (1979) and Smith and Rongstad (1980). Total protein values in our study were lower (Table 2) than those reported from the same 2 studies. Elevated BUN coupled with lowered TP levels can signify protein catabolism due to energy deprivation caused by inadequate winter nutrition, a condition we suspect is occurring in coyotes on HMNAR.

Calcium level was significantly lower in this study compared to levels from Smith and Rongstad (1980) and Rich and Gates (1979; Table 2). We believe these lower values were also due to dietary deficiency (Robbins 1983).

Among disease prevalences, the high percentage of HMNAR coyotes with titers to CPV was the most interesting and the only result that we presently consider could influence coyote condition. High CPV titers may indicate that most of the coyotes on our study area had been infected with CPV. Such high antibody prevalence rates are usually associated with a highly contagious but nonfatal infection (Thomas et al. 1984). Mech and Goyal (1995), however, predicted that the winter gray wolf population in Minnesota would decline when CPV prevalences in adults consistently exceeded 76%. They believe that CPV may be important in limiting wolf populations. The population data displayed by Windberg (1995) also illustrate the potential impact CPV can have on coyote populations. In his study, CPV contributed to high juvenile loss in 1980 and severely reduced recruitment of that age class the next year. If HMNAR coyote numbers decline over the next few years, it is possible, based on our data, that CPV may be involved.

HMNAR coyotes are old aged, at a relatively high density, and stable. Nutrition for these animals may be marginal to deficient during winter. The disease and parasite prevalences we observed did not appear to have any

measurable negative influence on HMNAR coyote condition, although the high percentage of our sample with CPV may have future relevance. While we are unable to draw direct conclusions relating the parameters we sampled to predation rates on pronghorn fawns at this time, we will continue some aspects of our work so that we may do so. The data we do present, however, are relevant for an unexploited coyote population.

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HISTORICAL VARIATIONS IN $\delta^{13}\text{C}_{\text{LEAF}}$ OF HERBARIUM SPECIMENS IN THE SOUTHWESTERN U.S.

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ABSTRACT.—The uncontrolled, global increase in atmospheric CO_2 concentration (ca 80 ppmv) and decline in $\delta^{13}\text{C}_{\text{air}}$ (ca 1.5‰) since industrialization provide experimental boundary conditions by which to assess physiological response of vegetation. To examine consequences of these global atmospheric changes in the southwestern U.S., 350 specimens of *Atriplex confertifolia*, *A. canescens*, *Ephedra viridis*, *Pinus edulis*, *P. flexilis*, *Juniperus scopulorum*, and *Quercus turbinella* of precisely known age spanning the last 150 years were acquired from 9 herbaria. Cellulose analysis of $\delta^{13}\text{C}_{\text{plant}}$ and estimation of isotopic discrimination (Δ) permitted calculation of water-use efficiency (A/g). The $\delta^{13}\text{C}_{\text{plant}}$ chronologies of *C. Atriplex* spp. show some promise as a reliable proxy for $\delta^{13}\text{C}_{\text{air}}$ because their mean trends approximate the known $\delta^{13}\text{C}_{\text{air}}$ chronology. However, the high variability would necessitate multiple samples at any time period to accurately represent the mean. The generally increasing A/g trends of the 5 C_3 species are particularly pronounced for *P. edulis* and, after the 1950s, for *J. scopulorum*, but less evident for *P. flexilis*, *E. viridis*, and *Q. turbinella*, evidencing possible differences in species response to rising CO_2 concentrations. The trends are statistically noisy, however, possibly due to complex microclimates, extreme seasonality, and great interannual variability typical of the southwestern U.S. Herbarium specimens, at least in the Southwest, may be less useful for precise detection of direct CO_2 effects on plant physiology than tree rings, where the variability can be constrained to a single individual over time.

Key words: carbon isotopes, herbarium specimens, leaves, southwestern USA, northern Arizona, atmospheric carbon dioxide, isotopic discrimination, ecophysiology.

Effective methodologies to better decipher past environments and corresponding eco-physiological responses of flora often include analysis of a variety of plant materials, e.g., tree rings (Leavitt and Long 1988, Bert et al. 1997, Feng 1998), plants preserved in sediments and woodrat middens (Marino et al. 1992, Van de Water et al. 1994), and historically archived plant samples (Woodward 1987). Leaves would seem to be a particularly useful substrate from which to extract such information because they are at the forward edge of plant-atmosphere interactions and because current plant stable-carbon isotopic fractionation models are based on leaves (O'Leary 1981, Farquhar et al. 1982). The availability of historical sequences of leaves of known provenance, grown in natural settings under changing atmospheric environments, could help resolve important questions regarding the capacity of plants to maintain "set point" regulation (homeostasis) of eco-physiological parameters (Wong et al. 1979, Polley et al. 1993, Ehleringer and Cerling 1995,

Marshall and Monserud 1996), e.g., internal CO_2 concentration (C_i), ratio of internal to atmospheric CO_2 concentration (C_i/C_a), difference between internal and external CO_2 concentrations ($C_a - C_i$), and intrinsic water-use efficiency, A/g (where A is the rate of photosynthesis and g is the rate of stomatal conductance).

Herbarium leaves offer promise for assessing plant environmental response over the last several hundred years, the last 200 of which have been characterized by profound global-scale changes in atmospheric chemistry. Fossil-fuel consumption and land-use changes have driven an atmospheric CO_2 concentration increase of ca 30% (from ca 280 to 360 ppmv; Barnola et al. 1995) and a corresponding ^{13}C depletion in atmospheric CO_2 ($\delta^{13}\text{C}_{\text{air}}$) from ca -6.5‰ to -8.2‰ (Friedli et al. 1986, Keeling et al. 1989, 1995; Fig. 1). Leaves archived in herbarium collections in Europe from this time interval have already been exploited to

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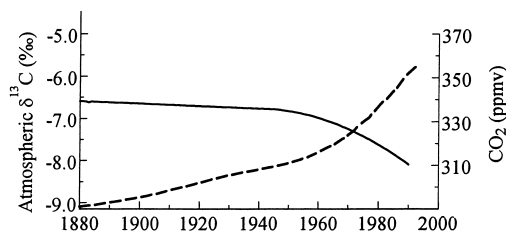


Fig. 1. Atmospheric changes in CO_2 (dashed line) and $\delta^{13}\text{C}$ (solid line) as determined from measurements of air trapped in bubbles of ice cores and direct atmospheric measurements (after Bert et al. 1997).

track effects of changing CO_2 as recorded in a stomatal density/stomatal index decline of ca 20–40% since 1800 A.D. (Woodward 1987, 1993, Peñuelas and Matamala 1990, Paoletti and Gellini 1993).

More recently, $\delta^{13}\text{C}$ of herbarium leaves has been used in efforts to further expose and define the influence of these global atmospheric changes. Peñuelas and Azcón-Bieto (1992) measured a $\delta^{13}\text{C}_{\text{plant}}$ shift of ca -1‰ in the averaged isotopic composition of C_3 leaves of several species from herbarium collections that was consistent with fossil-fuel effects, and a decrease in plant isotope discrimination, Δ (the difference between atmosphere and plant $\delta^{13}\text{C}$; see Methods). The $\delta^{13}\text{C}$ trend from 2 C_4 species was less uniform but also suggested decreased discrimination. Woodward (1993) measured $\delta^{13}\text{C}$ in herbarium leaves for the 8 species of British trees initially sampled for stomatal density (see Woodward 1987). $\delta^{13}\text{C}_{\text{leaf}}$ generally declined during the past 250 years, though there was considerable scatter attributed to marked annual variations in weather. $\delta^{13}\text{C}_{\text{leaf}}$ decline may be influenced by the continual depletion of $\delta^{13}\text{C}_{\text{air}}$ and/or an increase in water-use efficiency (calculated as A/g , rather than instantaneous water-use efficiency, A/E , where E is the transpiration rate) from leaf responses to atmospheric CO_2 enrichment. Woodward (1993) calculated A/g from $\delta^{13}\text{C}_{\text{leaf}}$ using historical trends in $\delta^{13}\text{C}_{\text{air}}$ and C_a in the computation, and found that A/g increased 28% over the past century, most likely through increases in C_a . Beerling et al. (1993) also found that $\delta^{13}\text{C}$ declined from -24‰ to -30‰ in *Salix herbacea* leaves collected in England between 1819 and 1985. They felt the increasing Δ represented by the large $\delta^{13}\text{C}$ decrease was consistent with decreasing

stomatal density in *S. herbacea* found by Beerling and Woodward (1993) because stomatal density and Δ are both “surrogate” indicators of water-use efficiency, responding to increasing atmospheric CO_2 . Toolin and Eastoe (1993) also analyzed $\delta^{13}\text{C}$ of herbarium specimens and modern samples of C_4 *Setaria* grass species, their results falling within the range of other records of recent $\delta^{13}\text{C}_{\text{air}}$ changes. Most of these herbarium $\delta^{13}\text{C}$ and stomatal density studies have been characterized by limited numbers of leaf samples for individual taxa and few replicates for particular years or decades. Also, many herbarium studies do not present or plot measurements from individual taxa. Instead, they plot multispecies averages of actual measurements or relative differences to represent historical trends in stomatal density and $\delta^{13}\text{C}_{\text{leaf}}$ (Woodward 1987, 1993, Peñuelas and Matamala 1990, Peñuelas and Azcón-Bieto 1992, Paoletti and Gellini 1993). Kelly and Woodward (1995) advocate multispecies approaches in plant isotopic studies, which we also endorse in the sense of identifying and understanding differential species responses. Simple multispecies averaging, however, is likely to confound rather than enhance detection of leaf responses to environmental forcing because of different lengths of growing season, different above- and belowground architecture, different strategies for coping with drought, etc.

This study examines variations in $\delta^{13}\text{C}$ (and other related ecophysiological parameters) of leaves from several species representing different functional types (e.g., C_3 vs. C_4 , angiosperms vs. gymnosperms) and growth forms within a confined area of the southwestern part of North America since 1850 A.D. Because of the large number of samples analyzed (each time series represents ca 50 $\delta^{13}\text{C}$ measurements per taxon), the response of isotopic parameters to changing atmospheric composition can be better recognized and quantified.

METHODS

Herbarium specimens from northern Arizona and northwestern New Mexico were targeted for analysis (Fig. 2), with the majority of samples coming from either the Mogollon Rim or the Colorado Plateau physiographic provinces. A spreadsheet containing the age, geographic location, and isotopic results for each

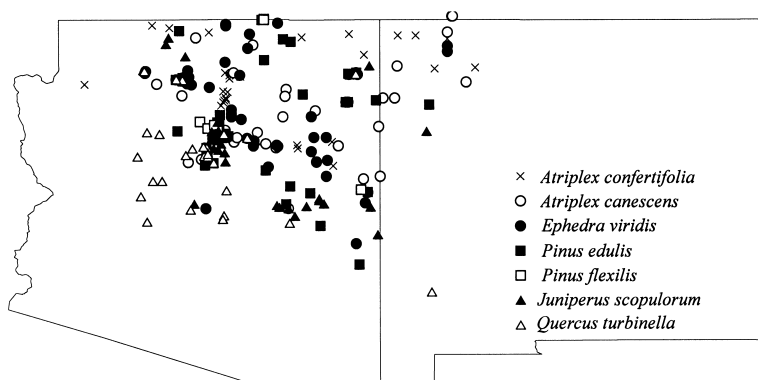


Fig. 2. Map of Arizona and New Mexico showing collection sites for herbarium specimens by species.

sample is available at http://www.paztcn.wr.usgs.gov/betancourt_table.html. The Rim is a topographic break oriented southeast to northwest between the Basin and Range Province (and Sonoran Desert) to the south and the Colorado Plateau to the north. The herbarium samples from the Rim come mostly from the deep valleys of the Verde River and its tributaries, which drain the Rim area south of Flagstaff. The Colorado Plateau consists of wind-swept mesas punctuated locally by volcanic terrain (e.g., the San Francisco Peaks near Flagstaff) and deeply incised, steep-walled canyons in nearly horizontal sedimentary formations.

We chose leaves of 7 species available from 9 herbaria to canvas 2 photosynthetic pathways: the C_4 pathway represented by the halophytes *Atriplex canescens* and *A. confertifolia*, and the C_3 pathway represented by the gymnosperms *Ephedra viridis*, *Pinus edulis*, *P. flexilis*, and *Juniperus scopulorum*, and the C_3 angiosperm *Quercus turbinella*. Herbarium specimens were selected to encompass a limited geographic and altitudinal range (a few degrees of latitude and longitude and less than ~ 1000 m difference in elevation) with a target of 50 specimens spanning 100–150 years for each species. For environmental uniformity, $\delta^{13}C_{\text{leaf}}$ studies should select leaves only from flowering shoots, with the assumption that they develop under a high irradiance from the outside of the tree crown (Woodward 1993). We note that botanists generally select flowering shoots in the field because most taxonomic studies require flowers. For convenience, botanists preferentially sample the outside of the plant's crown.

Four of our taxa (*A. confertifolia*, *A. canescens*, *E. viridis*, and *Q. turbinella*) are low shrubs less than 1.5 m tall; we are confident that most herbarium specimens from these species represent sun leaves from the top of the crown. The conifers (*P. flexilis*, *P. edulis*, and *J. scopulorum*) are relatively low (< 5 m) trees with open crowns and would have been sampled from the outside of the crown at 1.5–2 m heights. Desert scrub and woodland communities in this semiarid region are by nature open canopy; shading may be less confounding to leaf anatomy and physiology than in forested communities in more humid regions.

For *A. confertifolia* and *A. canescens*, we randomly selected 5 to 10 leaves from the herbarium specimens or from collections of previously detached leaves. Leaves were cut in half longitudinally along the central leaf vein, providing half for initial analysis and the remainder for replacement material if needed. We randomly chose 10 needles from multiple cohorts on single branches on *P. edulis* and *P. flexilis* herbarium sheets. One-third of the distal portion of each needle was removed and pooled into a single sample. The distal portions of 5 to 10 *J. scopulorum* twigs and 5 to 10 terminal joint segments from each *E. viridis* were likewise pooled. The *E. viridis* samples were cut in half perpendicular to their long axis. We removed 5 leaves for *Q. turbinella* from each sheet and cut them longitudinally along the central leaf vein. Leaf samples from living vegetation were collected in 1996 for some of the species from the Oak Creek Canyon area south of Flagstaff, Arizona.

The leaf material was milled to 20-mesh, soluble organic compounds were extracted with toluene and ethanol in a soxhlet extraction apparatus, and the remaining plant matter was delignified in a 70°C, acidified sodium chlorite solution (Leavitt and Danzer 1993) to obtain holocellulose. C_4 plant holocellulose was treated for 2 days with 10% HCl (after Baker 1952) to dissolve oxalates prior to combustion and analysis. The holocellulose was combusted with CuO in evacuated quartz tubes at 900°C for 2 hours and at 650°C for 2 hours (Boutton 1991). CO_2 was cryogenically collected and purified on a vacuum extraction line within 48 hours of combustion. It was then analyzed with a mass spectrometer (Finnigan Delta-S®), and $\delta^{13}\text{C}$ ($= [({}^{13}\text{C}/{}^{12}\text{C}_{\text{sample}} - {}^{13}\text{C}/{}^{12}\text{C}_{\text{standard}}) - 1] \times 1000$) calculated with respect to the international PDB standard (Craig 1957). Repeated analysis of a spruce wood holocellulose standard with the C_3 samples gave a standard deviation of 0.13‰ ($n = 32$), whereas repeated analysis of a sucrose standard with the C_4 samples gave a standard deviation of 0.35‰ ($n = 24$). In this study the lower precision on the C_4 standard should not restrict interpretations because inter-plant variability turned out to be approximately 10 times higher.

Whole-tissue $\delta^{13}\text{C}$ values used in calculating the physiological parameters were obtained by subtracting 1.5‰ (Van de Water et al. 1994) and 2.6‰ (Van de Water 1999) from holocellulose $\delta^{13}\text{C}$ values for C_3 and C_4 plants, respectively. We estimate these conversion factors are accurate to about $\pm 0.5\%$. $\delta^{13}\text{C}_{\text{air}}$ and CO_2 concentrations (C_a) were derived from a spline fit of ice core and direct atmospheric measurements (Bert et al. 1997; Fig. 1) and were used to calculate discrimination (Δ), C_i/C_a , C_i , and A/g from the following relationships (Farquhar et al. 1982, O'Leary 1993):

$$\Delta(\text{‰}) = (\delta^{13}\text{C}_{\text{air}} - \delta^{13}\text{C}_{\text{plant}}) / (1 + (\delta^{13}\text{C}_{\text{plant}}/1000)) \quad (1)$$

$$\delta^{13}\text{C}_{\text{C}_3 \text{ plant}}(\text{‰}) = \delta^{13}\text{C}_{\text{air}} - a - (b - a)C_i/C_a \quad (2)$$

$$\delta^{13}\text{C}_{\text{C}_4 \text{ plant}}(\text{‰}) = \delta^{13}\text{C}_{\text{air}} - a - (b_4 + b_3\phi - a)C_i/C_a \quad (3)$$

$$A/g = (C_a - C_i) / 1.6 \quad (4)$$

wherein a is the fractionation by diffusion into the stomata (4.4‰), b and b_3 are the fractionation caused by RuBP carboxylation (reported as ca 27–30‰; 27‰ and 29‰, respectively, are used in this study), C_i is the concentration of CO_2 in the intercellular leaf space, C_a is concentration of CO_2 in the air, b_4 is PEP-C

fractionation (–5.7‰, slightly temperature-dependent), ϕ is the fraction of CO_2 initially fixed in mesophyll by PEP-C that is decarboxylated in the bundle sheath cells but lost by diffusion before it can be fixed by RuBP, A is the assimilation rate, g is the leaf stomatal conductance to water vapor transfer, and 1.6 is the ratio of diffusivities of water vapor and CO_2 in air. Leakiness (ϕ) values range from 0.1 to 0.6, with no recorded values greater than 0.6 (Sandquist and Ehleringer 1995). For species subtypes, ϕ tends to be greater in dicots than among other C_4 subtypes (Farquhar 1983). In this study we used ϕ of 0.6 for all calculations involving C_4 species because in many cases lower ϕ values produced numerous unreasonable results such as $C_i/C_a > 1$ and negative A/g .

Third-order polynomial regressions do not have a mechanistic basis, but they were deemed flexible enough to identify trends in isotopic time series for this analysis and were especially useful to capture trends despite the scatter. These polynomials were sufficiently flexible to reveal isotopic changes in the last 50 years when exponential changes in atmospheric CO_2 and $\delta^{13}\text{C}_{\text{air}}$ have been most pronounced. Linear regressions of $\delta^{13}\text{C}$ with latitude, longitude, and altitude of each herbarium sample were employed to identify any geographical influences on each species.

RESULTS

Only 2 significant correlations of $\delta^{13}\text{C}$ with latitude, longitude, or elevation emerged, both at $P < 0.05$ with *J. scopulorum* (not shown). The 1st was a positive relationship of $\delta^{13}\text{C}$ with elevation ($r = 0.40$; regression slope = 0.0023‰ m^{-1}), and the 2nd was an inverse relationship with longitude ($r = -0.43$; regression slope = $-0.034\text{‰ degree longitude}^{-1}$). The relationship with longitude may be random, although the *J. scopulorum* sites generally are not at constant latitude but progressively lower latitudes moving eastward. Such a NW–SE alignment could imprint a signal of percent summer monsoon precipitation (versus annual total precipitation), which increases in the same direction. However, $\delta^{13}\text{C}$ is increasing toward the southeast, opposite of what might be expected if summer precipitation is increasing in that direction. The occurrence of depleted values at lower elevations

may result from a riparian association rather than from any overarching environmental gradients usually resulting in warmer, drier microclimate at progressively lower elevations. The distribution of $\delta^{13}\text{C}$ with elevation was strongly bimodal, with widely scattered values (range of -22‰ to -27.5‰) above 1700 m and depleted values (-24.5‰ to -27.5‰) below 1700 m. The most likely explanation is that below 1700 m *J. scopulorum* is restricted to riparian settings such as Oak Creek near Sedona, Arizona; trees in these settings were essentially being watered by permanent streams and would not reflect water stresses typical at lower elevations. Fortunately, sample elevations were distributed randomly throughout the *J. scopulorum* $\delta^{13}\text{C}$ chronology and would therefore be unlikely to force any trend in the chronology. Furthermore, in a separate study also on the Colorado Plateau, we measured $\delta^{13}\text{C}$ variations with elevation in modern populations of several species (including *P. edulis*, *E. viridis*, *A. confertifolia*, *A. canescens*). We found $\delta^{13}\text{C}$ variations with elevation to be largely nonsystematic (Van de Water 1999).

Figure 3 contains the leaf whole-tissue $\delta^{13}\text{C}$ chronologies for each species converted from holocellulose values. $\delta^{13}\text{C}$ values of *P. edulis* were constant through the time period, *P. flexilis* and to some extent *J. scopulorum* showed downward trends, and *A. confertifolia*, *A. canescens*, *Q. turbinella*, and *E. viridis* showed particularly pronounced $\delta^{13}\text{C}$ decreases after ca 1950. Discrimination (Fig. 4) increased markedly for *A. canescens* and *P. flexilis*. *Pinus edulis* exhibited clearly decreasing discrimination while the other species generally did not show a consistent long-term trend, although *A. confertifolia* and *E. viridis* exhibited an upturn after 1950 while discrimination of *J. scopulorum* declined. For *A/g*, *P. edulis* and *Q. turbinella* showed long-term increases, whereas *A. canescens* declined (Fig. 5). The other species showed limited long-term trends, although *P. flexilis* and *J. scopulorum* increased after 1950.

DISCUSSION

Altitude and Latitude Effects

Despite lack of significant correlations with altitude/latitude, there may yet remain altitude and latitude effects embedded in all of our isotopic results. For example, Körner et al. (1991) showed a $\delta^{13}\text{C}$ gradient of -0.036‰

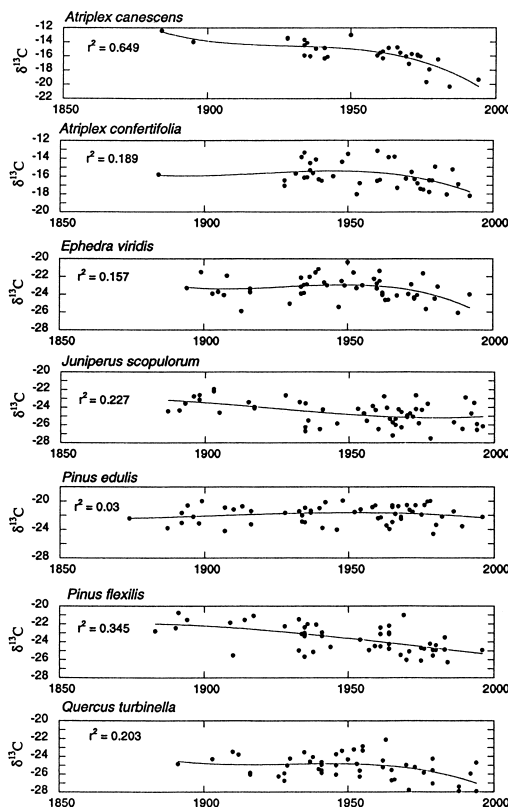


Fig. 3. Chronologies of herbarium leaf whole-tissue $\delta^{13}\text{C}$ for each of 7 species.

per degree of latitude for perennial herbaceous species growing across a span of 70° from the tropics to the poles. If this gradient is applied to the herbarium data in this study, which span at most 4° latitude, the latitude effect alone would make the most northerly samples only 0.14‰ more negative than the most southerly samples. Since this is well within our analytical error, any latitudinal influence should be negligible.

The effect of altitude on plant $\delta^{13}\text{C}$ is not fully understood and has been variously ascribed to temperature and partial pressures of CO_2 and O_2 ($p\text{CO}_2$ and $p\text{O}_2$; Körner and Diemer 1987, Körner et al. 1988, 1991, Morecroft and Woodward 1990, Kelly and Woodward 1995). Körner et al. (1988) found a $\delta^{13}\text{C}$ gradient of $+1.2\text{‰ km}^{-1}$ altitude irrespective of life form (trees, shrubs, forbs). This may be a consequence of lower C_i/C_a ratios at higher altitude (Körner and Diemer 1987, Körner et al. 1988). The mechanism suggested for the

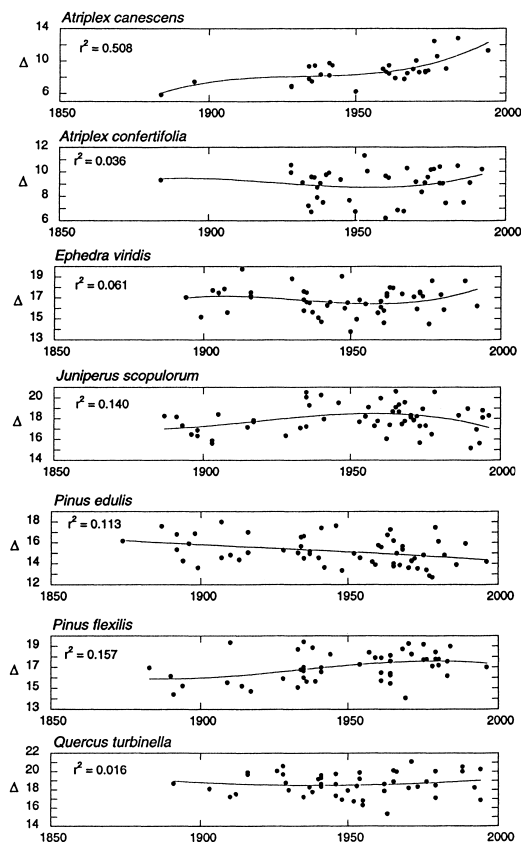


Fig. 4. Chronologies of herbarium leaf whole-tissue discrimination (Δ) for each of 7 species.

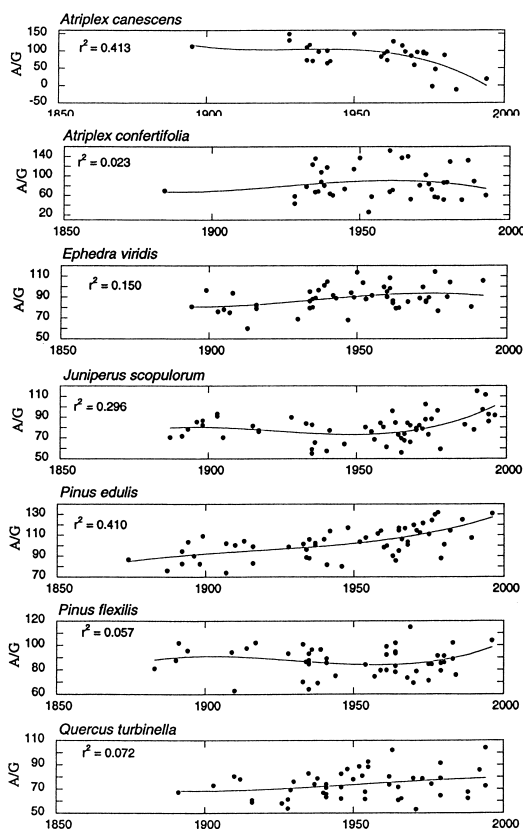


Fig. 5. Chronologies of herbarium leaf whole-tissue A/g (intrinsic water-use efficiency) for each of 7 species. These patterns would be identical to C_a - C_i plots.

decrease in C_i/C_a was higher carboxylation efficiency at higher altitudes. In contrast, Friend et al. (1989) determined that $\delta^{13}\text{C}$ either decreased or did not change at all with increasing altitude. Morecroft and Woodward (1990) found a similar relationship but concluded that, averaged over the globe, plants may show increasing $\delta^{13}\text{C}$ values with altitude although locally the slope could be negative, perhaps influenced by environmental factors such as soil water supply and water vapor pressure deficits. Kelly and Woodward (1995) reanalyzed data from Körner et al. (1988) and found that $\delta^{13}\text{C}$ actually does vary with life form, with more negative $\delta^{13}\text{C}$ values in taller plants. Kelly and Woodward (1995) concluded that differences in $p\text{CO}_2$ and $p\text{O}_2$ are sufficient to explain observed differences in carbon isotope composition. Vitousek et al. (1990), however, suggested that increasing leaf diffusion resis-

tance at higher elevations could cause the higher $\delta^{13}\text{C}$ values. Van de Water (1999) analyzed $\delta^{13}\text{C}$ of several taxa along 2 mountain gradients (1200–2600 m) in the southwestern USA. He found that most taxa exhibited either a slight decrease or no significant change in $\delta^{13}\text{C}$ with altitude. The depletion with altitude, compared to data sets elsewhere in the world, may be because isotopic discrimination decreases and A/g increases with water stress at more arid, lower elevations.

Within a given species, herbarium samples from altitudes 1000 m apart were not uncommon, and in a few cases up to 1500 m. If a gradient of $+1.2\text{‰ km}^{-1}$ altitude is applicable to this study, then elevation could have some measurable influence on $\delta^{13}\text{C}$ results. We did not apply altitude corrections, however, because (1) for all species, elevations were randomly distributed throughout the range of

ages of the herbarium samples; (2) there were no significant correlations of $\delta^{13}\text{C}$ of herbarium specimens with elevation (except *J. scopulorum*); (3) other field evidence indicates either no trend or decreasing $\delta^{13}\text{C}_{\text{leaf}}$ with altitude in the southwestern USA (Leavitt and Long 1983, Lajtha and Getz 1993, Van de Water 1999); and (4) there are large uncertainties in size and magnitude of any universal altitude effect.

C_4 Plants and Atmospheric $\delta^{13}\text{C}$

The case has been made (Francey 1986, Marino and McElroy 1991, Marino et al. 1992) that analysis of C_4 plants would permit exact reconstruction of past $\delta^{13}\text{C}_{\text{air}}$ when $\phi = 0.37$ because $\delta^{13}\text{C}_{\text{plant}}$ would be independent of C_i/C_a and discrimination would be constant (4.4‰); thus, $\delta^{13}\text{C}_{\text{plant}}$ would only be a function of $\delta^{13}\text{C}_{\text{air}}$. Small (up to 20%) deviations from $\phi = 0.37$ would produce fairly accurate reconstructions of $\delta^{13}\text{C}_{\text{air}}$, even if C_i/C_a was poorly known. Despite the scatter, the mean *Atriplex* herbarium trends generally follow the trend of atmospheric $\delta^{13}\text{C}$ changes, except for the pronounced negative departure of *A. canescens* after 1960. Both species, however, exhibit considerable isotopic variability, with a range of 3–4‰ among values within any given time interval. Thus, in the worst case, the value from an individual plant would be ca 2‰ from the average. If such a value had been used as a proxy for $\delta^{13}\text{C}_{\text{air}}$, then a 2‰ error in inferred $\delta^{13}\text{C}_{\text{air}}$ would translate to a ca 20% error in A/g for a C_3 plant. Clearly, multiple sampling and averaging of herbarium specimens of the same age or, by extension, packrat midden samples, could substantially reduce this error. The $\delta^{13}\text{C}_{\text{air}} - \delta^{13}\text{C}_{\text{plant}}$ offset is ca 8.3‰ (not shown). This 8.3‰ offset is much larger than ca 4.4‰ expected if $\phi = 0.37$, suggesting $\delta^{13}\text{C}_{\text{plant}}$ values of these specimens are not independent of C_i/C_a .

The scatter in the $\delta^{13}\text{C}$ data for these 2 C_4 plants may be related to factors that influence ϕ and/or C_i/C_a . For example, Buchmann et al. (1996) found that variable light levels and water availability influenced discrimination of C_4 grasses in controlled-growth experiments, which they attributed to changes in ϕ when assuming a constant C_i/C_a . Sandquist and Ehleringer (1995) studied *A. confertifolia* along a salinity gradient and noted that salinity may

influence ϕ by disrupting membrane properties or the “coordination” of C_3 and C_4 cycles in the mesophyll and bundle sheath cells (Peisker and Henderson 1992). With increasing salinity, leakiness (ϕ) increased and discrimination increased as much as 2‰, perhaps related to changes in bundle sheath permeability to CO_2 and/or biochemical activity of the enzymes rubisco and PEP-carboxylase. In contrast, Peisker and Henderson (1992) found that C_4 plants became isotopically heavier as salinity increased, inferring that stomata close at high salt concentrations with attendant decrease in C_i/C_a . There is no relevant information on specific salinity, light, or moisture conditions associated with individual herbarium specimens, and thus no corrections can be made for these factors. This lack of local plant micro-environmental information is an inherent drawback of these herbarium studies.

A leakage factor of 0.6 was arbitrarily used to calculate ecophysiological parameters such as A/g. Had a more conventional leakage factor been assumed, such as the 0.37 used by Marino et al. (1992) for *A. confertifolia*, then many unrealistic values would have resulted (e.g., negative A/g). Even with this high leakage factor, a few of the ecophysiological parameters calculated for herbarium *A. confertifolia* are unrealistic (see web spreadsheet). Additional uncertainty arises because the factor we used to convert the original cellulose $\delta^{13}\text{C}$ values to whole-tissue $\delta^{13}\text{C}$ for set-point calculations has an estimated error of about $\pm 0.5\%$, which might have been avoided if the whole tissue had been analyzed directly. However, even if this had been done, there would remain uncertainties about movement of mobile organic compounds in and out of the leaf that were not representative of the leaf photosynthates at the time of manufacture. Also, the PEP-C fractionation term b_4 has a slight temperature dependence (Sandquist and Ehleringer 1995) that could also influence the results.

In view of the unusually high ϕ assumed in order to produce generally realistic ecophysiological parameters, the greatest utility of these inferred parameters may be in their patterns and trends rather than their absolute values. Additionally, the *Atriplex* species have among the most negative $\delta^{13}\text{C}$ values of C_4 plants, probably attributable to their general leakiness (Farquhar 1983).

Although both *Atriplex* species show declining $\delta^{13}\text{C}$, particularly pronounced after 1940–1960, the *A. canescens* data points lie much closer to their fitted 3rd-order polynomial. The steep negative slope of *A. canescens* is much greater than the actual change in $\delta^{13}\text{C}_{\text{air}}$ of ca 1.5‰ over this time period. The *A. confertifolia* $\delta^{13}\text{C}$ slope more closely approximates the actual change in $\delta^{13}\text{C}_{\text{air}}$, but the scatter about the mean is much higher. Additionally, ecophysiological parameters such as A/g show little change for *A. confertifolia* but large changes for *A. canescens*. Although the certainty of the trends of the calculated ecophysiological parameters is limited by assumptions in equations 1–4 already discussed (e.g., the whole-tissue $\delta^{13}\text{C}$ vs. cellulose $\delta^{13}\text{C}$ correction factor), we are comparing trends of what are our best estimates.

C₃ Plants

C₃ plants in this study represented 4 gymnosperms (*P. edulis*, *P. flexilis*, *J. scopulorum*, and *E. viridis*) and 1 angiosperm (*Q. turbinella*). Mean $\delta^{13}\text{C}$ values for each species show *P. edulis* as isotopically heaviest (mean = -21.84‰ , $s = 1.26\text{‰}$) and *Q. turbinella* lightest (-25.17‰ , 1.34‰). *Juniperus scopulorum* was the lightest gymnosperm (-24.67‰ , 1.36‰), yet only 0.56‰ heavier than *Q. turbinella*. *Pinus flexilis* and *E. viridis* were intermediate, with mean $\delta^{13}\text{C}$ values of -23.68‰ ($s = 1.50\text{‰}$) and -23.32‰ (1.26‰), respectively. Previous comparisons of wood cellulose $\delta^{13}\text{C}$ have suggested gymnosperms are from ca 1‰ (Leavitt and Newberry 1992) to 3‰ (Stuiver and Braziunas 1987) ^{13}C -enriched compared to angiosperms, and *Q. turbinella* is indeed more ^{13}C -depleted than all the gymnosperms except *P. flexilis*.

The atmospheric $\delta^{13}\text{C}$ chronology shows a decrease as atmospheric CO_2 increases (Fig. 1), and most of the C₃ species also show various $\delta^{13}\text{C}$ declines, the most pronounced exception being *P. edulis* for which $\delta^{13}\text{C}$ remains constant. The constant *P. edulis* $\delta^{13}\text{C}$ is in sharp contrast to the *P. edulis* tree-ring results from this region by Leavitt and Long (1988) that show a downward $\delta^{13}\text{C}$ trend. This discrepancy may be a consequence of (1) tree rings more effectively integrating the influence of numerous crown microenvironments, (2) the selection of trees from more open woodlands

in the tree-ring study, and (3) different (and unknown) average microenvironmental conditions of the trees sampled for herbarium specimens.

Herbarium leaves of *P. flexilis* are the most spatially restricted of the 7 species used in this study, with all but 2 samples coming from the San Francisco Peaks near Flagstaff, Arizona. Additionally, because 40 of 50 samples were from a narrow 2600- to 3000-m elevational range, environmental conditions should have been uniform for this suite of samples. *Pinus flexilis* does show the clearest $\delta^{13}\text{C}$ declining trend, although there remains considerable scatter of up to ca 5‰ among samples of similar age. Furthermore, the *P. flexilis* $\delta^{13}\text{C}$ decline was 2–3 times greater than the ca 1.5‰ decrease in $\delta^{13}\text{C}_{\text{air}}$. Long- and short-term climate variability in north central Arizona may account for some of these isotopic characteristics.

As expected, greater scatter than that observed in the *P. flexilis* $\delta^{13}\text{C}$ chronology was found in the other 4 C₃ species whose provenance is more extensive. In addition to long- and short-term regional climate effects, individual microsite variability may exist, such as riparian associations of low-elevation *J. scopulorum* trees. Intra-canopy and inter-tree leaf $\delta^{13}\text{C}$ variability in the amount of 1–2‰ has been previously observed in *P. edulis* and juniper (*Juniperus* spp.; Leavitt and Long 1983, 1986). The leaf $\delta^{13}\text{C}$ variability with height in the canopy may be an effect of variable light and respired CO_2 concentrations at different heights below the canopy top (Medina and Minchin 1980, Garten and Taylor 1992).

There is the possibility that climate variability influences some of the chronologies in Figures 3–5. For example, in Figure 3 the apparent plateau of elevated $\delta^{13}\text{C}$ values for *A. confertifolia* and *E. viridis* coincides with mid-century, below-average precipitation in this region and what was possibly the worst drought in the Southwest during the past several hundred years (Meko et al. 1993, Swetnam and Betancourt 1998). In addition to the longer-term climate influences, short-term episodes such as El Niño may contribute to year-to-year variation, which might be lost if only the best-fit smoothed polynomial curves are examined.

Although an original goal of sample acquisition, samples could not always be found every 2 or 3 years through this century-long time

frame. The earlier part of this century has fewer samples in the chronology of each species, thereby providing unequal weighting of the best-fit polynomial curves. The reliability of the early part of many of the chronologies will therefore generally not be as high as the more recent portion of the curves.

Discrimination should increase if the CO_2 increase promotes elevated C_i/C_a ratios. Only *P. flexilis* exhibits increasing discrimination, while *E. viridis*, *J. scopulorum*, and *Q. turbinella* have no consistent long-term trends, and *P. edulis* discrimination actually decreases during the past ca 100 years. Discrimination can also be particularly susceptible to water availability such that drought conditions can reduce discrimination (Leavitt and Long 1988) as stomata tend to stay closed longer to reduce water loss. In addition to CO_2 partial pressures and water stress, other environmental factors such as irradiance, relative humidity, vapor pressure deficit, temperature, and nutrient content may influence C_i/C_a and therefore discrimination (Farquhar et al. 1982, Tieszen 1991). These environmental factors are typically related to rates of stomatal conductance and the chloroplast demand for CO_2 (rates of assimilation) that contribute to C_i/C_a differences (Ehleringer and Cerling 1995).

An anticipated consequence of elevated CO_2 is higher A/g. Woodward (1987) found an overall reduction in stomatal density from 1787 A.D. to the present and concluded that during pre-industrial times, when atmospheric CO_2 levels were only ca 270 ppmv, maintaining CO_2 uptake would have been costly in terms of plant water loss. Reductions in stomatal conductance or leaf area might have helped reduce water losses (Woodward 1993). Polley et al. (1993) demonstrated increases in A/g in growth-chamber experiments in which CO_2 was varied from subambient (180 ppmv) to double (700 ppmv) present CO_2 levels. Among herbarium species, A/g increased in *P. edulis* over the full period of record. For the other species, patterns were less pronounced, but *P. flexilis* and *J. scopulorum* exhibited increasing A/g ($\approx C_a - C_i$) since 1950–1960. A previous study with ancient *P. flexilis* leaves (Van de Water et al. 1994), however, found that both C_i and $C_a - C_i$ increased during deglaciation as atmospheric CO_2 increased ca 80 ppmv. A tree-ring $\delta^{13}\text{C}$ study with other modern conifers by Marshall and Monserud (1996) showed that

$C_a - C_i$ remained constant for Douglas fir, ponderosa pine, and western white pine as both C_i and the C_i/C_a ratio increased with rising CO_2 . The recent work of Feng (1998) for several western conifer species showed most exhibited increasing C_i , but $C_a - C_i$ trends in the 20th century were variable among species. Feng (1999) also found a trend of increasing water-use efficiency in these trees. Thus, a clear, common homeostatic physiological response for A/g does not emerge, even among conifers alone, although influences other than CO_2 changes may vary in the other studies. The leaf studies, however, represent many different trees, whereas the tree-ring studies analyze a few individuals through time.

Comparing overall A/g results for the 5 C_3 species, it is possible to identify differences among gymnosperms and angiosperms. In this study *P. edulis* has the highest average A/g compared to the other C_3 plants. This is consistent with an observed link of high A/g with plants that rely heavily on summer precipitation, a less stable source of water (Flanagan et al. 1992). *Juniperus scopulorum* and *Q. turbinella* have the lowest average A/g; *J. scopulorum* grows in more mesic environments (more moisture at the higher elevations), which may contribute to its lower A/g, and *Q. turbinella*, as an angiosperm, characteristically has lower $\delta^{13}\text{C}$ (and lower A/g by inference) than gymnosperms. In addition, it has been observed that plants with access to groundwater tend to have a lower A/g than plants using a more unstable source of water like summer precipitation in the Southwest (Flanagan et al. 1992).

CONCLUSIONS

There was high isotopic variability in the herbarium leaf samples. Analysis of a single C_4 *Atriplex* plant leaf is inadequate to serve as a proxy for atmospheric $\delta^{13}\text{C}$ at any point in time, but analysis of many leaf samples of the same age will more accurately represent $\delta^{13}\text{C}_{\text{air}}$, especially if more environmental variables are held uniform, i.e., light, salinity, etc. Application of C_4 proxy $\delta^{13}\text{C}_{\text{air}}$ results to prehistoric C_3 plant $\delta^{13}\text{C}$ would greatly benefit calculation of their ecophysiological parameters. The herbarium results suggest *A. confertifolia* better tracks atmospheric $\delta^{13}\text{C}_{\text{air}}$ than does *A. canescens*, although the scatter for *A.*

canescens seems to be lower where the values best track the atmospheric $\delta^{13}\text{C}$ prior to ca 1968 A.D. Among C_3 species, strategies for maximizing photosynthesis and minimizing water loss appear to be species specific. Over the past 100–150 years, only *P. flexilis* and *J. scopulorum* exhibited increasing A/g, while A/g for *E. viridis*, *J. scopulorum*, and *Q. turbinella* remained nearly constant.

Previous herbarium studies often present decadal or multidecadal averages, in some cases averaging across species; e.g., Peñuelas and Azcón-Bieto (1992) displayed only 4 data points for the last 240 years, each point representing a pooling of all the C_3 species analyzed in the study. It may be difficult to make appropriate conclusions when many species are averaged together from various sites. Even where the species can be held constant, inherent variability in herbarium data may make it difficult to detect and explain trends.

Intra-tree and intra-site variability in tree rings is much smaller than the variability observed in these herbarium samples, which may offer an advantage for some studies. An inherent problem with herbarium specimens is that they represent a single plant for which the year of collection is known exactly, but the exact year in which the leaves were produced is generally not. As a result, it is unlikely that it represents variability across populations. In fossil deposits, like packrat middens, a population of leaves from a single species probably represents several individual plants across decades (Van de Water et al. 1994). Midden leaves probably integrate spatially and temporally, whereas each herbarium sheet represents a single individual. It is clear that herbarium studies may provide some relevant information on gas-exchange properties in plants, such as dramatic increase in A/g of *P. edulis*. However, caution is required in interpreting previous and future isotopic measurements and physiological calculations made with herbarium specimens.

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SAMPLING EFFORT AND VEGETATIVE COVER ESTIMATES IN SAGEBRUSH STEPPE

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ABSTRACT.—The goal of this study was to identify relationships between sampling effort, using a point frame, and the precision of estimates of vegetative cover in sagebrush steppe. Data for 208 point-frame samples were randomly drawn and 95% confidence intervals were identified for varying sample sizes of individual species and species groups. Confidence interval widths decreased rapidly as sample sizes increased from 1 to 50, and more slowly as sample sizes were increased further. For the more abundant species, sample sizes of fewer than 50 frames were sufficient to reduce the 95% confidence interval to less than one-half of average cover. For species with average cover less than 5%, the sample size required to achieve the same relative confidence was much larger. Analyses were repeated to compare point frames with 36 versus 50 sample points per frame. Using a point frame with 50 sample points decreased the number of frames required to achieve the same level of confidence; however, the reduction in sample size was less than the 28% reduction in sample points per frame. Because of the time required to establish transects and position the point frame, it may still be worth sampling more points per frame.

Key words: sagebrush steppe, point frame, vegetative cover, sampling effort.

Methods commonly used to estimate vegetative cover include line interception (Canfield 1941, Lucas and Seber 1977, DeVries 1979), visual estimation of cover classes (Daubenmire 1959), and point interception (Floyd and Anderson 1987). The method that is most precise, giving the most accurate measure of cover, and the method that is most efficient, providing a given level of precision with the least effort, probably vary with vegetation type and with goals of the study. Hanley (1978) compared line interception and visual estimation within quadrats in big sagebrush communities. He concluded that line interception gave higher precision but that quadrat estimation could be a faster method for less precise cover estimates. Floyd and Anderson (1987) compared line interception, cover-class estimation, and point interception in sagebrush steppe vegetation. They concluded that line and point interception were more precise than cover-class estimation for sampling species other than the dominant shrubs and that point interception was the more efficient of those 2 sampling methods because it required less effort to achieve the same degree of precision.

The goal of this study was to identify sample sizes required to characterize, with various levels of precision, vegetation in a sage-steppe

community using a point-interception technique. I performed Monte Carlo simulations using data from 4 transects in each of 4 plots to calculate the range in cover estimates and 95% confidence intervals for varying numbers of point frames. I also compared 2 types of point frame samples, one that used 50 sample points per frame and another that used 36. Results presented here can help in designing an efficient sampling protocol that will result in a desired level of confidence.

STUDY SITE

This study was conducted at the Idaho State University (ISU) ecological research area located southeast of the ISU campus on Barton Road, Pocatello, Bannock County, Idaho. This roughly 26-ha area is situated at 1450 m elevation on the east side of the Portneuf River valley, 25 km south of the Snake River plain. The climate is semiarid, with cold winters, moist springs, and warm, dry summers. Annual precipitation at the Pocatello Airport (17 km from the site, 1359 m elevation) averages 30.8 cm, with July–October having the lowest average monthly total precipitation. Because of the local topography, average precipitation at the study site is probably slightly greater than at

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the Pocatello Airport. Soils at the site are deep, well-drained, calcareous silt loams that are neutral to moderately alkaline near the surface and moderately to strongly alkaline at depths of 20–150 cm (McGrath 1987).

The study area, acquired by ISU in 1995 and designated as an ecological research area in 1996, has not been cultivated but may have been subjected to low levels of grazing by domestic livestock during the latter part of the 20th century, prior to 1990. From about 1990 to 1996, anthropogenic disturbance was limited to occasional horseback riding and hiking, primarily along established paths.

METHODS

Four 20 × 20-m plots were established in April 1996 in a 1.4-ha area that was fenced to minimize disturbance from humans and domestic livestock. Plots were separated by at least 5 m; the greatest distance between 2 plots was about 60 m. Plot locations were chosen to have similar cover of the dominant shrubs and to avoid drainage channels that were 20–60 cm lower than adjacent areas.

Four 12-m-long transects were established within each plot. The ends of each transect, marked with metal stakes approximately 30 cm high, were located 4 m from the east and west sides of each plot. Transects were spaced 4 m apart with 4 m between the outside transects and the north and south sides of each plot.

During the period 13–19 July 1999, I sampled the vegetation, estimating percent cover using a point frame, modified from Floyd and Anderson (1987). The point frame held 2 layers of strings, one 14 cm above the other. Each layer consisted of a 5 × 10 grid of strings spaced 10 cm apart, with 5–6 cm between the outside strings and the inside of the wooden frame. The point frame was placed and leveled at 1-m intervals along each transect, with the long axis of the frame perpendicular to the transect. For the first sample along each transect, a corner of the frame was placed at the beginning of the transect (0 m), and for the last sample along each transect the same corner was placed at the end of the transect (12 m), for a total of 13 frames per transect and 52 frames per plot. At each location I recorded cover of the 50 points that fell below vertical pairs of grid intersections. Shrubs and forbs were recorded only if a leaf or stem fell under a

point. Perennial bunchgrasses were recorded only if the base of the bunchgrass fell under a point. If 2 vascular plant species were present under a point, I recorded both species.

For the purposes of this study, I treated each point frame as a separate sampling unit. To characterize the relationship between cover estimate and sample size (# frames), the frames were drawn in random order, without replacement, and total and average cover were calculated after the addition of each frame until all 208 frames were drawn. This process was repeated 1000 times, and 95% confidence intervals (CIs) were estimated by identifying the high and low cover estimates that included 950 of 1000 values for each sample size. This analysis was performed separately for individual vascular plant species, shrubs, perennial grasses, and forbs.

This process was repeated to compare the effectiveness of sampling 50 points per frame with Floyd and Anderson's (1987) point-frame design that used 36 points for each frame. For this analysis a 4 × 9 grid of points was selected from the same relative position in each frame and the randomization procedure was performed in the same manner as the full 50-point samples.

Various criteria can be used to assess whether a sample is sufficient to adequately characterize vegetative cover. The approach I have used is to consider the width of the 95% confidence interval relative to the mean. The required level of precision may vary depending on the specific goals of a given study. Here I present results in terms of sample sizes required to achieve a 95% confidence interval that is equal to either the mean or one-half of the mean.

RESULTS

Shrub cover ranged from 25.1% to 35.0% on individual plots (mean of 52 frames on each plot) and averaged 30.6% over the 4 plots (mean of 4 plot means). Perennial grass cover averaged 22.0% (19.7–26.7% on individual plots), and forb cover averaged 2.1% (1.1–3.7% on individual plots). The dominant shrub species on all plots was *Artemisia tridentata* spp. *tridentata*, which was responsible for more than 95% of the shrub cover. Cover of *A. tridentata* averaged 29.3% on the 4 plots; individual plot averages ranged from 24.5% to 33.8%.

The most abundant perennial grasses were *Elymus lanceolatus* spp. *lanceolatus* (thick-spiked wheatgrass; 16.5% cover), *Stipa comata* (needle-and-thread grass; 3.8% cover), and several species of *Poa*, which are combined here because of uncertainties in identification. *Sitanion hystrix* (bottlebrush squirreltail) was recorded on 2 plots, with cover values of 0.04% and 0.12%. Twelve forb species were recorded on the plots, none of which contributed more than 2% cover on any plot, and none of which averaged more than 0.6% cover. The 2 forb species that had the highest average cover were *Plantago patagonia* (desert plantain; 0.6% cover) and *Phlox hoodii* (0.3% cover). The most abundant annual plant was *Bromus tectorum* (cheatgrass), which contributed an average of 34.3% cover (19.0–50.4% on individual plots).

Sets of 1000 random draws were sufficiently large to give fairly smooth relationships between estimated cover and sample size (Fig. 1). The 4 lines in each figure converge at a sample size of 208 because this was the total sample of frames, and random draws were done without replacement. The range of cover estimates and the width of the 95% CIs decreased rapidly as sample size increased from very small numbers and then decreased more slowly until the number of frames approached 200 (Figs. 1, 2). The number of frames required for the 95% CI to be equal to average cover varied considerably among species and was much larger for species with lower average cover. For more abundant species or groups

(e.g., shrubs, perennial grasses, *Artemisia tridentata*, *Elymus lanceolatus*, *Bromus tectorum*), sample sizes of fewer than 50 frames were adequate to achieve a 95% CI equal to one-half of the species' average cover. For rarer species or groups (e.g., forbs), the same sample size was not sufficient to reduce the width of the 95% CI to the average cover of the group or species.

Figure 3 shows relationships between sample sizes required to achieve a 95% CI equal to either mean cover or one-half of the mean. In both cases the relationship can be fitted with a power function ($Y = aX^{-b}$) that is statistically significant.

When the number of points per frame was reduced from 50 to 36, the number of frames required to achieve a given width of CI was in nearly all cases increased. The absolute increase in number of frames was small for more abundant species or groups (e.g., from 43 to 45 for shrubs, from 20 to 24 for perennial grasses), but was larger for less abundant species (e.g., 147 to 155 for forbs).

DISCUSSION

Floyd and Anderson (1987) compared 3 methods for estimating plant cover in a shrub steppe community and reported that point interception was more efficient than line interception or cover-class estimation for obtaining cover estimates for most species in the plant community. In this study I examined the effectiveness of point estimation more closely, asking

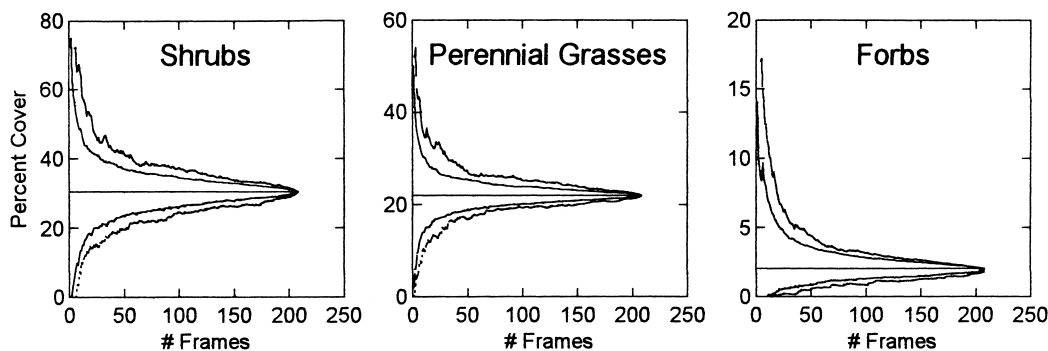


Fig. 1. Relationships between estimated cover and sample size for 3 species groups. For each graph, the horizontal line shows average cover for all 208 frames, and the outside curved lines represent minimum and maximum cover estimates for each sample size. The area between the 2 inner curved lines contains 95% of the cover estimates. The y -axis, which is scaled differently for each graph, was truncated so that maximum values for very small numbers of frames are not shown.

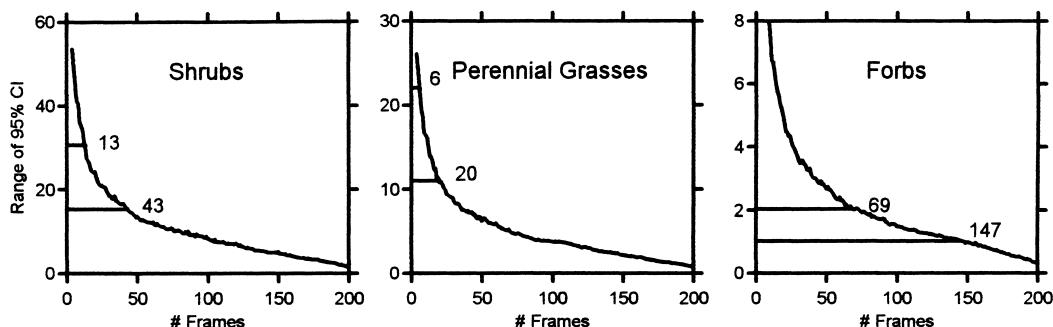


Fig. 2. Relationships between the width of the 95% confidence interval and the number of sample frames for 3 species groups. The upper horizontal line shows average cover; the number at the intersection of that line and the curved line is the number of frames required to achieve a 95% CI equal to that value. The number associated with the lower horizontal line is the number of frames required to achieve a 95% CI equal to one-half of average cover.

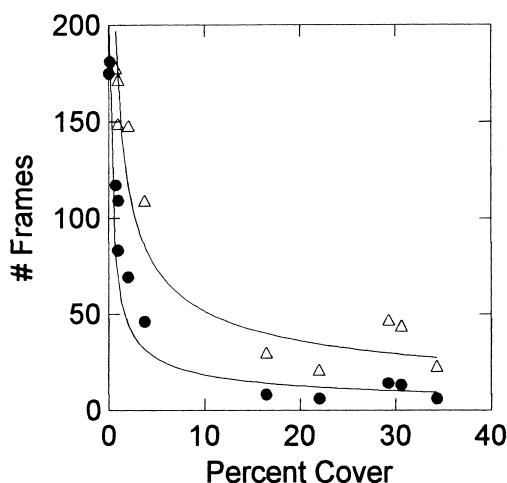


Fig. 3. Number of sample frames required to achieve a 95% CI equal to average percent cover (open triangles) or equal to one-half of average percent cover (closed circles). Each point in this figure represents 1 species or 1 group of species (e.g., shrubs). Curves drawn through each set of points are power functions of the form $Y = aX^{-b}$; both relationships are statistically significant ($P < 0.01$).

how large a sample size was needed to achieve a particular confidence interval and how the required sample size was influenced by the number of points per sample frame.

The wide range of cover estimates obtained with sample sizes less than 40 reflects the spatial heterogeneity that is typical of shrub steppe communities. At a gross scale these communities consist of shrubs and intershrub spaces, and cover estimates vary widely until the number of samples is large enough to include

this spatial variation. This was true even for the most abundant species and species groups. At sample sizes of 50–150, the range of cover estimates decreased much more slowly, indicating a smaller increase in precision with increased sampling effort. The precise nature of the relationship between sample size and precision at the largest sample sizes is suspect because samples were randomly drawn without replacement, and thus the largest sample sizes mostly comprised the same set of samples.

As average cover declined below 4%, the number of sample frames required to achieve a 95% CI equal to the average increased dramatically (Fig. 3). Setting a goal of reducing the 95% CI to the average is likely to be unrealistic for these species. Instead, reducing the width of the 95% CI to an arbitrary value (e.g., 2%) may be more realistic. Even for rare species this usually could be achieved with sample sizes less than 100 (74 for forbs).

Reducing the number of points per sample frame from 50 to 36, the number used by Floyd and Anderson, increased the required number of frames to achieve a given 95% CI. The increase in frames, however, was less than the 28% decrease in points per frame. This is because the size of the sample frame (0.5×1 m) is small relative to the spatial variation in vegetation; adding points within a frame will provide a better estimate of local cover but will be less effective at sampling the community as a whole. In terms of sampling efficiency, however, there is still likely to be an advantage in sampling more points per frame. Much of the time associated with this sampling technique

is devoted to establishing transects and locating and leveling the sample frame. Sampling 14 additional points per frame requires a relatively small increase in sampling effort.

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ORIENTATION AND VERTICAL DISTRIBUTION OF RED-NAPED SAPSUCKER (*SPHYRAPICUS NUCHALIS*) NEST CAVITIES

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ABSTRACT.—It has been hypothesized (1) that the compass direction in which woodpeckers excavate breeding cavities depends on nest thermoregulatory needs, and (2) that when multiple cavities are placed in the same tree across years, each new cavity is placed above previous cavities. We tested these hypotheses for Red-naped Sapsuckers (*Sphyrapicus nuchalis*) in central Nevada and found some evidence that cavities are oriented for thermoregulatory advantage, but we rejected the hypothesis that active cavities are always the highest.

Key words: woodpecker, habitat use, microhabitat use, behavior.

Primary cavity nesters, such as woodpeckers, select where on a tree to excavate a cavity. Decisions might be driven by predator avoidance (Nilsson et al. 1991), by efforts to manipulate nest microclimate (Inouye et al. 1981, Korol and Hutto 1984), in response to physical characteristics of the nest tree, such as the presence of heart rot fungus or bole slope (Conner 1975, Conner et al. 1976), or to avoid prevailing weather conditions (Conner 1975). One choice, vertical placement (i.e., how high from ground, above or below existing cavities), has been shown to be nonrandom in some woodpeckers (e.g., McAuliffe and Hendricks 1988). Avian studies also report nonrandom nest orientation for a variety of species, apparently intended for thermoregulatory advantage (Austin 1974, Högstedt 1978, Martin and Roper 1988) or to avoid prevailing winds or rains, which also could be thermoregulatory (Ferguson and Siegfried 1989, Haggerty 1995). Patterns of cavity orientation have been examined in woodpeckers, with some species showing distinct patterns while others do not. For example, Locke and Conner (1983) found a westward cavity orientation in Red-cockaded Woodpeckers (*Picoides borealis*), while there are conflicting reports for Gila Woodpeckers (*Melanerpes uropygialis*; no pattern: Kerpez and Smith 1990; pattern: Inouye et al. 1981, Korol and Hutto 1984), and Gutzwiller and Anderson (1987) found no patterns for Red-headed

or Downy Woodpeckers (*M. erythrocephalus* and *P. pubescens*, respectively).

Here we present results from a study of cavity placement by Red-naped Sapsuckers (*Sphyrapicus nuchalis*) nesting in central Nevada. This species, a riparian specialist in this habitat, is thought to be a keystone species (Daily et al. 1993). Red-naped Sapsuckers in Colorado are reported to excavate progressively higher nest cavities in the same tree year after year (Daily 1993). Published studies examining the orientation of sapsucker nest cavities report nonrandom patterns, with a southern bias (Inouye 1976) or a bimodal distribution (Red-naped Sapsucker, east and southwest [Dobkin et al. 1995]; Yellow-bellied Sapsuckers [*S. varius*], southeast and west [Lawrence 1967]). It is not known whether these orientations are for thermoregulatory advantage. We tested the hypotheses that Red-naped Sapsucker cavity orientation is nonrandom and consistent with thermoregulatory needs in this desert-riparian community, and that when multiple cavities are placed in the same tree, the active cavity is above other cavities.

METHODS

We located Red-naped Sapsucker nests in multiple stream basins of the Toiyabe Range of central Nevada (Lander and Nye counties), USA (39°N, 117°W). Study sites were located

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in narrow strips of riparian habitat composed primarily of aspen or cottonwood (*Populus* spp.) intermingled with willow (*Salix* spp.) and western birch (*Betula occidentalis*), and surrounded by either pinyon-juniper (*Pinus monophylla*–*Juniperus* spp.) woodlands or sagebrush (*Artemisia* spp.). Further descriptions of the area can be found in Linsdale (1938).

During May–July 1994 and 1995, we systematically searched riparian habitat with mature aspens for signs of sapsucker activity. Early in the season we located nests by looking for fresh woodpecker excavations and by following adult birds. Later in the season, nests were located by listening for food-begging calls of chicks in the cavity and by following adults that were carrying food. Inactive cavities were recorded only when we thought they were made by sapsuckers, a designation made based on size and shape of the cavity entrance (Fleury 2000). At the termination of breeding activities, we measured tree height, number and height of cavities, relative position of active cavities in trees with multiple cavities, nest entrance orientation, whether or not the cavity was used during the current breeding season, and whether or not the nest tree was alive. Tree heights were measured using a clinometer. Heights of cavities below 7 m were measured with a tape measure; cavity heights above 7 m were measured using a clinometer. Nest entrance orientation was measured with a compass and placed into 1 of 16 classes (N, NNE, NE, ENE, E, etc.).

Using Arc/Info Grid Module, we ran the Arc Macro Language program Solarflux (Herrick et al. 1993) using a 30-m horizontal resolution digital elevation model provided by Rick Connell at the Toiyabe National Forest. The following independent variables were estimated: (1) daily insolation on summer solstice (21 June), which indicated the amount of solar radiation incident at the cavity tree's location for clear skies, and (2) number of hours of direct sunlight expected on summer solstice, which was used to estimate the amount of solar radiation received at the nest cavity. Values for cavity tree locations were obtained by overlaying locations onto the derived insolation grids. Because these methods are indirect, they do not account for the potential of local shading by adjacent trees.

We used a *t* test to compare heights of active nest cavities in trees containing multiple cavi-

ties to heights of nest cavities in trees containing a single cavity. Orientation data were analyzed using a Rayleigh test (Zar 1996), including calculating mean angle and angular deviation. Correlations of orientation data with insolation data and hours of sunlight were done by ignoring the east–west aspect of the orientation (i.e., values range from 0° to 180°, and so cavities facing NE and NW received the same value) and finding the Pearson correlation coefficient between north–south orientation gradient and insolation variables.

RESULTS

We found nests in 9 different stream basins, 7 of which drained to the west of the range, 2 to the east. We made measurements on 38 active nests and 51 inactive nest cavities in trees containing active nests. The number of cavities per nest tree ranged from 1 to 6, with a mean of 2.3 (± 1.4 s). Nest trees ranged in height from 1.5 m (broken top) to 20.0 m (mean = 11.7 ± 4.4 m). Most nest trees (60%; 23/38) contained more than one cavity, although only a single active nest. The active cavity was in the highest position in 43% (10/23) of the trees containing more than one cavity, and in the lowest position in 43% (10/23; Table 1). Mean height of active cavities in trees containing more than one cavity (4.4 ± 2.2 m, $N = 23$) was not significantly different from the height of active cavities in trees containing only one cavity (3.5 ± 3.5 m, $N = 15$; $t = 0.86$, $df = 21.0$, corrected for unequal variance, $P = 0.40$).

We found nest cavity entrances facing all compass directions. When combined, active and inactive nests ($N = 89$) tended to be oriented in southern or eastern directions, although there was high variability; mean angle

Table 1. Relative position of the active nest cavity in trees with multiple cavities.

Relative position	Number of cavities in trees				
	2	3	4	5	6
Top	2	6	1	1	—
2nd	5	1	—	—	—
3rd		2	2	—	—
4th			1	—	—
5th				—	—
6th					2

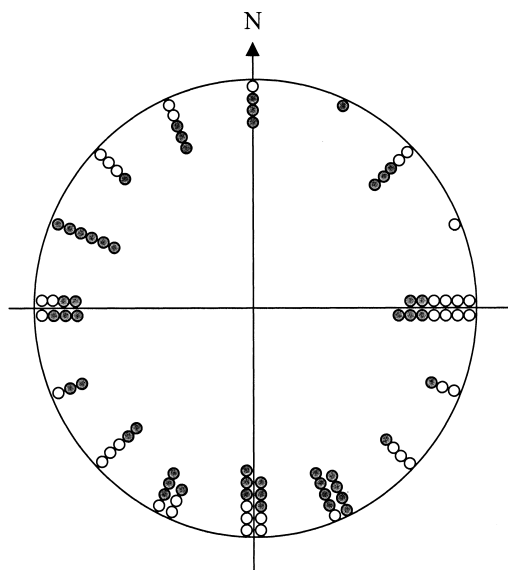


Fig. 1. Circular distribution of nest entrance holes; open dots are active cavities and closed dots are inactive cavities.

= 180° , angular deviation = 73° ($Z = 2.82$, $P < 0.05$; Fig. 1). It is possible that other woodpecker species excavated some of the inactive nest cavities (e.g., Hairy Woodpeckers [*Picoides villosus*] and Downy Woodpeckers are present in low densities in the study area). Thus, we repeated the analysis using only active nest cavities ($N = 38$). Again, there was a predominantly southern orientation with high variability (mean angle = 148° , angular deviation = 71°), but the pattern was not statistically significant ($Z = 1.97$, $P > 0.1$; Fig. 1).

GIS data were available only for the 32 nests located during the 1995 breeding season. A significant negative correlation was found between the north–south orientation gradient and the number of hours of direct sunlight received at the nest site on the summer solstice (Pearson product-moment correlation, $r = -0.41$, $P = 0.02$; Fig. 2). This result was strongly influenced by 3 nests at 10 and 11 hours; if they are removed, the result loses significance ($P > 0.1$). We did not find a significant relationship between the orientation gradient and insolation. Our data suggest a threshold in hours of sunlight and orientation (represented by a vertical line in Fig. 2). Although not statistically significant, we found that nest cavities receiving fewer than 12 hours of sunlight

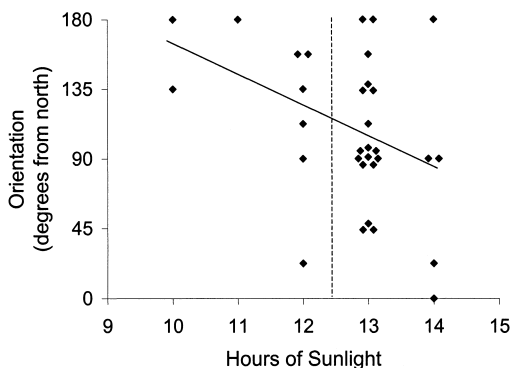


Fig. 2. Relationship between nest orientation and hours of sunlight. East–west directions were ignored, and so due east and west are 90° . Regression line is significant, $r = -0.4$, $P = 0.02$. Vertical line represents a proposed threshold where cavities receiving less than the marked amount of solar radiation (left) are oriented toward the sun, while those receiving more (right) are not; see text for discussion.

per day were oriented southward, while nest cavities receiving 12 or more hours of sunlight per day were oriented in any direction ($t = 1.6$, $P = 0.11$).

DISCUSSION

Active Red-naped Sapsucker nests in our study were located in the highest position in only 43% of the trees with multiple cavities, with the same proportion being the bottom-most cavity. Also, we found no significant difference in the heights of active nest cavities in trees containing one cavity versus multiple cavities. These patterns differ from those reported by Daily (1993) for this species in Colorado. In trees containing multiple cavities, Daily (1993) found the active cavity in the highest position 86% of the time and never in the lowest position. Daily (1993) also found that active nest cavities in trees containing no other cavities were significantly lower than active nest cavities in trees containing multiple cavities. From these data, Daily hypothesized that Red-naped Sapsuckers excavate progressively higher nest cavities in subsequent nesting in an attempt to minimize predation risk from non-arboreal predators. Our data do not support this hypothesis. Either the pattern Daily found was a sampling artifact or sapsuckers there were responding to selective pressures not present in our study area.

When we include both active and inactive cavities in our analyses, we find a significant southerly orientation for all woodpecker cavities recorded in our study, which is consistent with other studies (Inouye 1976, Dobkin et al. 1995). However, the pattern was not strong, and possibly some of the inactive woodpecker cavities were misclassified as being excavated by Red-naped Sapsuckers. When only active cavities are included in the analysis, the mean orientation is still southerly, but statistically the cavities are oriented randomly. We found a significant correlation between the north-south aspect of orientation and the number of hours of direct sunlight received at the nest site. This is consistent with the hypothesis that nest orientation is influenced by thermoregulatory needs. A tree's trunk is significantly warmer on the side facing the sun (Derby and Gates 1966). Derby and Gates (1966) found that aspen at 3000 m elevation in Colorado showed as much as 12°C difference in trunk temperature between the tree side facing the sun during daylight hours and the side facing away. From the plot of our data, we hypothesize that there is a threshold amount of sunlight that falls on a potential cavity site, below which the cavity tends to be oriented to capture sunlight (southerly) and above which orientation is random. We propose this threshold to be at approximately 12 hours of sunlight on summer solstice. If this pattern is supported by other research, it suggests that cavities in central Nevada placed on trees that receive relatively low amounts of direct sunlight are oriented to maximize exposure to sunlight for heat to maintain the desired microclimatic characteristics of the nest cavity.

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BIRD POPULATIONS IN RIPARIAN AREAS OF SOUTHEASTERN ARIZONA IN 1985–86 AND 1994–95

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Key words: breeding birds, population trends, riparian, Arizona.

Numbers of Nearctic migrant birds are apparently in decline, especially in the eastern United States (e.g., Sauer and Droege 1992, Hagan 1993, Rappole 1995). Declines have also been noted for some western Nearctic migrant species (DeSante and George 1994), although not in all instances (e.g., see review in James and McCulloch 1995). Partially as a result, declines have been questioned by some researchers (e.g., James and McCulloch 1995, Peterjohn et al. 1995), and this issue is difficult to resolve because few studies besides the Breeding Bird Survey (Robbins et al. 1986) have been conducted long-term (Morrison et al. 1996).

In the summers of 1984–1986, Strong and Bock (1990) conducted point counts of birds in riparian stretches in and around the Huachuca Mountains, Arizona, to determine patterns of vegetation use by different species. Western riparian areas support high densities and diversities of migrant breeding birds (Carothers et al. 1974, Knopf 1985, Rosenberg et al. 1991, Skagen et al. 1998), and Strong and Bock's study collected baseline information on abundances of many species of migrants and residents. In the summers of 1994 and 1995, we conducted bird surveys on the same points using the same methods as Strong and Bock to compare the relative abundances and richness of bird species a decade after the initial study, and to bolster the database initiated by them for use in future monitoring studies.

Details on the study areas and sampling methods are in Strong and Bock (1990). In summary, the study area is located in southeastern Arizona, Cochise and Santa Cruz counties

(31°32'N, 110°22'W), primarily in the foothills of the Huachuca Mountains. Birds were counted in riparian vegetation along the Babocomari River on the Babocomari Ranch (1387–1418 m elevation), which has an upland containing moderately grazed grassland with scattered oaks (*Quercus* spp.), cottonwood (*Populus fremontii*) gallery forests, walnuts (*Juglans major*), and willows (*Salix* spp.) along the river. At slightly higher elevations (1418–1494 m), we sampled in riparian areas on ungrazed land on the National Audubon Society Appleton-Whittell Research Ranch (ungrazed since 1967 [Bahre 1977]), the Nature Conservancy Canelo Hills Preserve, and the Coronado National Forest. These areas are covered in the upland by grasslands with scattered oaks and have several different riparian tree species, including Arizona walnut, velvet ash (*Fraxinus velutina*), cottonwood, desert willow (*Chilopsis linearis*), Arizona sycamore (*Platanus wrightii*), and willow. Counts also were done on the Fort Huachuca Military Reservation where grazing did not occur. The riparian sampling area in the foothills of the fort (1448–1524 m) is surrounded in the uplands by grass and mesquite (*Prosopis* spp.), and riparian plants include desert willow, velvet ash, sycamore, and cottonwood. Riparian sampling areas in the mountains (1601–1921 m) are located within the oak-juniper (*Juniperus deppeana*) and pine (*Pinus* spp.)-oak upland belt; riparian plant species in the area include cottonwoods, big-tooth maples (*Acer grandidentatum*), pines, oaks, and sycamores.

In the decade between 1984 and 1995 few apparent changes in the vegetation structure

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and composition occurred on any of the sites, and those vegetation category designations defined by Strong and Bock (1990) remained constant. Changes in vegetation and land structure occurred only on Fort Huachuca, with construction of a ca 6-ha disposal site in the foothills and cessation of tank training. Grazing occurred at a moderate stocking rate on the Babocomari Ranch both during our study and Strong and Bock's study.

In 1984 Strong and Bock (1990) established 132 riparian area point counting stations within the study area. They conducted variable circular plot counts (Reynolds et al. 1980) 6 times during the period 1 May–15 July 1984 to 1986. In 1994 we relocated 123 of the stations (the remaining 9 points could not be accurately relocated) and conducted point counts 3 times from 1 May to 15 July 1994 and 1995. Sampling occurred only 3 times in our study due to time constraints. In both studies birds were not counted in weather conditions (e.g., rain, excessive wind, or low temperatures) that might have inhibited their activities or reduced their detectabilities. Although detection rates of birds can vary among vegetation types, for this research we assumed that detection did not change between study periods because vegetation structure did not change at points.

Three repetitions of counts from both 1985 and 1986 were selected to correspond to the dates we counted in 1994 and 1995; counts from 1984 were not used due to some missing data files from that year. The 3 counts from both 1985 and 1986 were combined across the 2 years, as were counts from 1994 and 1995 (i.e., for each of the 123 points, the number of birds of each species was summed across the 6 total counts in each study [1985 and 1986; 1994 and 1995] at each point). Our objective was to analyze long-term change in the bird community and not to evaluate inter-year variation in bird numbers. Therefore, we combined adjacent count years to derive an average bird abundance for 1985–86 and 1994–95.

Due to similarities in some species' call notes or to our inability to always distinguish between certain species when they flew quickly past a counting station, Brown-headed and Bronzed Cowbirds (scientific names given in Appendixes 1 and 2) were grouped together as "cowbirds," and Chihuahuan and Common Ravens were grouped as "ravens." We observed, as

did Strong and Bock, several hummingbird species but did not determine the abundances of these birds because they sometimes flew so quickly past points that positive identifications were not possible. Species richness for each study was calculated as the total number of different species observed at a count station across the 2 years of each study. For each study we calculated the relative abundance of each bird species at each point as the total number of individual birds observed divided by the number of times that point was counted over the 2 years. These relative abundance estimates, which were not normally distributed, were then used to compare average abundances between the 2 studies using Mann-Whitney *U* tests (Zar 1984:138). Comparisons were made only for bird species that were observed at ≥ 3 points during both studies because fewer observations resulted in too few records for analysis. Those migrant birds that were known not to breed in the area and birds for which point counts are not applicable (e.g., hawks, owls; Fuller and Mosher 1981) were not used in abundance comparisons, but they were included in richness comparisons. We used SPSS/PC+ for all analyses (Norusis 1992), and *P*-values ≤ 0.05 were considered significant.

Strong and Bock counted 121 species in 1985–86 across the 123 count stations; 86 of those species were Nearctic breeding migrants and 7 were nonbreeding migrants. In 1994–95, we counted 129 total species; 83 were breeding migrants and 13 were nonbreeding migrants. Thirteen bird species were unique to the Strong and Bock study, whereas 21 were unique to our study (Appendix 2).

There were 80 species (Appendix 1) for which we calculated abundance estimates. These included 21 resident species, of which 3 (Gambel's Quail, Greater Roadrunner, Montezuma Quail) had significantly lower abundances, and 3 (Canyon Towhee, Rufous-crowned Sparrow, White-breasted Nuthatch) had significantly higher abundances in 1994–95 than 1985–86 (Appendix 1). Of the 59 Nearctic migrants, 4 species (Band-tailed Pigeon, cowbirds, Lesser Goldfinch, Western Kingbird) had significantly lower abundances, and 6 (Botteri's Sparrow, Cassin's Kingbird, Hepatic Tanager, Mourning Dove, Spotted Towhee, Virginia Warbler) had higher abundances in 1994–95 (Appendix 1). The differences found between study periods significantly ($P < 0.05$)

differed from what would be expected from random chance alone (Sokal and Rohlf 1981: 158–159). Our results did not show an overall decline in bird abundances from the mid-1980s to the mid-1990s. Only 14% of resident species and 7% of Neartic migrant species declined over the decade, and 14% and 10% of the bird species, respectively, showed increases. Our study area has changed little over the past decade, and this is seen in the few significant changes in bird populations (see below).

Changes in distribution (as measured by occurrences at count points) of species for which relative abundances were not calculated (e.g., Verdin, Black-throated Sparrow, Ruby-crowned Kinglet, Bell's Vireo, Cordilleran Flycatcher, Indigo Bunting, Olive Warbler) could have been due to a host of factors, including (1) fine-scaled changes in the study area that we could not perceive, but which affected bird distribution; (2) region-wide changes in bird abundance and distribution; (3) potential biases in observers between study periods; and (4) changes on migratory routes and wintering grounds. However, our results can be used to prioritize species for more detailed evaluations of population status, and we have now bolstered the Strong and Bock database that can be used for future trend monitoring.

We did, however, count more bird species in 1994 and 1995 than did Strong and Bock in 1985 and 1986. In both studies there were unique species (Appendix 1); 8 of these species were nomadic, wide-ranging, or nocturnal (Barn Owl, Golden Eagle, Northern Goshawk, Sharp-shinned Hawk, Northern Pygmy-Owl, Spotted Owl, Wild Turkey, and Evening Grosbeak) that could not be adequately addressed by our methodology (e.g., no nocturnal counts).

Species that showed significant declines could be prioritized for additional research. For example, both Montezuma and Gambel's Quail declined, indicating that environmental conditions might be degrading for quail in general. Alternatively, numbers of both Canyon and Spotted Towhee increased, indicating more favorable conditions for these species. Quail and towhees present an interesting paradox and both groups occupy similar habitats. The decline identified for cowbirds is similar to a general decline in the western United States for these species and could be due to reduced livestock grazing in the region (Ortega 1998).

In conclusion, over the past decade our study area has seen little disturbance and few significant changes, overall, in bird abundances or richness. We have not seen effects of breeding ground or wintering ground disturbances on Neartic migrants or resident species overall, although a few individual species did exhibit declines. Because of the multiplicity of interacting factors that could impact both Neartic migrant and temperate resident landbird populations (Rappole and McDonald 1994), however, it is important to continue monitoring these animals in both disturbed and undisturbed areas to increase our knowledge of the trends and possibly elucidate the causes of any declines. With this knowledge, research and management measures can be focused more precisely on those species that are exhibiting declines.

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APPENDIX 1. Bird species (84) included in the analyses of relative abundances between studies, and the number of points at which they were counted in 1985–86 and 1994–95. Asterisk indicates significantly different values between study periods (Mann-Whitney tests, $P \leq 0.05$), southeastern Arizona.

STATUS	Number of points		Relative abundances		P-value
	1985–86	1994–95	1985–86 (\bar{s}_x)	1994–95 (\bar{s}_x)	
RESIDENTS					
Gambel's Quail (<i>Callipepla gambelii</i>)	9	22	0.944 (0.486)	0.288 (0.194)	0.001*
Scaled Quail (<i>Callipepla squamata</i>)	18	16	0.454 (0.312)	0.385 (0.369)	0.177
Montezuma Quail (<i>Cyrtonyx montezumae</i>)	41	16	0.431 (0.271)	0.202 (0.077)	<0.001*
Greater Roadrunner (<i>Geococcyx californianus</i>)	36	18	0.241 (0.109)	0.178 (0.040)	0.037*
Acorn Woodpecker (<i>Melanerpes formicivorus</i>)	55	68	0.709 (0.602)	0.782 (0.583)	0.419
Ladder-backed Woodpecker (<i>Picoides scalaris</i>)	37	29	0.203 (0.070)	0.201 (0.069)	0.678
Gila Woodpecker (<i>Melanerpes uropygialis</i>)	6	17	0.639 (0.245)	0.680 (0.485)	0.832
Strickland's Woodpecker (<i>Picoides stricklandi</i>)	19	14	0.272 (0.138)	0.210 (0.081)	0.225
Common Raven (<i>Corvus corax</i>) and Chihuahuan Raven (<i>Corvus cryptoleucus</i>)	17	41	0.304 (0.079)	0.315 (0.210)	0.978
Mexican Jay (<i>Aphelocoma ultramarina</i>)	66	81	1.967 (0.136)	2.298 (1.758)	0.400
Steller's Jay (<i>Cyanocitta stelleri</i>)	11	8	0.439 (0.239)	0.292 (0.194)	0.122
Bridled Titmouse (<i>Parus wollweberi</i>)	32	52	0.599 (0.404)	0.606 (0.524)	0.590
Bushtit (<i>Psaltiriparus minimus</i>)	18	34	0.787 (0.548)	0.588 (0.497)	0.112
White-breasted Nuthatch (<i>Sitta carolinensis</i>)	44	69	0.360 (0.313)	0.394 (0.217)	0.056*
Bewick's Wren (<i>Thryomanes bewickii</i>)	102	101	1.046 (0.759)	0.985 (0.566)	0.953
Canyon Wren (<i>Catherpes mexicanus</i>)	13	25	0.500 (0.379)	0.440 (0.369)	0.431
Cactus Wren (<i>Campylorhynchus brunneicapillus</i>)	13	33	0.667 (0.379)	0.568 (0.390)	0.349
Curve-billed Thrasher (<i>Toxostoma curvirostre</i>)	8	35	0.188 (0.059)	0.269 (0.172)	0.141

APPENDIX I. Continued.

STATUS	Number of points		Relative abundances		P-value
	1985–86	1994–95	1985–86 ($s_{\bar{x}}$)	1994–95 ($s_{\bar{x}}$)	
RESIDENTS (continued)					
Rufous-crowned Sparrow (<i>Aimophila ruficeps</i>)	65	105	0.354 (0.192)	0.776 (0.484)	<0.001*
Canyon Towhee (<i>Pipilo fuscus</i>)	53	50	0.302 (0.196)	0.392 (0.251)	0.038*
Abert's Towhee (<i>Pipilo aberti</i>)	3	6	0.278 (0.193)	0.389 (0.172)	0.347
MIGRANTS					
Killdeer (<i>Charadrius vociferus</i>)	23	10	0.464 (0.301)	0.267 (0.139)	0.087
Cooper's Hawk (<i>Accipiter cooperi</i>)	6	6	0.094 (0.068)	0.183 (0.018)	0.387
Red-tailed Hawk (<i>Buteo jamaicensis</i>)	22	14	0.296 (0.145)	0.329 (0.240)	0.944
Swainson's Hawk (<i>Buteo swainsoni</i>)	4	3	0.167 (0.001)	0.167 (0.000)	1.000
Turkey Vulture (<i>Cathartes aura</i>)	19	17	0.544 (0.657)	0.502 (0.482)	0.945
American Kestrel (<i>Falco sparverius</i>)	12	20	0.403 (0.399)	0.292 (0.161)	0.735
Elegant Trogon (<i>Trogon elegans</i>)	15	19	0.357 (0.211)	0.435 (0.214)	0.263
Mourning Dove (<i>Zenaida macroura</i>)	78	84	0.684 (0.463)	0.855 (0.525)	0.031*
White-winged Dove (<i>Zenaida asiatica</i>)	83	87	0.918 (0.630)	0.835 (0.521)	0.615
Band-tailed Pigeon (<i>Columba fasciata</i>)	6	9	0.417 (0.204)	0.189 (0.055)	0.010*
Yellow-billed Cuckoo (<i>Coccyzus americanus</i>)	13	6	0.250 (0.073)	0.389 (0.272)	0.100
Common Nighthawk (<i>Chordeiles minor</i>)	29	33	0.305 (0.223)	0.420 (0.427)	0.834
Northern Flicker (<i>Colaptes auratus</i>)	62	80	0.387 (0.204)	0.485 (0.310)	0.115
Vermillion Flycatcher (<i>Pyrocephalus rubinus</i>)	14	24	0.488 (0.436)	0.368 (0.208)	0.852
Western Kingbird (<i>Tyrannus verticalis</i>)	38	28	0.588 (0.419)	0.330 (0.198)	0.006*
Cassin's Kingbird (<i>Tyrannus vociferans</i>)	93	100	1.213 (1.000)	1.568 (1.029)	0.007*
Dusky-capped Flycatcher (<i>Myiarchus tuberculifer</i>)	45	49	0.459 (0.322)	0.522 (0.396)	0.642
Ash-throated Flycatcher (<i>Myiarchus cinerascens</i>)	86	98	0.603 (0.354)	0.674 (0.436)	0.467
Sulphur-bellied Flycatcher (<i>Myiodynastes luteiventris</i>)	16	18	0.625 (0.628)	0.548 (0.598)	0.815
Western Wood-Pewee (<i>Contopus sordidulus</i>)	56	55	1.324 (1.014)	1.069 (0.741)	0.307
Greater Pewee (<i>Contopus pertinax</i>)	8	9	1.146 (1.451)	0.704 (0.389)	0.922
Black Phoebe (<i>Sayornis nigricans</i>)	11	13	0.288 (0.168)	0.295 (0.169)	0.924
Say's Phoebe (<i>Sayornis saya</i>)	8	4	0.354 (0.274)	0.208 (0.083)	0.219
Buff-breasted Flycatcher (<i>Empidonax fulvifrons</i>)	6	7	0.778 (0.502)	1.214 (0.685)	0.223
White-throated Swift (<i>Aeronautes saxatalis</i>)	11	10	1.546 (1.951)	1.217 (1.843)	0.395
Northern Rough-winged Swallow (<i>Stelgidopteryx serripennis</i>)	4	13	0.333 (0.136)	0.346 (0.308)	0.950
Violet-green Swallow (<i>Tachycineta thalassina</i>)	4	8	0.417 (0.289)	1.063 (0.868)	0.198
House Wren (<i>Troglodytes aedon</i>)	5	20	0.267 (0.149)	0.300 (0.207)	0.910
Northern Mockingbird (<i>Mimus polyglottos</i>)	84	62	0.952 (0.600)	0.889 (0.513)	0.115
American Robin (<i>Turdus migratorius</i>)	22	25	0.629 (0.524)	0.701 (0.475)	0.567
Eastern Bluebird (<i>Sialia sialis</i>)	12	23	0.361 (0.223)	0.304 (0.139)	0.618
Loggerhead Shrike (<i>Lanius ludovicianus</i>)	12	13	0.236 (0.150)	0.308 (0.202)	0.392
Phainopepla (<i>Phainopepla nitens</i>)	29	27	0.793 (0.909)	0.394 (0.287)	0.335
Plumbeous Vireo (<i>Vireo plumbeus</i>)	18	25	0.630 (0.456)	0.643 (0.573)	0.921
Hutton's Vireo (<i>Vireo huttoni</i>)	9	24	0.241 (0.169)	0.281 (0.159)	0.187
Warbling Vireo (<i>Vireo gilvus</i>)	8	5	0.208 (0.118)	0.200 (0.075)	0.816
Black-throated Gray Warbler (<i>Dendroica nigrescens</i>)	11	14	0.439 (0.217)	0.250 (0.118)	0.153
Painted Redstart (<i>Myioborus pictus</i>)	17	23	0.470 (0.408)	0.596 (0.399)	0.177
Grace's Warbler (<i>Dendroica graciae</i>)	7	13	0.500 (0.347)	0.749 (0.643)	0.441
Virginia's Warbler (<i>Vermivora virginiae</i>)	3	14	0.167 (0.000)	0.393 (0.192)	0.044*
Lucy's Warbler (<i>Vermivora luciae</i>)	70	57	0.614 (0.525)	0.563 (0.348)	0.658
Yellow Warbler (<i>Dendroica petechia</i>)	9	20	0.426 (0.313)	0.595 (0.643)	0.960
Common Yellowthroat (<i>Geothlypis trichas</i>)	45	44	0.582 (0.459)	0.727 (0.625)	0.313
Yellow-breasted Chat (<i>Icteria virens</i>)	7	8	0.238 (0.089)	0.208 (0.077)	0.480
Red-winged Blackbird (<i>Agelaius phoeniceus</i>)	21	20	0.841 (1.086)	0.405 (0.318)	0.105

APPENDIX 1. Continued.

STATUS Species	Number of points		Relative abundances		<i>P</i> -value
	1985–86	1994–95	1985–86 ($s_{\bar{x}}$)	1994–95 ($s_{\bar{x}}$)	
MIGRANTS (continued)					
Eastern Meadowlark (<i>Sturnella magna</i>)	67	60	0.826 (0.875)	0.859 (0.589)	0.177
Brown-headed Cowbird (<i>Molothrus ater</i>) and Bronzed Cowbird (<i>Molothrus aeneus</i>)	103	94	0.694 (0.448)	0.466 (0.343)	0.001*
Bullock's Oriole (<i>Icterus bullockii</i>)	41	28	0.370 (0.304)	0.355 (0.265)	0.802
Scott's Oriole (<i>Icterus parisorum</i>)	33	57	0.253 (0.151)	0.267 (0.125)	0.216
Western Tanager (<i>Piranga ludoviciana</i>)	18	20	0.209 (0.163)	0.265 (0.121)	0.739
Summer Tanager (<i>Piranga rubra</i>)	37	44	0.320 (0.194)	0.423 (0.351)	0.114
Hepatic Tanager (<i>Piranga flava</i>)	14	29	0.238 (0.126)	0.315 (0.119)	0.040*
Grasshopper Sparrow (<i>Ammodramus savannarum</i>)	11	18	0.212 (0.078)	0.263 (0.146)	0.392
Botteri's Sparrow (<i>Aimophila botterii</i>)	37	34	0.460 (0.394)	0.912 (0.569)	<0.001*
Spotted Towhee (<i>Pipilo maculatus</i>)	27	51	0.438 (0.311)	0.743 (0.487)	0.007*
Black-headed Grosbeak (<i>Pheucticus melanocephalus</i>)	62	70	0.524 (0.407)	0.413 (0.238)	0.460
Blue Grosbeak (<i>Guiraca caerulea</i>)	66	64	0.366 (0.205)	0.345 (0.205)	0.434
House Finch (<i>Carpodacus mexicanus</i>)	66	72	0.586 (0.433)	0.588 (0.498)	0.714
Lesser Goldfinch (<i>Carduelis psaltria</i>)	30	24	0.728 (0.626)	0.438 (0.395)	0.021*

*Number of points at which the species was observed.

APPENDIX 2. Bird species counted at point counting stations in southeastern Arizona that were not included in abundance estimates of Appendix 1. Species consist of nonbreeding Nearctic migrants that were counted early in each breeding season; hummingbirds; nocturnal species; species unique to 1985–86 or 1994–95; and species counted during both studies but at ≤ 2 points in one study.

When observed STATUS Species	No. points	
	1985–86	1994–95
Observed during both 1985–86 and 1994–95		
RESIDENT		
Great Horned Owl (<i>Bubo virginianus</i>)	6	6
Crissal Thrasher (<i>Toxostoma crissale</i>)	1	1
Yellow-eyed Junco (<i>Junco phaeonotus</i>)	2	7
BREEDING MIGRANT		
Mallard (<i>Anas platyrhynchos</i>)	2	3
Great Blue Heron (<i>Ardea herodias</i>)	2	2
Whip-poor-will (<i>Caprimulgus vociferus</i>)	1	1
Anna's Hummingbird (<i>Calypete anna</i>)	2	2
Costa's Hummingbird (<i>Calypete costae</i>)	1	1
Barn Swallow (<i>Hirundo rustica</i>)	11	2
Brown-crested Flycatcher (<i>Myiarchus tyrannulus</i>)	1	6
Brown Creeper (<i>Certhia americana</i>)	1	8
Rock Wren (<i>Salpinctes obsoletus</i>)	8	2
Hermit Thrush (<i>Catharus guttatus</i>)	3	2
European Starling (<i>Sturnus vulgaris</i>)	13	1
Red-faced Warbler (<i>Cardellinarubifrons</i>)	1	4
Lark Sparrow (<i>Chondestes grammacus</i>)	12	2
Cassin's Sparrow (<i>Aimophila cassini</i>)	1	15
Green-tailed Towhee (<i>Pipilo chlorurus</i>)	4	1
Lazuli Bunting (<i>Passerina amoena</i>)	1	13
NONBREEDING MIGRANT		
Yellow-rumped Warbler (<i>Dendroica coronata</i>)	7	6
Townsend's Warbler (<i>Dendroica townsendi</i>)	1	1
Wilson's Warbler (<i>Wilsonia pusilla</i>)	12	8
Chipping Sparrow (<i>Spizella passerina</i>)	1	

APPENDIX 2. Continued.

When observed STATUS Species	No. points	
	1985–86	1994–95
Observed only in 1985–86		
RESIDENT		
Barn Owl (<i>Tyto alba</i>)	1	0
Great-tailed Grackle (<i>Quiscalus mexicanus</i>)	2	0
Pyrrhuloxia (<i>Cardinalis sinuatus</i>)	2	0
BREEDING MIGRANT		
Golden Eagle (<i>Aquila chrysaetos</i>)	1	0
Sharp-shinned Hawk (<i>Accipiter striatus</i>)	1	0
Northern Goshawk (<i>Accipiter gentilis</i>)	4	0
Hairy Woodpecker (<i>Picoides villosus</i>)	4	0
Cliff Swallow (<i>Hirundo pyrrhonota</i>)	1	0
Black-throated Sparrow (<i>Amphispiza bilineata</i>)	3	0
Pine Siskin (<i>Carduelis pinus</i>)	5	0
NONBREEDING MIGRANT		
Ruby-crowned Kinglet (<i>Regulus calendula</i>)	1	0
Orange-crowned Warbler (<i>Vermivora celata</i>)	1	0
White-crowned Sparrow (<i>Zonotrichia leucophrys</i>)	1	0
Observed only in 1994–95		
RESIDENT		
Wild Turkey (<i>Meleagris gallopavo</i>)	0	1
Spotted Owl (<i>Strix occidentalis</i>)	0	1
Northern Pygmy-Owl (<i>Glaucidium gnoma</i>)	0	2
Verdin (<i>Auriparus flaviceps</i>)	0	10
Pygmy Nuthatch (<i>Sitta pygmaea</i>)	0	2
Black-tailed Gnatcatcher (<i>Poliophtila melanura</i>)	0	7
Northern Cardinal (<i>Cardinalis cardinalis</i>)	0	7
Evening Grosbeak (<i>Coccothraustes vespertinus</i>)	0	2
BREEDING MIGRANT		
Cordilleran Flycatcher (<i>Empidonax occidentalis</i>)	0	2
Northern Beardless-Tyrannulet (<i>Camptostoma imberbe</i>)	0	1
Blue-gray Gnatcatcher (<i>Poliophtila caerulea</i>)	0	11
Bell's Vireo (<i>Vireo bellii</i>)	0	7
Olive Warbler (<i>Peucedramus taeniatus</i>)	0	1
Hooded Oriole (<i>Icterus cucullatus</i>)	0	16
Black-chinned Sparrow (<i>Spizella atrogularis</i>)	0	7
Song Sparrow (<i>Melospiza melodia</i>)	0	2
Indigo Bunting (<i>Passerina cyanea</i>)	0	1
NONBREEDING MIGRANT		
Dusky Flycatcher (<i>Empidonax oberholseri</i>)	0	1
Horned Lark (<i>Eremophila alpestris</i>)	0	1
American Goldfinch (<i>Carduelis tristis</i>)	0	3
Hummingbirds observed but not analyzed		
Broad-billed Hummingbird (<i>Cynanthus latirostris</i>)	0	1
Broad-tailed Hummingbird (<i>Selasphorus platycercus</i>)	9	20
Magnificent Hummingbird (<i>Eugenes fulgens</i>)	5	5
Black-chinned Hummingbird (<i>Archilochus alexandri</i>)	83	34

THE EFFECT OF ROADS AND TRAILS ON MOVEMENT OF THE OGDEN ROCKY MOUNTAIN SNAIL (*OREOHELIX PERIPHERICA WASATCHENSIS*)

Dwayne W. Meadows¹

Key words: snail, *Oreohelix peripherica wasatchensis*, road avoidance, movement, habitat fragmentation, Utah.

Pathways for human movement are ubiquitous in most landscapes, including managed “wilderness” areas. For example, U.S. national forests contain 10% of U.S. road miles but only 8% of the land area (Forman and Alexander 1998). The effects of roads on wildlife populations are diverse and widespread, although most frequently studied near major urban areas (Gilbert 1989, Forman and Alexander 1998, Spellerberg 1998). It is known that roads are a source of introduced species, soil erosion, and various forms of pollution and disturbance. Moreover, roads lead to edge effects that spread into the surrounding habitat, resulting in altered microclimate and other disturbances. In addition, roads alter or prevent animal movement, possibly leading to habitat fragmentation and genetic divergence of populations (Selander and Kaufman 1975, Mader 1984, Reh and Seitz 1990, Forman and Alexander 1998). Between 15% and 20% of U.S. land area is affected by roads (Forman and Alexander 1998). For smaller and less mobile animals, narrow walking trails may have similar effects.

Small mammals, birds, frogs, turtles, beetles, and a snail avoid roads or trails (Baur and Baur 1990, Forman and Alexander 1998). However, it is not clear whether this avoidance is due to features of pathway habitats per se, preference for natural habitat, or avoidance of secondary disturbances associated with human use, as experiments have not been conducted. Correlative studies suggest birds avoid traffic noise (Reijnen et al. 1997) or poor food availability (Tabor 1974), while road salt may deter amphibians (Forman and Alexander 1998). Other possible causes of avoidance are various disturbances, pollutants, or predators (Forman

and Alexander 1998). This study examines road avoidance and its proximate causes in the terrestrial land snail *Oreohelix peripherica wasatchensis* (Hemphill in Binney 1886), the Ogden Rocky Mountain snail. Movement preference relative to pathways was assessed in the field, while habitat features causing pathway avoidance were assessed with laboratory choice studies.

The oreohelcid snail *O. p. wasatchensis* occurs in a 17-ha area in the Wasatch Mountains 1 km south of Ogden Canyon (Fig. 1) in Ogden, Utah (41°14'N, 111°55'W; altitude 1310–2020 m). It is a hermaphroditic, pulmonate snail that feeds on vegetation and detritus and lives under leaf litter (usually maple) and/or limestone or quartz rocks (Pilsbry 1939, Clarke 1993, personal observation). The main snail habitat is a normally dry draw that runs approximately east to west upslope. Vegetation is mostly bigtooth maple (*Acer grandidentatum*). A largely treeless area within 100 m either side of the main draw also contains *O. p. wasatchensis* under scattered patches of bigtooth maple, sagebrush (*Artemisia tridentata* and *A. ludoviciana*), and a variety of small shrubs. Two U.S. Forest Service trails cross the study area, as well as 2 dirt access roads for public utilities and numerous unnamed trails increasingly frequented by hikers, joggers, and mountain bikers.

Four sites were chosen for the study: 2 near pathways and 2 control sites away from pathways (Fig. 1). One pathway site is along the eastern edge of the upper road (which is 5 m wide), while the 2nd is along the southern edge of a trail (0.7 m wide). Test snails were gathered from downslope of the study sites in

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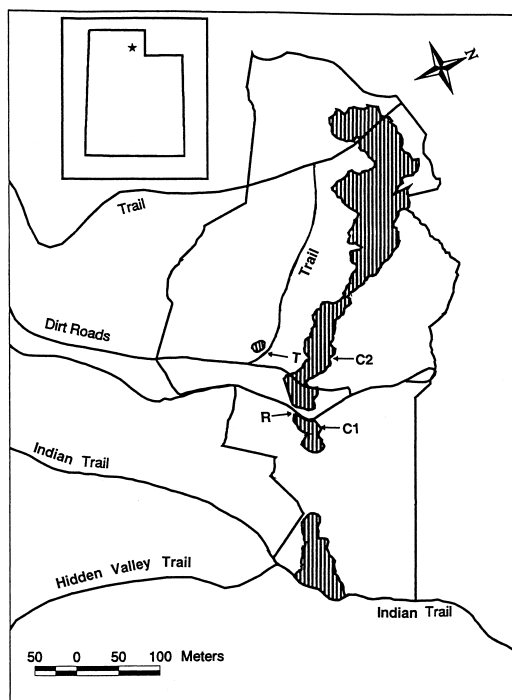


Fig. 1. Location and study sites of *O. p. wasatchensis*. Crosshatched areas indicate the maple groves where most snails occur, though living snails extend into the more open habitats enclosed by the solid line. C1 and C2 identify the control locations for the movement study, while R is the road site and T is the trail site.

summer 2000. At each site 30 randomly selected and individually marked snails were placed in 2 parallel 4-m-long lines which were 25 cm apart and paralleled the pathway, with one line of snails directly on the edge of the pathway. Snails were separated by 25 cm along each line. Stakes were placed every meter to establish a baseline axis for movement measurements. Initial snail positions were recorded using x -, y -coordinates from this design. The next day I again recorded positions of all recovered snails to the nearest centimeter. Snail movement direction was determined trigonometrically. The 0–180° axis of movement was parallel to the nearby pathway rather than being absolute direction. Preferred movement angles between 0° and 180° thus signify movement away from pathways. For control sites the 0–180° axis was arbitrary. Rayleigh's test (Zar 1984) was used to test angular direction preference (ϕ) at each site.

To determine whether pathway avoidance was related to habitat features per se, I con-

ducted choice tests in the lab using $25 \times 17 \times 8$ -cm terraria. Test substrates were gathered from the natural snail habitat. Half of each terrarium was filled 4 cm deep with one test substrate and half with the other. I used the following substrate combinations: (1) natural snail substrate plus leaf litter versus road material, (2) natural snail substrate alone versus road material, (3) wet natural snail substrate versus dry natural snail substrate, (4) road substrate plus leaf litter versus natural substrate, (5) natural substrate plus dry leaf litter versus dry natural substrate without litter, and (6) natural substrate plus artificial leaves (Michaels Crafts Inc., stock number 5517300999) versus natural substrate. A snail was placed in the center of each terrarium, after which both substrates were equally watered (unless wetness was a choice factor). Temperature was 21–24°C with a 12:12 light:dark cycle. The snails were then given 24 hours to make a habitat choice. A second 24-hour trial was then run using the same snail but with substrates switched 180° to control for environmental gradients. The data for each snail thus consisted of the results of 2 trials per substrate combination. In any test each individual could have consistently chosen one substrate or the other, or had a mixed preference. Chi-square tests were used to determine whether the distribution of these outcomes differed from chance for sets of 12 to 17 snails tested with each substrate combination. Snails were reused in different tests but not within the same test.

Control site snails had no directional movement preference (site C1: $n = 13$, $Z = 0.4$, $P > 0.5$; C2: $n = 16$, $Z = 1.9$, $P > 0.10$), while road and trail site snails moved away from pathways (road: $n = 12$, $Z = 6.0$, $P < 0.002$, $\phi = 95.2^\circ$, trail: $n = 23$, $Z = 10.0$, $P < 0.001$, $\phi = 102.5^\circ$).

Snails preferred natural substrate with leaf litter to road material ($n = 12$, $\chi^2 = 22.0$, $P < 0.001$), but they showed no preference between natural substrate and road material ($n = 15$, $\chi^2 = 1.8$, $P > 0.05$). There was no significant preference for wet vs. dry natural substrate ($n = 17$, $\chi^2 = 1.0$, $P > 0.05$). There was a significant preference for natural substrate with dry leaf litter over natural substrate without litter ($n = 15$, $\chi^2 = 30.5$, $P < 0.001$), as well as for leaf litter on road substrate over natural substrate alone ($n = 13$, $\chi^2 = 31.5$, $P < 0.001$). Natural substrate with artificial leaves was

chosen over natural substrate alone ($n = 14$, $\chi^2 = 8.2$, $P < 0.05$).

The field and experimental results show that *O. p. wasatchensis* avoids areas without leaf litter. The first choice test showed preference for natural substrate and/or avoidance of road substrate. The only secondary effect of pathways not eliminated by this test was soil pollution. However, the snail did prefer road substrate if it was covered with leaf litter, and so avoidance of pollutants is unlikely. The first choice test also does not show whether the snail's preference is for natural substrate or for the effect(s) of learning or food availability, predator protection, shelter, and/or extra moisture retention provided by leaf litter, and thus does not discern the primary factor in natural substrate preference. The lack of preference in the test involving natural snail substrate without leaf litter versus road material, and the significant preference for leaf litter on road substrate over natural substrate alone, suggest that it is some quality provided by leaf litter that is most important to snail habitat choice. Thus, pathway avoidance appears to be a function of preference for leaf litter. The definitive field experiment of adding leaves to pathways was attempted twice, but trail users destroyed it.

The lack of preference for wet versus dry natural substrate and the preference for dry leaf litter versus no leaf litter when both were on natural substrate suggest that substrate moisture or leaf moisture retention are not the main proximate factors that affect preference for leaf litter. Furthermore, the preference for artificial leaves suggests that shelter and cover are important factors in snail habitat choice. However, I cannot completely rule out the role of leaf litter as a food source, since the artificial leaf test results were barely significant in comparison to other tests, and because it is difficult to completely eliminate potential food using artificial leaves.

Although Baur and Baur (1990) found pathway avoidance in the field in the European snail *Arianta arbustorum*, they did not isolate the proximate factors involved. Baur (1986) did find that slope affected movement preference in *A. arbustorum*, but slope probably did not affect my results since all study sites had similar inclinations. Goodfriend (1983) found that the snail *Cepaea nemoralis* moved upwind,

but this factor is also unlikely here since my sites experienced similar wind direction.

My results imply that pathways create barriers to movement in this species. Consequently, this snail's habitat may be fragmented by pathways into numerous subpopulations that may be genetically divergent, as has been shown for other snails (Selander and Kaufman 1975) and frogs (Reh and Seitz 1990). Consequently, these subpopulations may fluctuate more widely in abundance and with a higher probability of extinction (Soulé 1987, Opdam et al. 1993, Schilthuisen and Lombaerts 1994). This may be a major threat to *O. p. wasatchensis*, which only occurs at this location and is a U.S. candidate endangered species and Utah Species of Special Concern. Future research should explore this possibility.

C. Meadows and M. Morin helped develop the sampling protocols, and S. Linssen did the GPS mapping. L. England and S. Zeveloff provided valuable comments on the material that formed the basis for this work.

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A NEW STATE RECORD FOR
CICINDELA NIGROCOERULEA NIGROCOERULEA LECONTE
(COLEOPTERA: CICINDELIDAE) IN NEVADA

Michael G. Kippenhan¹

Key words: tiger beetles, *Cicindela*, *Coleoptera*, *Nevada*.

Tiger beetles are a well-studied and popular family of Coleoptera. Adults occupy a large variety of habitats with individual species exhibiting microhabitat preferences and marked seasonal activity. Due to these specialization factors, tiger beetles have become an important element for assessing conservation planning (Cassola and Pearson 2000). Adults of the Holarctic genus *Cicindela* are represented in North America with 92 species (Freitag 1999), most of which exhibit attractive colors and markings as well as diurnal habits. The distribution of these species has been well documented and recorded throughout the United States (Pearson et al. 1997).

Cicindela nigrocoerulea LeConte (Fig. 1) is a species of the southwestern United States and northern Mexico, with 3 recognized subspecific forms (Freitag 1999). In the United States the nominate form is known to inhabit the largest geographic area, which comprises Arizona, California, Colorado, Kansas, New Mexico, Texas, and Utah (Freitag 1999). *Cicindela n. nigrocoerulea* exhibits a summer adult activity period and is associated with moist alkali soil of grasslands or along water edges.

On 17 and 18 August 2000, the author collected 9 specimens (4 ♂♂, 5 ♀♀) of this species along the Virgin River near Mesquite, Clark County, Nevada. The specimens were active along the edges of short grasses bordering muddy, alkali-encrusted patches on a wide sand bar in the channel of the river. Other cicindelids occurring in this habitat were *C. haemorrhagica arizonae* Wickham along the water's edge and *C. praetextata pallidofemora* Acciavatti on the muddy areas throughout the

sand bar. The sand bar was searched extensively and it was verified that *C. n. nigrocoerulea* could be located only in close proximity of the alkali encrustations.

This collection of *Cicindela n. nigrocoerulea* represents the first published record of this species from Nevada (Sumlin 1976, Pearson et al. 1997, Freitag 1999). Records from St. George, Utah (Tanner 1929), indicate that this species is an inhabitant of the upriver Virgin River system, and therefore it is surprising that it has not previously been recorded from Nevada.

Richard Freitag (Lakehead University, Ontario), Boris C. Kondratieff (Colorado State University, Fort Collins), and Dave Pearson (Arizona State University, Tempe) reviewed the manuscript and offered helpful comments.

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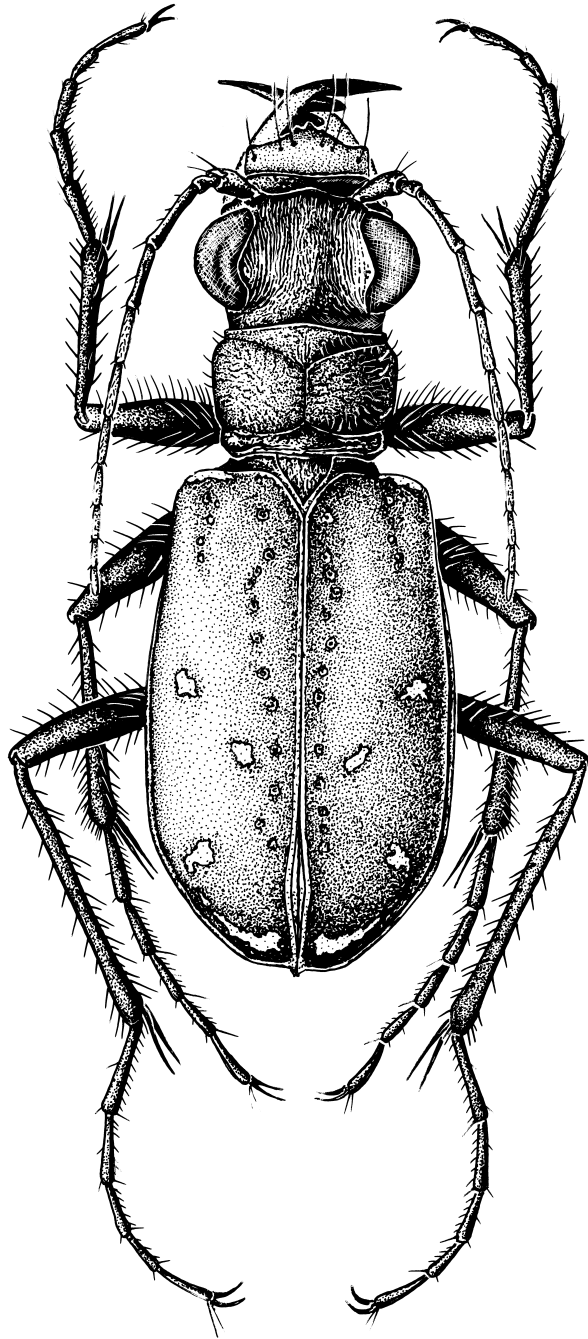


Fig. 1. *Cicindela n. nigrocoerulea* LeConte, male.

BOOK REVIEW

The Geology of the Parks, Monuments, and Wild-lands of Southern Utah. Robert Fillmore. University of Utah Press, Salt Lake City. 2000. \$19.95, paperback; 268 pages. ISBN 0-87480-652-6.

It is so easy to love the towering cliffs and red layered cakes of sandstone and siltstone of the Colorado Plateau. These formidable rock formations dissected by narrow slot canyons and vast gray plains are attractive to most people. Unless (or especially if), you have lost a cow in a slot, or a jeep in a flash flood-filled wash, or have only a few hours to cross them on the highway on a trip to less important destinations.

This is a good book for all those folks, and I particularly recommend it to novices and diletantes, like me, wishing to understand southern Utah geology. I have worked extensively in southern Utah on biological surveys and am always looking for ways to better understand the rocks and geologic history of the area. For these reasons I picked up this book and could hardly put it down until I had read every word.

The book is divided into 2 sections by the author, but I considered it to be divided into 3: basic principles of geology, a general tour through the geologic time periods, and a road log with specific examples of rock features along the principal highways of the Grand Staircase-Escalante National Monument and adjacent areas. I was especially pleased with the redundancy and parallel construction of these parts. These devices helped emphasize what I thought the author had chosen to be the most important messages concerning the area: the comparable stratigraphy across long distances (despite different type section names), the mountain-building events, the general and stupendous uplift of the plateau, and the inter-fingering of sediments during repetitive erosive and depositional series resulting from regressive and transgressive seas and rivers through time. These concepts finally hit home with me. I now better understand the sometimes confusing array of sediments encountered in the area. For the first time I understand why not all layers are spread uniformly across the Colorado Plateau!

Fillmore introduced the general principles clearly, followed by events of various time periods for the region as a whole (in a more global context), and then the road log gave specific examples of the phenomena in rock-hard, layers-in-your-face locations that should be easy to find on a road trip. I must admit, however, that I did not check any mileages for accuracy. That is something I will do during my next field season as I traverse the area.

The book was easy to read and combined technical knowledge with general information. The index worked well, and I used it repeatedly to check concepts handled earlier in my reading.

Inquisitive readers could access additional information by consulting references in the brief bibliography associated with each of the chapters covering a particular geologic time period. There was a sparse bibliography given in the road log section, and I was surprised that it did not include Hintze (1988, *A Field Guide to Utah's Rocks: Geologic History of Utah*) or Rigby (1976, *Northern Colorado Plateau: Field Guide*), both of which can be valuable companions to this work. As a biologist, I would have appreciated more information concerning the fossils of the area, but that is not a major fault as it would have increased the book's length. I will just need to go elsewhere.

As more and more people come to see the dissected, cake-like stratigraphy for which the Colorado Plateau is world famous, they will have additional choices in the interpretation that this book provides. This sturdy paperback will fit easily into most glove compartments of sports utility vehicles of tourists as well as the battered trucks of natural history professionals and ranchers crisscrossing the red rock country, looking for cows, avoiding floods, and moving on down the road.

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