

A GIS MODEL TO PREDICT THE LOCATION OF FOSSIL PACKRAT (*NEOTOMA*) MIDDENS IN CENTRAL NEVADA

Scott A. Mensing¹, Robert G. Elston, Jr.¹, Gary L. Raines²,
Robin J. Tausch³, and Cheryl L. Nowak³

ABSTRACT.—Fossil packrat (*Neotoma*) middens provide an important source of paleoecologic data in the arid West. This study describes and tests a predictive GIS model that uses the weights-of-evidence method for determining areas with a high probability of containing fossil middens in central Nevada. Model variables included geology, elevation, and aspect. Geology was found to be the most important variable tested. We produced a map of 4 probability classes validated by field-checking 21 randomly selected 1-km² sites throughout the study area. Our high-probability category reduced the search area to only 3.5% of the total study area. Fossil middens were found on 8 of 21 sites (38%). Geologic types that contained middens were granite, limestone, and volcanic tuff. A 2nd run of the model with the new midden localities added to the training set helped narrow the total search area even further. This analysis demonstrates that the weights-of-evidence method provides an effective tool both for guiding research design and for helping locate midden sites within specific localities. With only a limited training dataset and a simple set of mapped criteria, a model can be constructed that is both predictive and testable. We intend to continue development of the model to improve our ability to predict the location of Pleistocene-age middens and to locate middens on low-probability sites. This method, designed for mineral exploration, has wide potential application within the natural sciences.

Key words: GIS predictive model, weights-of-evidence, fossil packrat middens, Nevada, *Neotoma*.

Plant and animal macrofossils preserved in fossilized packrat (*Neotoma*) middens are an important source of evidence for reconstructing paleoclimate and vegetation change in the arid West (Betancourt et al. 1990). Middens contain plant fragments, fecal pellets, bone fragments, and other debris collected within approximately a 1-ha area of a *Neotoma* den (Finley 1990, Spaulding et al. 1990). *Neotoma* spp. repeatedly urinate on their collections and, over time, the mass hardens into a material called amberat, which protects the midden contents from decay. A den may be abandoned and reinhabited many years later, leading to the accumulation of multiple strata in the midden. Middens can be as large as 7 m high and 10 m wide, but middens of 1–2 m are more common. Although *Neotoma* inhabit a broad range of habitats and are widely distributed (Vaughan 1990), fossil middens are found only in sites sheltered from rain and runoff, such as caves or under overhanging rocks, because amberat dissolves in water.

Characteristics that define fossil midden locations in the Great Basin are cave-forming

substrate, mid-elevations, and southwest to easterly exposure (Webb and Betancourt 1990). On some rocky sites Holocene middens are very common. However, the Great Basin is geologically complex, and sites where fossil middens are abundant are often widely separated. One of our research goals was to reconstruct plant species migration patterns over distance and elevation across the central Great Basin. This effort requires a high-resolution spatial network of fossil middens. Much of central Nevada has limited road access, and systematically searching all potential midden localities is logistically prohibitive. A predictive model that maps the probability of finding fossil middens would both focus search efforts, increasing the efficiency of valuable field time, and identify new areas that may not have been expected to have middens.

Geographic information systems (GIS) models have been used to predict locations of rare orchid habitat (Sperduto and Congalton 1996), black bear habitat (van Manen and Pelton 1997), squirrel distribution (Rushton et al. 1997), breeding bird distributions (Tucker et al. 1997),

¹Department of Geography, University of Nevada, Reno, NV 89557.

²United States Geological Survey and Adjunct Faculty, Department of Geosciences, University of Nevada, Reno, NV 89557.

³USDA Forest Service, Rocky Mountain Research Station, 920 Valley Road, Reno, NV 89512.

and rare mineral deposits, particularly gold (Bonham-Carter et al. 1988, Agterberg et al. 1990, Xu et al. 1992). In this paper we present a GIS model to predict the location of fossil *Neotoma* midden sites in central Nevada. The goal of this study was to test the effectiveness of this approach for identifying specific search locations within a very large study area. Once developed, and with additional data, such a model could then be refined to improve our ability to find Pleistocene-age middens or to identify potential sites in localities where fossil middens are less common.

METHODS

Weights-of-Evidence Method

Weights-of-evidence is a quantitative method originally designed as a medical data-driven system for combining information about symptoms to predict disease (Xu et al. 1992, Bonham-Carter 1994). The method was adapted for mineral exploration using geologic and geochemical datasets to predict the location of specific ore deposits (Bonham-Carter et al. 1988). Recently, a software package for calculating weights-of-evidence was developed as an extension to run with the ArcView™ Spatial Analyst GIS program (ESRI, Redlands, CA). A beta version of the weights-of-evidence ArcView™ extension (Kemp et al. 1999) was used in this research.

The weights-of-evidence program uses a set of training points (in this case, known fossil midden locations), a spatially defined study area, and a set of thematic maps (evidential themes), which represent variables that are considered predictive of the training point data. Evidential themes are assumed to be conditionally independent with respect to training points. Training points are compared against each evidential theme to calculate the measure of spatial association between the points and each class or attribute in the theme. A weight is calculated for each class in a theme, with a positive weight (W^+) if the class is present and a negative weight (W^-) if the class is absent. The difference between weights is the contrast (Bonham-Carter 1994), which measures the strength of the correlation between the training set and classes in the theme. Positive contrast values suggest that more training points occur in that class than would be expected by chance, and negative

contrast values suggest fewer training points than would exist by chance alone. Equations for the derivation of contrast are described in detail in Bonham-Carter et al. (1988), Bonham-Carter (1994), and Kemp et al. (1999). Positive contrast values of 0–0.5 are usually considered mildly predictive, 0.5–1.0 moderately predictive, 1.0–2.0 strongly predictive, and >2.0 extremely predictive (Bonham-Carter 1994). Contrast values are used to reclassify each evidential theme into a binary map with only 2 classes, ‘inside’ or predictive and ‘outside’ or not predictive. The user’s decisions on how high or low to set the predictive values in each evidential binary map influence the model outcome.

Before running the model, the program calculates prior probability by dividing number of training points, where each point represents a user-defined unit area, by total study area, assuming a random distribution of sites. This probability will invariably be less than the spatial density of all existing middens because the training set represents a small sample of existing middens in a large study area. However, it provides an initial probability to start the modeling. Evidential binary maps are then combined to give the posterior probability to each cell for each unique binary combination. For example, if 3 themes were combined, any cell containing the predictive variable, ‘inside’, in all 3 themes would have the highest posterior probability. Overlaying cells with ‘inside’ in 2 themes and ‘outside’ in 1 theme would meet only 2 predictive criteria and have a lower probability. Posterior probabilities higher than the prior probability suggest a nonrandom distribution and indicate that locations of training points are controlled by specific environmental variables.

To create a map that represents true probability, each evidential theme must be conditionally independent with respect to training points; however, this assumption is probably always violated to some extent (Bonham-Carter 1994). Weights-of-evidence software incorporates a test for conditional independence, which calculates the ratio between actual number and predicted number of training points. A value of 1 means the evidential themes are conditionally independent with respect to training points; a value of 0 means there is absolute dependence. Values >0.85 are generally considered acceptable for demonstrating

conditional independence (Agterberg 1994 personal communication).

Fossil Midden Training Dataset and Study Area

The training point dataset included 346 fossil midden samples from central Nevada. Fourteen samples had no location data and were discarded. Duplicate samples and middens from the same location were also discarded, reducing the dataset to 85 locations. These locations were then entered into the ArcView™ GIS program. Points were plotted on the 1:500,000 scale geology of Nevada (Stewart and Carlson 1978) and checked for accuracy. In several cases the location was on the wrong geologic type as recorded from field notes by the midden collector. This typically occurred in areas of complex geology where spatial resolution of the geologic map was insufficient to capture variability on the ground, making the midden location appear on the wrong geologic type. In these cases the midden location was moved to the correct geology. In general, points were not shifted more than 200 m, which is less than the spatial resolution of the 1:500,000-scale geology theme. Original aspect and elevation were unchanged.

A 1-km² lattice, representing the minimum spatial resolution of the weights-of-evidence model, was then laid over the geology. Where more than 1 training point occurred on the same geology within a 1-km² cell, duplicate points were discarded. The weights-of-evidence method calculates the posterior probability of a point occurring in a unit cell, 1 km² in this case. Consequently, the method cannot consider multiple points per cell, which is a limitation of the method. The final training point dataset had 60 midden locations. Only 58 points were used in model 1 because 2 middens fell outside the study area. If these 58 training points somehow are a biased sample, for example, if a particular geologic unit or elevation were never sampled, then the resulting model will be influenced by this bias. The authors are unaware of any bias in this sample of midden locations.

The study area was restricted to central Nevada counties where our training points were concentrated (Fig. 1). All major geologic formations in the state and many of the largest mountain ranges are found in this region. Elevation as calculated by the digital elevation

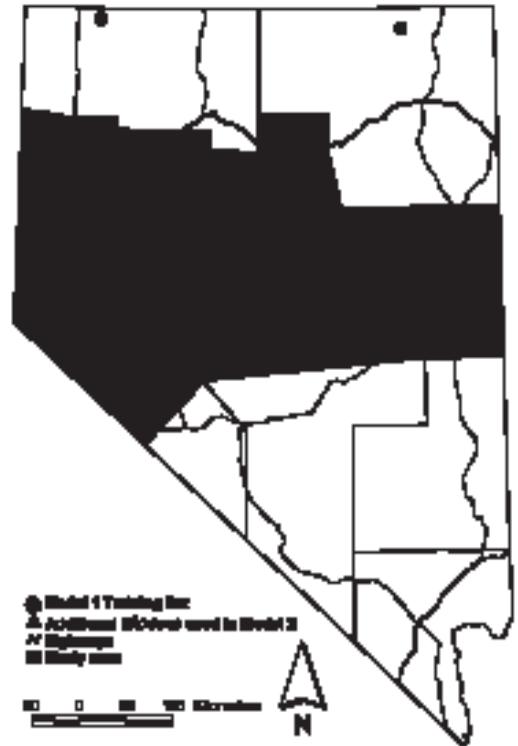


Fig. 1. Map of the model study area with training point locations. Open circles represent the original training set used to create model 1. Open triangles represent middens found during field validation of model 1 and added to the original training set to create model 2.

model ranged from 1000 m in Dixie Valley to 3949 m at Wheeler Peak in Great Basin National Park.

Creation of Evidential Themes

Four evidential themes were considered for this model: geology, elevation, slope, and aspect. These themes provide information on the 3 major characteristics of midden locations: substrate, elevation, and exposure.

The geology evidential theme was created from the 1:500,000 U.S. Geological Survey geologic map of Nevada (Stewart and Carlson 1978). Large-scale geologic maps (>1:100,000) would have included smaller features and isolated rock outcrops; however, coverage of the study area was unavailable at these scales. Geology at a 1:250,000 scale was available, but it was constructed from 13 county maps with different definitions of geologic formations. Consequently, geologic map units did not

match across county lines and were inconsistent across the state. Only the 1:500,000 scale provided a consistent geologic base map across the entire study area. The original vector coverage was rasterized by use of 276×276 -m pixels. This cell size was selected to adequately represent the information content of the geologic map. Weights-of-evidence does not require that evidential themes be degraded to a consistent cell size. The user-defined unit cell, 1 km^2 , defines that each training point will be counted as 1 km^2 and evidential themes will be measured in units of 1 km^2 .

We were concerned that the 1:500,000-scale map would lack resolution necessary to identify small outcrops of suitable geology that fell below the minimum mapping resolution threshold. To test the loss of resolution associated with moving to a small-scale map, we compared minimum mapping resolution and changes in lithologic boundaries between 3 map scales, the Austin 1:62,500 quadrangle (McKee 1978), Lander County 1:250,000 map (Stewart and McKee 1977), and USGS 1:500,000 Nevada map (Stewart and Carlson 1978). The test area contained 6 midden sites, 4 of which were mapped on granitic rock and 2 on limestone. Granitic formations remained consistent through all 3 map scales, including general polygon size and lithologic boundary. A section of Quaternary alluvium at the base of the granitic rock was mapped as a 200-m-wide strip at 1:62,500 scale, but shrank to a 100-m-wide strip at 1:250,000 scale and disappeared altogether at 1:500,000 scale. Loss of this detail did not influence the geologic type associated with midden sites. Limestone was mapped as 4 distinct units with 2 different named formations on the 1:62,500 map. The 1:250,000-scale map had 2 formations and only 2 rock units. At the 1:500,000 scale the limestone had been reduced to 1 named formation and 1 mapped unit; however, middens were still located on the correct lithology. Although our analysis was necessarily limited due to a lack of 1:62,500 geologic maps, it demonstrated that the 1:500,000 map was consistent with larger-scale maps.

Aspect, slope, and elevation evidential themes were constructed from a U.S. Geological Survey digital elevation model (DEM) of Nevada with an initial cell size of 92 m. Cell size was resampled to 276 m to be consistent with the geology theme. The elevation eviden-

tial theme was created by classifying the DEM into 30 elevation classes of 98.3 m each. Aspect and slope evidential themes were derived from the DEM by use of the ArcView™ Spatial Analyst algorithms. Aspect was classified into 16 classes with 22.5° in each class. Slope and geology were found to be conditionally dependent with respect to middens, and slope was eliminated from the model.

Weighting of Evidential Themes

Contrast values were calculated for geology, elevation, and aspect evidential themes. In selecting optimal weights for creating binary evidential maps, we took a conservative approach and restricted the model to classes with highest contrast values.

Training points occurred on 23 of 85 geologic types in the study area (model 1, Table 1). Four geologic types had contrast values <0.5 , five had values of 0.5–1.0, seven had values of 1.0–2.0, and 7 had values >2.0 . The 15 geologic types with contrast ≥ 0.966 (strongly predictive) were classified as ‘inside’ for model 1, and the remaining 70 were classified as ‘outside’. Of 58 training sites, 42 (72%) fell within these 15 geologic types. This criterion was used to provide a prediction that was tightly focused on the most favorable geologic types.

Model 1 contrast values for aspect and elevation are graphed in Figure 2. For aspect classes 4–10, representing compass bearings from east-northeast to south-southwest (67.5° – 247.5°), contrast was generally positive with moderate to strongly predictive values. The negative value for class 6 (east-southeast aspect) was disregarded as a minor deviation in an otherwise continuous interval. This aspect may represent minor sampling bias in the training set. Aspect classes 4–10 were classified as ‘inside’ and all other aspects as ‘outside’. Of 58 training sites, 41 points (71%) fell within this range of aspects.

Elevation had a bimodal distribution, with classes 6–7 and 11–14 (1492–1688 m and 1983–2376 m) having positive contrast values and most other elevation classes having negative or only weakly positive contrast values (Fig. 2). Contrast values in these 2 class ranges were moderate to strongly predictive. Thirty-nine (67%) training points were associated with these elevation classes. The gap between 1688 and 1983 m may be an artifact of a limited set

TABLE 1. Variation of weights-of-evidence for geologic type ranked by contrast value. Note that the rank for contrast value changes under model 2. The points column is the number of cells containing a training point. Geologic descriptions are Tmi, intrusive mafic; Jd, JTRsv, Osv, Ts3, sedimentary/tuff; Tgr, Kgr, MZgr, granitic; Jgb, Tb, Tba, basalt; Tr2, Tr1, intrusive/rhyolitic; Tt3, Tt2, TRk, volcanic tuff; Dc, Oc, Os, PPc, JTRs, MDs, sedimentary/limestone; and Ta3, andesite.

Geology	Area (km ²)	Model 1		Model 2	
		Points	Contrast	Points	Contrast
Tmi	44	3	5.077	3	4.836
Jd	142	1	2.703	1	2.469
Tgr	229	1	2.223	3	3.125
Jgb	241	1	2.170	1	1.936
Tr2	252	1	2.123	1	1.893
Kgr	2015	7	2.089	11	2.347
Tt3	266	1	2.071	1	1.837
Tb	2111	5	1.665	5	1.416
Dc	1727	4	1.628	6	1.818
TRk	424	1	1.604	1	1.370
JTRsv	1185	2	1.278	3	1.461
Oc	1190	2	1.274	6	2.197
MZgr	2099	3	1.122	4	1.184
Tba	4676	6	1.049	6	0.795
Ta3	3298	4	0.966	5	0.959
Os	991	1	0.746	1	0.513
PPc	994	1	0.744	1	0.510
JTRs	2020	2	0.737	2	0.499
Osv	1100	1	0.641	1	0.407
Tr1	1319	1	0.458	1	0.224
MDs	1415	1	0.387	1	0.153
Tt2	10651	7	0.345	7	0.087
Ts3	4004	2	0.035	2	-0.201

of training sites. However, another possibility relates to topography. The base elevation for mountain ranges in central and eastern Nevada is higher than in the western part of the state. The 1688–1983 m elevation range approximately coincides with the elevation of basin floors and alluvial fans in central and eastern Nevada. These geomorphic features rarely preserve fossil middens due to repeated periods of erosion and deposition. For the purpose of constructing the model, we followed the data and classified elevations 6–7 and 11–14 as ‘inside’ and all others as ‘outside’.

Validation

To validate the model, we randomly selected a set of 1-km² sites to field-search. We placed a 1-km² lattice within an 8-km buffer of all major roads in the study area. In testing the model, we chose to follow a conservative, practical approach. If a randomly chosen 1-km² site inside the 8-km buffer had at least 3 high-probability cells (approximately 25% of the plot), it was considered a high-probability site and included for field-checking. We

selected 75 sites for potential field-checking. Selected sites averaged 6 high-probability cells (approximately 50% of the plot). The intent of the model was to guide a user to the best potential sites for collecting fossil middens. We felt that if at least 25% of any given 1-km² area was predicted to have middens, that was sufficient information to locate a site that should contain fossil middens.

We selected both a moderate- and low-probability site within a 25-km² matrix near each high-probability site to test the accuracy of our predictive criteria. The 25-km² matrix was subjectively placed so that secondary sites were never farther from a main road than the primary site. Within this matrix, however, secondary sites were randomly selected. If no moderate- or low-probability sites were available within the matrix, then the nearest available site was chosen. We chose this approach for efficiency. The study area covered 120,000 km², and although secondary sites may not be truly independent, we wanted to visit the maximum number of sites within the limited time available for fieldwork.

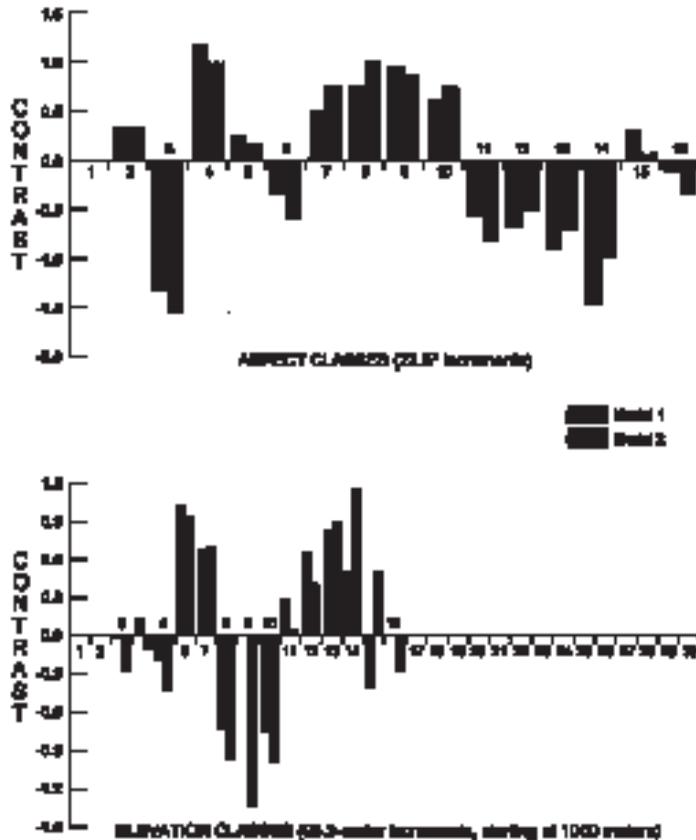


Fig. 2. Contrast values for aspect and elevation evidential themes for model 1 and model 2. Abscissas represent the entire range found in the study area. Aspect classes represent 22.5° increments (1 = 0°–22.5°, 2 = 22.5°–45°, etc.). Elevation classes represent 98.3-m increments.

At each validation site we walked the entire 1-km² plot looking for collectible fossil middens, defined as having a brown to black weathering rind and a volume of no less than 1–2 L. In a few cases poor road access and vertical terrain prevented searching on foot. Here we used high-powered sighting scopes to search the site. Our experience has shown that caves with middens can be positively identified with this method, although we verified such sightings on foot whenever possible. In only 1 case did we sight middens through the scope that we could not actually get close to for positive identification, and this was on a moderate-probability site. New midden locations found during the validation process were added to the training set for the 2nd model run.

RESULTS

Two models predicting distribution of middens were created from reclassified evidential themes. Model 1 had an acceptable conditional independence ratio of 0.87. Prior probability of a random cell containing a fossil packrat midden was 0.0005. Posterior probability for each combination of class values is given in the unique conditions table (Table 2). Geology was clearly the most important variable in determining probability of fossil midden locations (Table 3). For purposes of this study, we considered ranking of probabilities as sufficient.

Under the model all cells that were strongly predictive for all 3 themes, geology, aspect, and elevation, had a probability of 0.0067. Nineteen training points (33%) were in this category.

TABLE 2. Unique conditions table for the 3 evidential themes, geology, elevation, and aspect, used in model 1 and model 2 where 2 = desired condition present and 1 = desired condition absent. The points column is the number of training points with that unique condition. Value simply ranks each unique condition by probability.

Value	Geology	Elevation	Aspect	Points	Area (km ²)	Probability
MODEL 1						
1	2	2	2	19	4,285	0.0067
2	2	2	1	7	4,710	0.002
3	2	1	2	10	5,044	0.002
4	2	1	1	6	5,845	0.0005
5	1	2	2	11	14,727	0.0005
6	1	2	1	2	19,336	0.00015
7	1	1	2	1	25,397	0.00014
8	1	1	1	2	40,765	0.00004
MODEL 2						
1	2	2	2	23	2,908	0.0123
2	2	2	1	8	3,113	0.0035
3	2	1	2	10	2,787	0.0031
4	2	1	1	5	3,105	0.0009
5	1	2	2	15	17,551	0.0008
6	1	2	1	6	22,553	0.0002
7	1	1	2	4	26,208	0.0002
8	1	1	1	2	41,886	0.00006

These cells represented the highest probability of containing a fossil midden according to the model and were classified as high (Fig. 3). Total area of high-probability cells was 4285 km², equal to 3.5% of the study area.

Cells that were strongly predictive for geology plus either elevation or aspect had a probability of 0.002. Seventeen training points (29%) were in this category. The probability of a midden's being on these sites was higher than the prior probability that assumed random distribution, and these cells were classified as moderate.

If a cell was only strongly predictive for geology, or elevation and aspect, the probability of its containing a midden was no better than random (0.0005), and these sites were classified as low. Another 17 training points (29%) were in this category. The remaining area had a posterior probability (0.00014) below the prior probability, and these sites were classified very low. Five training points (9%) were in this category. The map of probability classes (Fig. 3) was used to select sites to validate the model.

We field-checked 21 of 75 sites randomly selected from across the entire study area. Limited field time (6 d) and difficult access over a large area prevented us from visiting more sites. Sixteen sites were on limestone/sedimentary (Oc, Dc), granite (Kgr, Tgr, MZgr), or andesite/volcanic tuff (Ta3), and 5 sites were

on basalt (Tb). The 6 other geologic types used in the model (Tmi, Jd, Jgb, Tr2, Tt3, and TRk) are each limited in extent (total area for these rock types ranged between 43 and 425 km²). None of the randomly chosen sites fell on these geologic types.

Fossil middens were found on 8 of 21 sites (38%). This percentage is significantly higher than the probability predicted by the model ($\chi^2 = 422.48$, 1 df, $P < 0.001$). Of these 8 sites, all had middens on the high-probability plots, 5 had middens on moderate-probability plots, and 2 on low-probability plots for a total of 15 new midden locations. Four sites (8 middens) were on granitic rock, 3 (6 middens) on limestone/sedimentary, and 1 (1 midden) on a volcanic welded tuff. None of the basalt sites held middens.

We added the 15 new midden sites discovered in validating model 1 to the training set and reran the model to test whether contrast

TABLE 3. Weights and contrast values for each evidential theme used in model 1. Each theme is reclassified into a binary map prior to running the model using the classes 'inside' or predictive (W⁺) and 'outside' or not predictive (W⁻). A strongly predictive theme produces a higher contrast value.

Theme	W ⁻	W ⁺	Contrast
Geology	-0.8905	1.8519	2.7424
Elevation	-0.7609	0.6192	1.3801
Aspect	-0.7149	0.5494	1.2643

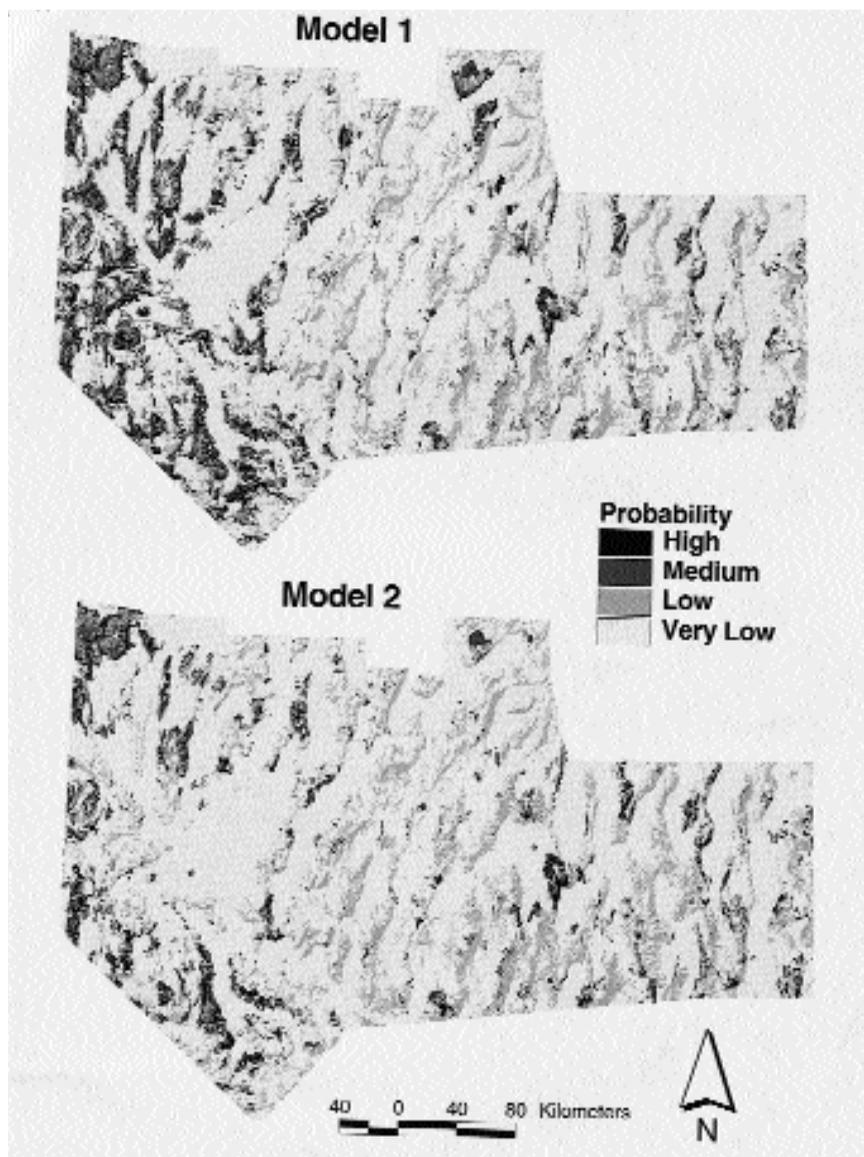


Fig. 3. Map of probability classes for model 1 and model 2 (levels are defined in the text).

values strengthened and posterior probability improved. As expected, contrast values changed for geologic types with additional training points (model 2, Table 1). The order of rank also changed; however, the 15 geologic types used in the 1st model still had highest overall contrast values. For model 2, contrast values >1.0 were classified as 'inside' for geology, which removed Ta3 from the predictive set. The large area (3298 km²) coupled with low number of points (5 training points) makes this geologic type only moderately predictive. With

more training points this geologic type may prove to be a reliable predictor.

Contrast values for aspect and elevation are graphed in Figure 2. For aspect, classes 4–10, representing compass bearings from east-northeast to south-southwest (67.5° – 247.5°), continued to have highest contrast and were classified as 'inside'. The addition of sites at higher elevations shifted significant elevation classes so that classes 6–7 and 11–15 (1492–1688 m and 1983–2474 m) were classified as 'inside'.

Prior probability for model 2 improved to 0.0006. The test for conditional independence returned a value of 0.86, an acceptable level of conditional independence. Posterior probability for each possible combination of class values is given in the unique conditions table (Table 2). Posterior probability values were mapped as 4 generalized classes, >0.004 (high), >0.001 and ≤ 0.004 (moderate), >0.0003 and ≤ 0.001 (low), and ≤ 0.0003 (very low; Fig. 3). Posterior probability for cells with optimal geology, aspect, and elevation was 0.012. Probability was higher than in model 1 because total area within the highest probability was reduced to 2908 km² (2.4% of the total study area) and number of training points increased from 19 to 23. Eighteen training points (25%) were on cells with a probability of 0.0031–0.0039 that we ranked as moderate because the value was greater than prior probability but lower than highest probability. Twenty sites (27%) were located on cells with a probability roughly equivalent to prior probability and were ranked low, and 12 sites (16%) were below prior probability

DISCUSSION AND CONCLUSIONS

Our purpose was to construct a GIS model from a small training set that would rank suitable sites for finding fossil *Neotoma* middens across a large portion of Nevada. The model performed well in both limiting the area to search and guiding us to collectible fossil middens. The high-probability category in model 1 reduced the search area to 3.5% of the total study area. Field validation of the model found fossil middens on 38% of the sites. This percentage was significantly higher than the probability predicted by the model and suggests that middens are particularly common on high-probability sites. A 2nd model with additional data changed probability values. Additional training data would likely result in a refinement of the ranking of key geologic types, improving the model as a field research tool.

The model performed well ranking the probability of potential midden occurrence within a site. Eight field-checked sites had middens on high-probability sites. Only 5 of these also had middens on moderate-probability sites, and 2 had middens on low-probability sites. In no cases did we find middens at

low- or medium-probability sites but not at high-probability sites. This suggests that when the model predicts an area is likely to have middens, they may also be found in proximity to highest probability sites, although the greatest likelihood of finding a midden is on high-probability sites.

We have demonstrated that the model can accurately predict the most common sites for fossil middens. Our goal now is to refine the model and improve our ability to predict very old middens and middens on low-probability sites. Pleistocene-age middens tend to be in more specialized locations, and as more data become available, the model could be refined to focus on these sites. Approximately 40% of training points ended up on sites with low or very low probability of having middens. We need to examine additional evidential themes that may help predict middens on these types of sites. For example, our field-testing included 5 sites on basalt, none of which contained middens. Although basalt had a relatively high contrast value in the initial model, fossil middens are usually found at the edge of flows where cliff faces form. Much of the area dominated by flood basalts in Nevada may have little chance of containing a midden; however, if we can use GIS to identify cliff faces within basalt, we may increase the probability of finding middens associated with this geology. Basalt and andesite cover large portions of western Nevada and have potential for containing fossil middens. These geologic types and others warrant further research to improve our search criteria.

The weights-of-evidence method used in this analysis demonstrates that with a limited set of known sites, and a simple set of search criteria in the form of digital maps, a well-defined model can be constructed that is both predictive and testable. A larger training dataset can potentially produce a model with very high predictive value. Although the software was designed for mineral exploration, it has been successfully applied in a biological context. The method has wide potential application for problems requiring identification and understanding of habitat for specialized taxa, or for a variety of exploration questions, including finding populations of rare and endangered species or identifying potential archaeological sites. Continued development of high-resolution digital datasets will enhance our

ability to improve field exploration through the use of geographic information systems.

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CARBON ISOTOPE DISCRIMINATION AND WATER RELATIONS OF OAK HYBRID POPULATIONS IN SOUTHWESTERN UTAH

David G. Williams¹ and James R. Ehleringer²

ABSTRACT.—The evergreen oak *Quercus turbinella* and the deciduous *Q. gambelii* form natural hybrids in southwestern Utah and northern Arizona. Hybrid individuals also are found in northern Utah in a region where only *Q. gambelii* currently exists, indicating that *Q. turbinella* has recently retreated southward. Our objectives were to (1) examine the ecophysiology of parental taxa and hybrids under natural conditions in southeastern Utah, and (2) investigate the level of integration between leaf carbon isotope discrimination (a synthetic gas exchange trait) and structural and chemical traits of leaves in morphologically variable hybrid populations. Leaf length, width, mass-to-area ratio (LMA, g m^{-2}), and nitrogen concentration (N, g g^{-1}) within 2 hybrid populations near New Harmony, Utah, were highly intercorrelated. Variation within the hybrid populations spanned mean values for these traits observed in parental taxa from adjacent “pure” populations of each species. Carbon isotope discrimination (Δ), an integrated measure of the ratio of intercellular to ambient CO_2 concentration, ranged from 16.1‰ to 19.6‰ within the 2 hybrid populations and was positively correlated with leaf nitrogen concentration and negatively correlated with LMA; individuals in hybrid populations with leaves resembling *Q. gambelii* had the highest leaf Δ and N concentrations and lowest LMA compared with leaves from plants that resembled *Q. turbinella*. CO_2 uptake is limited by stomatal conductance and possibly by mesophyll resistance to a greater extent in *Q. turbinella* phenotypes than in intermediate or *Q. gambelii* phenotypes. δD of stem xylem water (an indication of active rooting depth) and predawn water potential during the peak monsoon period in August were not correlated to leaf Δ values within the hybrid populations. Several individuals that were morphologically similar to *Q. turbinella* in the hybrid populations maintained high predawn water potentials and derived moisture from winter recharge that presumably was taken from deep soil layers. Apparently, a few adult individuals of the *Q. turbinella* phenotype in hybrid populations accessed water from deep in the soil profile, which enabled them to avoid summer drought. Reduced monsoonal activity may have been an important, but not the single, determinant of *Q. turbinella*’s retreat from northern Utah during the recent Holocene.

Key words: oak hybrids, *Quercus turbinella*, *Quercus gambelii*, leaf structure, leaf nitrogen, carbon isotope discrimination, $\delta^{13}\text{C}$, δD , water potential.

Fossil records reveal dramatic shifts in woody species’ distributions during the late Pleistocene through the recent Holocene in the American Southwest (Van Devender and Spaulding 1979, Spaulding and Graumlich 1986, Betancourt et al. 1990, Miller and Wigand 1994). One such migration involves the southward retreat of *Quercus turbinella* Greene, an evergreen diffuse-porous oak, from northern Utah. This species hybridizes with *Quercus gambelii* Nutt., a deciduous ring-porous oak, in contact zones in southwestern Utah and northwestern Arizona (Cottam et al. 1959). Relict hybrid clones occur in northern Utah along the western front of the Wasatch Mountain Range almost 400 km north of the current contact zone (Fig. 1). Cottam et al. (1959) argued that hypsithermal warming was

responsible for the northward migration of both species through the Arizona-Utah region, and more recent cooling has resulted in extirpation of the evergreen *Q. turbinella* from northern Utah, leaving behind the more cold-tolerant hybrid individuals. Neilson and Wullstein (1983, 1985), however, found that successful seedling establishment in both *Q. turbinella* and *Q. gambelii* depends on summer moisture and argued that the northern range limits for both species are controlled synergistically by 2 distinct air mass boundaries: the polar front that controls the probability of late spring frost, and the summer “monsoon” that controls summer moisture availability. Biogeographic implications of seedling stress tolerance and demography, however, do not reveal why hybrid individuals have persisted and

¹School of Renewable Natural Resources, University of Arizona, Tucson, AZ 85721.

²Department of Biology, University of Utah, Salt Lake City, UT 84112.

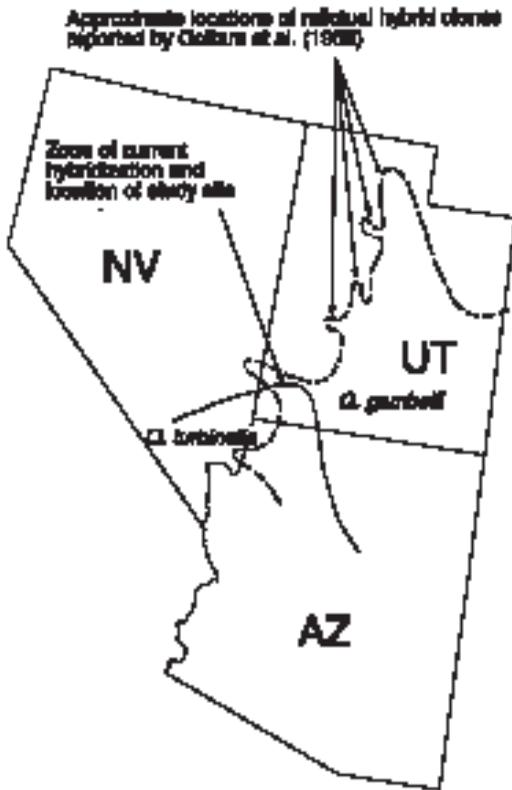


Fig. 1. Map of current northern boundaries of *Quercus gambelii* and *Q. turbinella* in the Intermountain region and location of relict hybrid clones in north central Utah. Map is based on information in Cottam et al. (1959) and Little (1971).

adult *Q. turbinella* individuals have disappeared from northern Utah in spite of the fact that clones of these oaks have long life spans.

The present northern limit of *Q. turbinella* is geographically more closely related to the sharp summer moisture gradient in the Southwest than is that of *Q. gambelii*. Ecophysiological studies conducted in natural populations and in common gardens reveal that adult individuals of *Q. gambelii* do not take up summer precipitation but instead use winter moisture stored in deep soil layers during the growing season (Phillips and Ehleringer 1994). Ehleringer and Phillips (1996) demonstrated that adult *Q. turbinella* in a common garden near Salt Lake City, far north of *Q. turbinella*'s present northern boundary, took up water from shallow soil layers following summer rains. The tradeoff associated with having roots deployed in shallow soil layers is that

plants experience very low and potentially damaging soil water potentials during the summer months in the absence of significant monsoon storms. Hybrid individuals between these 2 oaks appear to have an intermediate rooting depth that allows them to persist in the summer-dry region of northern Utah, where the intensity of the summer monsoon has apparently declined over the recent Holocene. Greater drought tolerance and higher water-use efficiency are commonly found among species or populations that extract water only from shallow soil layers compared to taxa that have access to a stable water source deep in the soil profile (Knapp and Fahenstock 1990, Flanagan et al. 1992, Williams and Ehleringer 1996). Ehleringer and Phillips (1996) and Ehleringer and Smedly (1988) showed that stomatal conductance is lower and carbon isotope discrimination (Δ) is higher in the drought-tolerant *Q. turbinella* compared to that in the moisture-requiring *Q. gambelii*. In C_3 plants, Δ depends upon c_i/c_a , the ratio of internal to ambient CO_2 concentration (Evans et al. 1986, Farquhar et al. 1989) and thus records the tradeoff between biochemical demand for CO_2 by photosynthetic enzymes in the chloroplasts and CO_2 supply through the stomata. Flanagan et al. (1992) found that leaf Δ and depth of water extraction from the soil (inferred from δD values of xylem water) were positively correlated among 4 woody species of the pinyon-juniper ecosystem in southern Utah. Since Δ is often correlated with stomatal conductance and water-use efficiency, it is an important parameter for unraveling the potential effects of hybridization on the water balance of woody perennials such as oak.

Hybrid oak populations in southern Utah also are useful for examining leaf structural and physiological controls on photosynthesis. The dependence of carbon isotope discrimination (Δ) on leaf structural and chemical traits is typically studied at the interspecific and interpopulation level (Vitousek et al. 1990, Meinzer et al. 1992, Sparks and Ehleringer 1997). Generally, Δ has been shown to decrease with leaf mass-to-area ratio and leaf nitrogen content. The *Q. gambelii* \times *Q. turbinella* hybrid zones are intriguing because these species represent extreme leaf morphological types; small, thick-leaved *Q. turbinella* grade into large, thin-leaved *Q. gambelii* types in these extremely

variable hybrid populations. Integration between leaf structural and chemical traits and carbon isotope discrimination should be retained in these hybrid populations if c_i/c_a is strongly controlled by these characters.

This study evaluated plant water relations, leaf Δ , and leaf structural and chemical traits in *Q. gambelii*, *Q. turbinella*, and their natural hybrids in southwestern Utah. We predicted that these 2 oaks would show differential capacities to take up summer rains in this natural setting and that hybrids would have intermediate water use and leaf gas exchange characteristics, similar to patterns observed in F1 hybrids in common gardens in Salt Lake City (Ehleringer and Phillips 1996). Of interest also was whether leaf structural and chemical traits that are often linked to Δ also would be correlated to Δ in hybrid populations, where there is a high potential for loss of trait integration because of recombination and back crossing.

MATERIALS AND METHODS

The study was conducted in southeastern Utah in Washington County near the town of New Harmony within a large area of hybridization between *Quercus gambelii* and *Q. turbinella* (Fig. 1). Hybridization between these 2 oak species contributes to substantial leaf morphological variation in this area (Cottam et al. 1959, Tucker et al. 1961). Two hybrid populations were selected for study. Hybrid population 1 (HP1; 37°30'N, 113°19'W, 1707 m), located on a broad alluvial terrace above an ephemeral drainage (Pace Draw), is approximately 5 km north of the town of New Harmony. Hybrid population 2 (HP2; 37°30'N, 113°19'W, 1713 m) is 2 km northwest of HP1 near the same drainage. Vegetation at both sites is open scrub-oak woodland.

Twelve plants were selected from within each of these 2 hybrid populations for detailed morphological and physiological measurements. All plants used in the study were multi-stemmed adult plants and were 2–4 m in height. Plants were selected haphazardly with the intent of including the full range of leaf morphological variation that distinguishes the 2 oak species. Between 8 and 10 leaves were collected for morphological analysis on 24 August 1994 from each selected plant in the 2 hybrid populations and also from 5 plants from 1 nonhybrid population of each *Quercus*

species. The “pure” stand of *Q. gambelii* (37°31'N, 113°20'W, 1798 m) was 3 km northwest of HP2 at the mouth of a mesic canyon feeding the drainage that passes near HP1 and HP2. The nonhybrid population of *Q. turbinella* was approximately 18 km south of New Harmony (37°20'N, 113°18'W, 1340 m).

Blade length, width, 1-sided area, and dry mass were determined for each leaf collected from the populations and averaged for each plant. Leaf mass-to-area ratio (LMA, g m^{-2}) was calculated from average mass and 1-sided area values from the leaves collected from each plant. These same leaves were analyzed for stable isotope ratios of carbon ($\delta^{13}\text{C}$) and total nitrogen concentration (N , g g^{-1}). $\delta^{13}\text{C}$ was determined on finely ground, oven-dried (70°C for 48 h) blade tissue using an isotope ratio mass spectrometer (Delta S, Finnigan MAT, San Jose, CA) attached on-line to a CHN combustion furnace at the University of Utah Stable Isotope Facility for Environmental Research (SIRFER). $\delta^{13}\text{C}$ was converted to carbon isotope discrimination values (Δ) using an atmospheric $\delta^{13}\text{C}$ value of -8‰ (Ehleringer and Osmond 1989, Farquhar et al. 1989). Nitrogen concentration was measured on these same samples using a Perkin-Elmer 2400 CHN analyzer (Norwalk, CN).

Predawn leaf water potential (Ψ_{pd}) was determined for the same plants sampled above from all populations on 25 August 1994 using a Scholander-type pressure chamber (PMS Instruments, Corvallis, OR). Ψ_{pd} was measured between 0300 and 0530 h local time within 1 to 2 min after twigs were cut from the plants to minimize changes in Ψ due to water loss.

Plant water sources (winter recharge or summer monsoon-derived soil moisture) were inferred from δD values of plant xylem water. Although we did not measure isotopic values of soil, precipitation, or groundwater, it has been shown repeatedly for this region that winter moisture stored in deep soil layers is depleted in deuterium compared to water from surface soil layers that has been subjected to evaporative enrichment and mixed with isotopically heavy summer precipitation (Ehleringer et al. 1991, Flanagan et al. 1992, Phillips and Ehleringer 1994). Our interest here was simply to evaluate the covariation of δD with other physiological measurements rather than to identify the exact depth of water extraction by these trees or the proportion of water

obtained from different sources. We cut 3–4 suberized twigs at midday from different locations on a tree canopy the same day that Ψ_{pd} measurements were taken. Cut twigs were immediately enclosed and sealed in screw-cap glass vials using Parafilm and kept frozen in the lab until water was extracted using a cryogenic vacuum distillation technique (Ehleringer and Osmond 1989). Samples were then prepared for hydrogen isotope analysis by reacting 3 μL of the extracted water with 100 mg of zinc at 500°C for 1 h in sealed Pyrex tubes (method modified from Coleman et al. 1982). Zinc was obtained from J.M. Hayes, Departments of Chemistry and Geology, Indiana University. Hydrogen gas was analyzed for δD in the same manner as for $\delta^{13}\text{C}$ at SIRFER. Standard lab waters were calibrated against samples of the international standards GISP and V-SMOW and were used in linear corrections of raw values obtained from the mass spectrometer.

Correlation, linear regression, and t tests were used to evaluate leaf morphological variation within and between oak populations and the associations between plant ecophysiological characteristics, leaf morphology, and chemistry. All analyses were performed using the JMP statistical software for Macintosh (Version 3.1, SAS Institute Inc. 1995).

RESULTS

Data for leaf structural and chemical traits were pooled between the 2 hybrid populations to examine broad trends for these characteristics. Blade length, width, LMA, and N concentration within the 2 hybrid populations were highly intercorrelated (Table 1). As expected, blade length, width, and area were all positively correlated. LMA was negatively correlated to length, width, and area, indicat-

ing that larger leaves were also thinner and likely contained less mesophyll tissue per unit leaf surface area. Conversely, leaf N concentration was positively correlated to leaf size. Because LMA declined with leaf size and N concentration increased in these hybrid populations, leaf N content (mmol N m^{-2}) was constant over the range of leaf sizes (Table 1).

Leaf structural and chemical traits for plants in hybrid populations (HP1 and HP2) had values that spanned the range found in leaves from the 2 nonhybrid populations (Table 2). Leaves differed significantly between nonhybrid populations of *Q. gambelii* and *Q. turbinella* for all morphological traits and for leaf N concentration (Table 2). Larger leaves of *Q. gambelii* had lower LMA, higher N, but did not differ from leaves of *Q. turbinella* for leaf N content. Plants in the 2 hybrid populations, because of the high degree of trait variation, did not differ significantly from each other for any leaf morphological or chemical trait (Table 2).

Dependence of carbon isotope discrimination (Δ) on leaf structural and chemical traits and plant water relations traits in the 2 hybrid populations were evaluated by regression (Figs. 2, 3). Variation in Δ was related significantly to leaf N concentration and LMA, but not to leaf nitrogen content (Fig. 2). Δ ranged almost 4‰ within these hybrid populations, with plants resembling *Q. turbinella* (high LMA and low leaf N concentration) having the lowest Δ values (near 16‰), and plants with leaves resembling those of *Q. gambelii* (low LMA and high N concentration) having the highest Δ values of up to 20‰.

Several rain events that preceded our sampling provided necessary conditions to evaluate water source variation within hybrid populations. Ψ_{pd} and δD were highly variable

TABLE 1. Pearson correlation coefficients for leaf morpho-physiological traits within a *Quercus gambelii* \times *Q. turbinella* hybrid zone. Data for the correlations were from average per leaf values from each plant and are pooled from 2 hybrid populations near New Harmony, Utah. Correlation coefficients in italics are significant ($P < 0.05$) after sequential Bonferroni corrections for multiple comparisons (Rice 1989).

	Leaf length	Leaf width	Leaf area	LMA	N (%)
Leaf width	<i>0.98</i>				
Leaf area	<i>0.97</i>	<i>0.97</i>			
LMA	<i>-0.83</i>	<i>-0.81</i>	<i>-0.80</i>		
N (%)	<i>0.81</i>	<i>0.83</i>	<i>0.75</i>	<i>-0.77</i>	
N (mmol m^{-2})	<i>-0.29</i>	<i>-0.23</i>	<i>-0.32</i>	<i>0.52</i>	0.11

TABLE 2. Mean ($\pm s_{\bar{x}}$), range (min, max), and significance levels (t tests) of leaf structural and chemical traits for nonhybrid and hybrid populations of *Quercus turbinella* and *Q. gambelii* near New Harmony, Utah, in August 1994. Parameters and hybrid populations are as in Figure 2.

Leaf trait	Nonhybrid populations			Hybrid populations		
	<i>Q. turbinella</i>	<i>Q. gambelii</i>	t test	HP1	HP2	t test
Length (mm)	26.9 (1.6) (23.1, 31.9)	80.8 (3.1) (70.3, 83.5)	***	57.0 (8.1) (27.2, 103.5)	47.6 (6.2) (25.0, 88.7)	n.s.
Width (mm)	19.3 (0.7) (17.7, 22.0)	53.2 (1.6) (48.4, 58.6)	***	36.7 (5.8) (16.2, 66.1)	33.2 (4.5) (15.4, 58.8)	n.s.
Area (cm ²)	24.9 (8.2) (15.1, 36.1)	138.2 (24.4) (108.8, 173.4)	***	65.5 (18.9) (22.3, 215.1)	56.4 (17.0) (20.8, 172.3)	n.s.
LMA (g m ⁻²)	199 (4) (188, 210)	115 (2) (110, 123)	***	143 (9) (100, 185)	160 (7) (111, 206)	n.s.
N (%)	1.2 (0.1) (1.0, 1.3)	2.0 (0.1) (1.8, 2.1)	***	1.8 (0.1) (1.4, 2.3)	1.7 (0.1) (1.2, 1.9)	n.s.
N (mmol m ⁻²)	173 (9) (140, 189)	161 (7) (143, 175)	n.s.	174 (7) (123, 207)	189 (7) (145, 226)	n.s.

*** $p < 0.001$

within hybrid populations; Ψ_{pd} ranged from -1.5 to -0.2 MPa and δD ranged from -90% to -58% . Groundwater and integrated summer precipitation collected from a site in Zion National Park, approximately 50 km to the east of our hybrid population site and at a similar elevation, were 95% and 30%, respectively. Surprisingly, the regression of leaf Δ on plant δD or Ψ_{pd} was not significant when hybrid populations were analyzed separately or together (Fig. 3). Although these water relations traits were not correlated with Δ , Ψ_{pd} was strongly correlated with δD (Fig. 4). Ψ_{pd} declined as δD increased across the 2 hybrid populations.

Although leaf N concentration differed significantly between the 2 nonhybrid populations (Table 2), Δ did not (Table 3). Leaf carbon isotope discrimination, furthermore, was substantially higher in the pure *Q. turbinella* population than would be predicted from relationships found in hybrid populations (Fig. 2). Δ was high in the nonhybrid population of *Q. turbinella* even though Ψ_{pd} was low. δD values for individuals within the nonhybrid *Q. turbinella* population were higher than for *Q. gambelii*, but these were not significantly different (Table 3).

DISCUSSION

Reduced monsoonal activity over the recent Holocene may have contributed to the extinc-

tion of *Quercus turbinella* from northern Utah, but other climatic factors cannot be eliminated as possible causes. Although the present study was limited in scope, we found few differences among intermediate and parental phenotypes of *Q. gambelii* and *Q. turbinella* for summer precipitation use in hybrid populations in southwestern Utah. A few individuals that morphologically resembled *Q. turbinella* within the hybrid populations had δD values that were identical to that of winter precipitation, and these same individuals had high predawn water potentials. Presumably, these *Q. turbinella* phenotypes avoid drought through the summer because of their access to water stored in deep soil layers. However, more detailed isotopic and root profile studies would be needed to verify this hypothesis. If our water relations measurements represent general patterns for the entire growing season, then at least some *Quercus turbinella* phenotypes have the potential to persist and maintain high physiological activity despite limited access to summer rainfall. Hybrid populations that occurred in northern Utah some time in the past presumably had comparable levels and patterns of variation for these water relations traits. Consequently, loss of monsoonal storms from the region would not have resulted in complete extirpation of *Q. turbinella* or morphologically similar individuals of hybrid origin. Although our conclusions are based on only a single sampling event during 1 yr, both

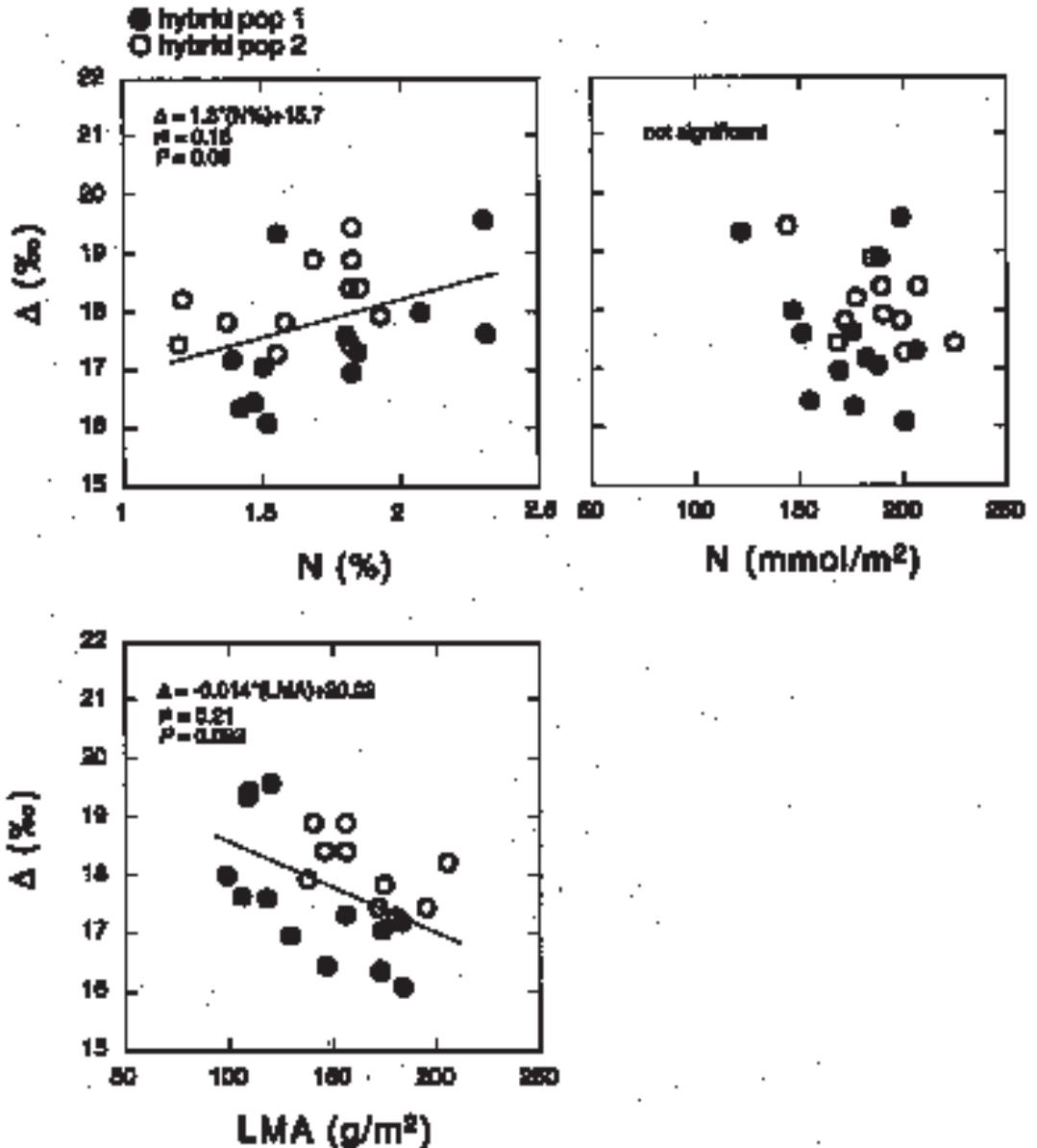


Fig. 2. Dependence of leaf carbon isotope discrimination (Δ) on leaf mass per unit area (LMA, g m⁻²), nitrogen concentration (% g⁻¹), and nitrogen content (mmol N m⁻²) for plants selected within hybrid populations (HP1 and HP2) near the town of New Harmony in southwestern Utah. Regressions were fit to the pooled data for the 2 populations.

hybrid populations in our study yielded similar results.

Based on biogeographic analysis and seedling stress studies, Neilson and Wullstein (1983, 1985) concluded that the northern limit of *Q. gambelii* in Utah is constrained by the summer monsoon gradient and the probability of late spring frost determined by the polar front gra-

dient. In addition to monsoon dynamics, the influence of freeze-thaw cycles may be exceptionally important in controlling the present northern limit of adult *Q. turbinella*. Hydraulic dysfunction caused by frost-induced xylem cavitation can be catastrophic for a diffuse-porous evergreen species (Sperry and Sullivan 1992, Sperry et al. 1994, Pockman and Sperry

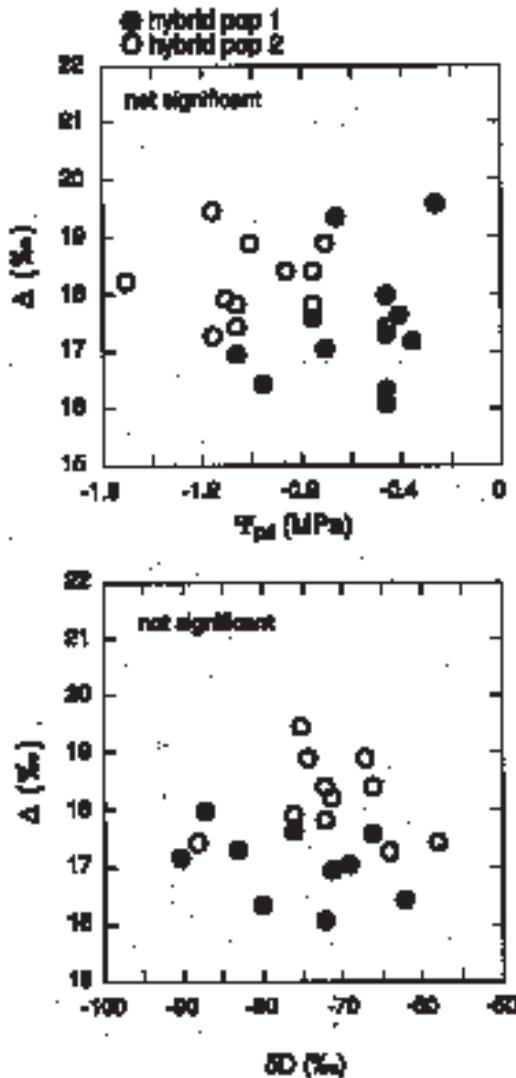


Fig. 3. Dependence of leaf carbon isotope discrimination (Δ) on plant predawn water potential (Ψ_{pd} , MPa) and xylem water isotopic composition (δD , ‰) for plants selected within hybrid populations (HP1 and HP2) near the town of New Harmony in southwestern Utah. Regressions were fit to the pooled data for the 2 populations.

1997). Apparently, the ring-porous *Quercus gambelii* will tolerate >90% loss of hydraulic conducting efficiency during winter and rely on new xylem production prior to leaf-out in spring to sustain high rates of transpiration (Sperry et al. 1994). Hybrid oak clones found in northern Utah are deciduous and potentially cope with freeze-thaw cycles in a manner similar to that in *Q. gambelii*. Neither the refilling of cavitated vessels with positive root

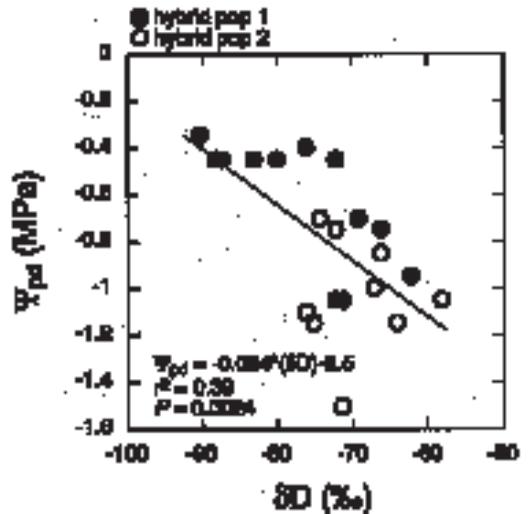


Fig. 4. Dependence of plant predawn water potential (Ψ_{pd}) on δD of xylem water for plants selected within hybrid populations (HP1 and HP2) near the town of New Harmony in southwestern Utah. Regressions were fit to the pooled data for the 2 populations.

pressure nor the ability to avoid freeze-thaw cavitation by having very small conducting elements seems like a plausible mechanism allowing the diffuse-porous and evergreen *Q. turbinella* to sustain significant hydraulic conducting efficiency in the cold climate presently characterizing northern Utah (Sperry et al. 1994). This diffuse-porous species likely experiences significant and nonreversible xylem dysfunction on an annual basis.

Carbon isotope discrimination in this study provides indirect evidence that hydraulic efficiency is reduced in *Q. turbinella* phenotypes in hybrid populations growing naturally near New Harmony in southwestern Utah and in an experimental garden at Salt Lake City studied by Ehleringer and Phillips (1996). Variation in Δ can be attributed directly to changes in stomatal conductance affecting c_i/c_a . Adjustments in stomatal conductance, furthermore, accompany changes in hydraulic conducting efficiency following hydraulic dysfunction in *Quercus* (Cochard et al. 1996). Low carbon isotope discrimination values measured in the common garden by Ehleringer and Phillips (1996) in northern Utah and at the northern limits of *Q. turbinella*'s range in the hybrid populations studied here may therefore reflect stomatal responses to reduced xylem conducting efficiency caused by frost. Notably, Δ in

TABLE 3. Mean leaf carbon isotope discrimination (Δ), δD of xylem water, and predawn water potential (Ψ_{pd}) for nonhybrid populations of *Quercus turbinella* and *Q. gambelii* near New Harmony, Utah, in August 1994. Data include $1 \pm s_{\bar{x}}$ (in parentheses) and significance levels from t tests (***, $P < 0.001$).

Plant trait	<i>Q. turbinella</i>	<i>Q. gambelii</i>	t test
Δ (‰)	18.0 (0.2)	18.2 (0.2)	n.s.
Ψ_{pd} (MPa)	-2.0 (0.1)	-0.4 (0.1)	***
δD (‰)	-82 (4)	-94 (6)	n.s.

the nonhybrid population of *Q. turbinella* at lower elevation and on a drier microsite south of New Harmony (18.0‰) was not different from that of *Q. gambelii* found in a common garden in northern Utah (18.8‰) or that of *Q. gambelii* in pure stands near New Harmony (18.0‰). Δ in *Q. turbinella* phenotypes was much reduced in the hybrid populations and in the common garden in Salt Lake City. It is likely that frost, in addition to reduced monsoonal activity, played a role in the loss of adult *Q. turbinella* from northern Utah, but the combination of these climatic effects on this migration requires further study.

Leaf nitrogen concentration was almost twice as high for *Q. gambelii* as it was for *Q. turbinella* in pure and hybrid populations. Bulk leaf N concentration often reflects concentrations of photosynthetic enzymes, pigments, and electron transport components in leaves and is positively correlated with maximum photosynthetic rate within and among species of C_3 plants (Evans 1989) and oaks (Reich et al. 1995). Plants morphologically similar to *Q. gambelii* in the hybrid populations maintained higher Δ (hence higher c_i/c_a) and leaf N concentration compared to *Q. turbinella* phenotypes. The positive relationship between Δ and N concentration in this study is opposite of what is expected if nitrogen forms a suitable proxy for photosynthetic capacity. Higher N (greater photosynthetic capacity) should cause c_i/c_a and Δ to decline, not rise. Furthermore, we found no correlation between Δ and nitrogen content per unit leaf area, and a negative relationship between Δ and LMA. Vitousek et al. (1990) observed similar correlations between leaf $\delta^{13}C$ and LMA for *Metrosideros polymorpha* across an elevational gradient in Hawaii, and attributed $\delta^{13}C$ variation to variation in leaf internal resistance.

High internal resistance reduces CO_2 concentration at sites of carboxylation in the chloroplast and potentially lessens discrimination against $^{13}CO_2$ (Evans et al. 1986). Although we found patterns of leaf carbon isotope variation and LMA in oak hybrid populations that were similar to that reported by Vitousek et al. (1990) for *Metrosideros*, we have no direct estimates of c_i/c_a from instantaneous gas exchange measurements to demonstrate conclusively the magnitude of internal resistance. In any event, some combination of high internal resistance and low c_i/c_a produced the relatively high discrimination values in *Q. turbinella* phenotypes in our study.

Carbon isotope discrimination in the oak hybrid populations was not related to water source (δD) or plant water potential (Ψ_{pd}) during our August sampling period. Tucker et al. (1961) noted that these oak populations apparently have undergone repeated hybridization and backcrossing. Hybridization and further recombination in these populations may have reduced the level of integration between traits that control rooting depth and leaf Δ . Leaf gas exchange traits and rooting patterns appear to be functionally integrated among parental and F1 hybrids in the artificially maintained common garden populations near Salt Lake City (Ehleringer and Phillips 1996), but these traits are not functionally integrated in natural hybrid populations in southwestern Utah. We found no correlation between either predawn water potential or δD and Δ within our hybrid populations (Fig. 3). Introgression of genes into populations of *Q. turbinella* that control development of a deep root system remains a possibility and would explain the high levels of variation in δD among *Q. turbinella* phenotypes in hybrid populations.

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DISTRIBUTION OF THE SUBTERRANEAN AMPHIPOD *STYGOBROMUS*
IN CENTRAL COLORADO STREAMS,
WITH NOTES ON THE INTERSTITIAL COMMUNITY

Steven P. Canton¹ and James W. Chadwick¹

ABSTRACT.—As part of a larger study on the aquatic life of streams in central Colorado, efforts were made to determine the distribution of interstitial organisms, with emphasis on the subterranean amphipod *Stygobromus*. In a preliminary screening-level study, sampling for *Stygobromus* was conducted in 1985 at 47 sites along the Front Range of Colorado at elevations generally matching the type locale for *S. coloradensis* and *S. pennaki* at the confluence of the North Fork of the South Platte River and its mainstem. A more intensive follow-up study was conducted in 1988 at 30 sites concentrating on the upper South Platte River basin. In the follow-up study both hyporheic and shore zone (phreatic) habitats were sampled using a variety of techniques (Bou-Rouch pump, Karaman-Chappuis technique, and a coarse-mesh wide-mouth net, as appropriate). In the preliminary study *Stygobromus* spp. were collected at only 12 of 47 study sites, with all collections in the vicinity of the type locale. In the follow-up study *Stygobromus* were found at 16 of 30 sites sampled, extending the known distribution in Colorado of *S. coloradensis* and *S. pennaki* well beyond the type locale. The use of multiple sampling techniques was important in locating these organisms. In addition to the amphipod *Stygobromus*, sampling sites in the follow-up study contained a rich interstitial community, including copepods, bathynellids, tardigrades, archiannelids, and ostracods.

Key words: *Stygobromus*, Colorado, hyporheic habitat, interstitial organisms.

The subterranean amphipod *Stygobromus* is found in groundwater or groundwater-related habitats throughout the United States (Holsinger 1967, 1974, 1978). There are roughly 100 described species of *Stygobromus*, with at least 30 as yet undescribed species (Holsinger 1978). The majority of recorded species are found in caves (i.e., cave springs, pools, etc.), with other species found in surface springs, wells, seeps, and deep lakes. Two new species, *Stygobromus coloradensis* and *S. pennaki*, were described from the lower North Fork South Platte River, Colorado (Ward 1977), providing the 1st known record of subterranean amphipods from the hyporheic stream gravel environment (Holsinger 1978, 1986). The term subterranean has been expanded in this case to include those species not in direct association with caves, yet still exhibiting the lack of eyes and pigmentation characteristic of cave forms (Holsinger 1986). Prior to the discoveries by Ward (1977), subterranean amphipods had not been reported from Colorado (Pennak and Rosine 1976).

Life histories of *S. coloradensis* and *S. pennaki* are not known. These Colorado species were collected by Ward (1977) only during

April, and in the study by Pennak and Ward (1986), they were also most abundant in spring, generally comprising a mixture of young and mature specimens. *Stygobromus* collected from Lake Tahoe included gravid females (with eggs) from May through December, with immature females, males, and juveniles also present throughout the year (Holsinger 1974). Other western species, which are basically restricted to caves, have been collected at various times throughout the year. What little evidence exists suggests that subterranean amphipods, compared with surface-dwelling amphipods, have longer life spans (>1 yr), produce fewer but larger eggs, and apparently breed continuously at a gradual rate (Holsinger 1986).

The presence of a diverse interstitial community in Colorado streams, in addition to *Stygobromus*, was first described by Pennak and Ward (1986), based on sampling at 1 site on the South Platte River at its confluence with the North Fork, southwest of Denver, Colorado. This work has been followed by additional studies on the South Platte River and other Colorado streams, providing distributional records for a variety of interstitial organisms (Ward and Holsinger 1981, Ward and

¹Chadwick Ecological Consultants, Inc., 5575 S. Sycamore St., Suite 101, Littleton, CO 80120.

Voelz 1990, 1994, Ward et al. 1992), as well as the discovery of new ostracod, copepod, and bathynellid species (Pennak and Ward 1985a, 1985b, Marmonier and Ward 1990, Reid 1992).

The present study was initiated to determine whether the type of interstitial community described by Pennak and Ward (1986) exists at other locations in central Colorado streams, with particular emphasis on the presence of *Stygobromus*.

SAMPLING STRATEGY

A preliminary screening-level study was conducted in the spring and fall of 1985 at over 40 sites along the Front Range of Colorado. This included sites on streams in the

“foothills zone” (Ward and Kondratieff 1992), which resembles the type locale of the North Fork of the South Platte River. Based on results of this preliminary study and Pennak and Ward’s previous study, it appeared that, when found, collections of *Stygobromus* were generally from stream gravels resulting from the decay of Pike’s Peak granite in central Colorado (Ward 1977, Pennak and Ward 1986). Pike’s Peak granite is a fine- to coarse-grained crystalline rock that weathers to a mixture of coarse sands and gravels (Hansen and Crosby 1982, von Guerard 1989). Based on the assumption that these coarse alluvial streambeds may provide suitable habitat for *Stygobromus*, the follow-up study concentrated on sampling

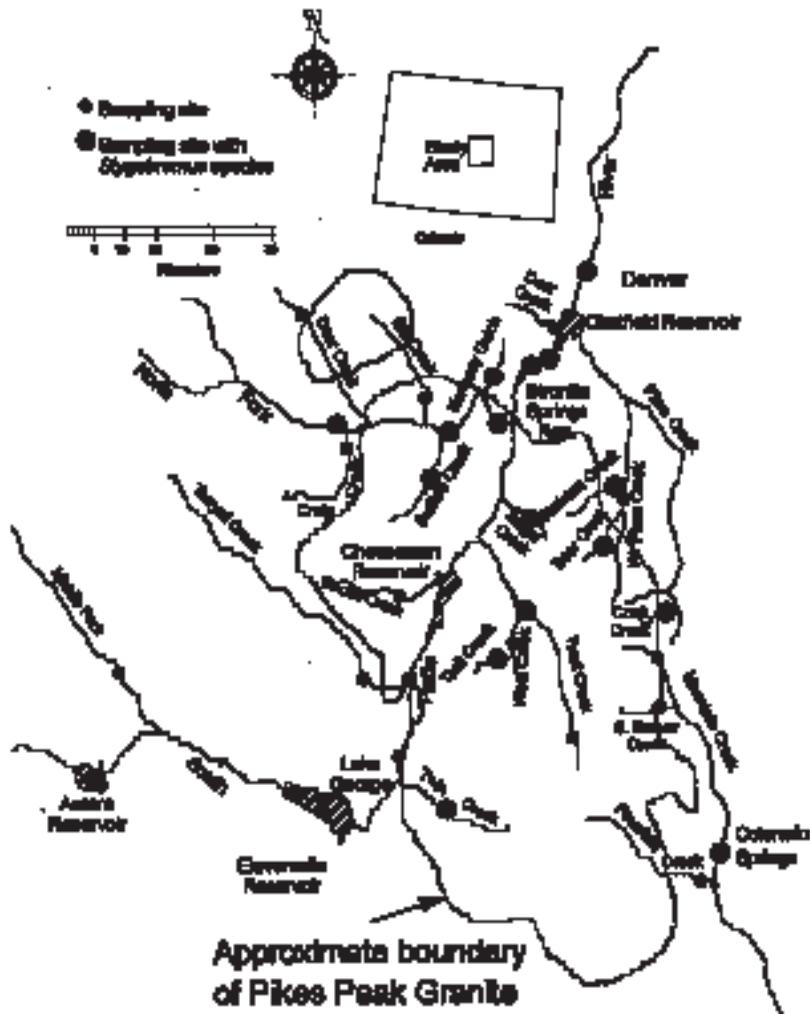


Fig. 1. Sampling locations for the intensive interstitial organisms study in spring 1988.

streams in central Colorado with substrates derived in large part from decomposed Pikes Peak granite (Fig. 1). Sampling was conducted 2 March–28 April 1988 at 30 sites in the South Platte, North Fork South Platte, Plum Creek, and upper Fountain Creek drainages in central Colorado (Fig. 1). *Stygobromus* appear to reach their greatest seasonal abundance in spring (Ward 1977, Pennak and Ward 1986).

During the preliminary study we restricted sampling to the hyporheic zone, which is the interstitial habitat under the streambed (Orghidan 1959). In the later study 2 habitat types were sampled at each stream site. These included (1) the hyporheic zone and (2) the shore zone, which is the boundary between the hyporheic and phreatic environments (Pennak and Ward 1986). These 2 habitats contained the richest assemblage of interstitial organisms in the South Platte River site studied by Pennak and Ward (1986).

METHODS

For the initial screening-level study, we sampled each site using a large-mouth net (90 cm wide by 50 cm high) with a relatively coarse mesh size of approximately 240 μm . This net was anchored to the stream bottom with steel rods. The substrate upstream of the

net was worked with a shovel to a depth of 30 cm. Displaced organisms and debris collected in the net were placed in a jar, preserved with 95% ethanol, and returned to the lab. In the lab, while other organisms were collected, samples were sorted only for *Stygobromus*. Although 240- μm mesh is too coarse for collecting most interstitial organisms, it was considered sufficient for the presence/absence determination of these amphipods in this initial study, given the overlapping cohorts.

In the later follow-up study, we used additional sampling techniques. For both the hyporheic and shore zone habitats, 10-L samples were collected with the Bou-Rouch groundwater pump (Bou 1974) from 50-cm depths when possible (Fig. 2). This was the method employed by Pennak and Ward (1986) in their study. The Karaman-Chappuis technique (Delamare Deboutteville 1960, Kolasa et al. 1987) was also used in the shore zone. This method involves digging a shallow pit in the shore zone adjacent to the stream, allowing it to fill with water, and then collecting 10 L (Fig. 2). Following collection of the water, samples from both the Bou-Rouch pump and Karaman-Chappuis techniques were strained through a plankton net (63- μm mesh) and washed into separate jars using 95% ethanol. The large-mouth (240- μm mesh) net described above

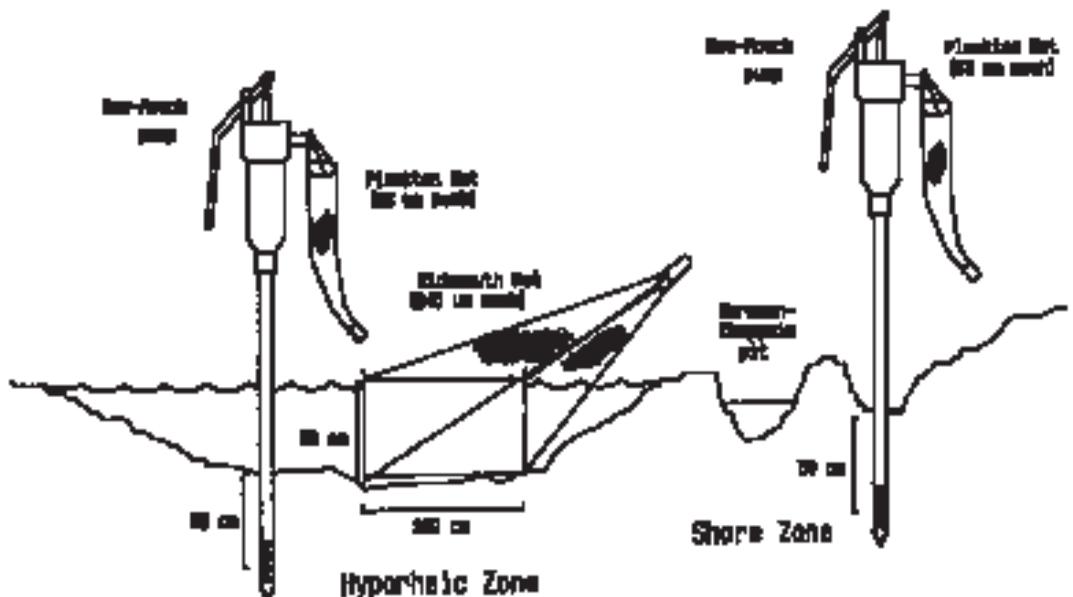


Fig. 2. Schematic representation of sampling methods used for collecting interstitial organisms.

was also used in riffle habitats. In the lab we sorted organisms from all samples from the debris using a dissecting microscope. As before, samples from the large-mouth net were sorted specifically for *Stygobromus* and any larger interstitial organisms, such as cyclopoid copepods. The Bou-Rouch and Karaman-Chappuis samples were sorted for all organisms.

Identification and enumeration of *Stygobromus* specimens were made using keys and descriptions of Holsinger (1967, 1974, 1978) and Ward (1977) and were checked against voucher specimens identified by Dr. John Holsinger, Old Dominion University. Preliminary identifications of other organisms (class or order level) provide additional information on the remainder of the interstitial community.

RESULTS AND DISCUSSION

Results of 1985 Preliminary *Stygobromus* Sampling

In this initial study a total of 219 *Stygobromus* were collected at 12 locations (Table 1). These sites are all near the type locale for these species (Ward 1977), as well as subsequent collections (Ward and Voelz 1990, 1994).

No *Stygobromus* were found at the other 35 sites along the Front Range. Generally when *Stygobromus* were found, both *S. coloradensis* and *S. pennaki* were present. The 3rd Colorado species described by Ward (1977), *S. holsingeri*, was not collected in this study. This species was originally collected from a small intermittent spring west of Fort Collins, Colorado. This spring flows only for a few meters during wet periods (Ward 1977). Although several springs similar to this site were sampled in this study, no *Stygobromus* were collected.

Rarely have 2 related *Stygobromus* species been reported occurring in the same location, usually where their respective distributional ranges overlap (Holsinger 1978). However, this is based primarily on the distribution of *Stygobromus* in the eastern United States, where they are largely restricted to caves and springs. Many western species are being collected from hyporheic and alluvial gravels of streams (Ward 1977, Ward and Holsinger 1981, Stanford and Ward 1988). In these habitats it appears to be rare that 2 or more species *do not* occur together. These 2 species do differ in size, with *S. coloradensis* averaging 3 mm long and *S. pennaki* 4 mm. This size difference

TABLE 1. Sampling locations and dates for sites on which *Stygobromus* spp. were collected in the South Platte River basin, spring 1985.

Location	Date sampled	Number of organisms collected	
		<i>Stygobromus coloradensis</i>	<i>Stygobromus pennaki</i>
NORTH FORK			
Between Kennedy Gulch and Dome Rock			
7.0 km upstream of South Platte River	9 April	7	—
200 m upstream of invertebrate site 8	5 April	17	4
100 m upstream of invertebrate site 8	3 April	17	5
Invertebrate site 8, 0.6 km upstream of	26 March	17	2
South Platte River	5 April	3	2
	9 April	9	5
100 m downstream of invertebrate site 8	5 April	2	3
200 m downstream of invertebrate site 8	5 April	2	—
At confluence with South Platte	5 April	17	5
	9 April	18	7
	6 Nov	30	14
SOUTH PLATTE			
Invertebrate site 6, 4.8 km upstream	19 March	—	2
of North Fork			
100 m upstream of North Fork	9 April	2	—
50 m downstream of North Fork	5 April	1	—
200 m downstream of North Fork	9 April	25	2
Invertebrate site 8, 0.75 km downstream	19 March	—	1
of North Fork			
Total collected		167	52

may allow them to utilize different size-related resources, such as food particle size, intragravel space, etc.

Of particular interest in the preliminary study was the occurrence of both species in a November sample. Earlier attempts to collect *Stygobromus* during fall low flows were not successful (Ward 1977). Both the spring and fall *Stygobromus* collections in this preliminary survey yielded a relatively large number of young and mature specimens of both species.

Results of 1988 Interstitial Sampling Efforts

DISTRIBUTION OF *STYGOBROMUS*.—During the follow-up study 192 *Stygobromus* were collected (Table 2). These again included *S. pennaki* and *S. coloradensis*. In addition, a 3rd, potentially new species was collected that appears to be related to *S. coloradensis* (J.R. Holsinger personal communication). However, too few specimens of this species were collected to allow a true description. Unlike the preliminary study, for these collections *S. pennaki* was generally more abundant than *S. coloradensis* (Table 2).

Prior to this follow-up study, *S. pennaki* and *S. coloradensis* had been reported only from locations on the mainstems of the South Platte River and North Fork South Platte River near their confluence (see above, also Ward 1977, Pennak and Ward 1986). However, in the follow-up study, 1 or both species were collected at 16 of 30 sampling sites, including locations on mainstem and tributary sites in the South Platte, North Fork South Platte, and Plum Creek drainages (Fig. 1, Table 2). The 3rd, undescribed species of *Stygobromus* was found at 2 locations, Monument Creek in the city of Colorado Springs, Colorado, and Twin Creek, directly west of the Monument Creek site near the town of Lake George, Colorado (Fig. 1).

When *Stygobromus* were collected, they were generally found at stream sites either within or downstream of the Pikes Peak granite formation (Fig. 1). This formation generally ranges from just south of Pikes Peak (west of Colorado Springs, Colorado) north to the North Fork of the South Platte River (Tweto 1979). At sites with *Stygobromus*, the substrate largely comprised coarse sands and gravels, consistent with decomposed Pikes Peak granite (von Guerard 1989). Two exceptions were

the collections of *Stygobromus* in Kennedy Gulch and the North Fork upstream of Craig Creek (Fig. 1), just upstream of the reported Pikes Peak granite formation (Tweto 1979). While the presence of stream substrates derived from Pikes Peak granite did not guarantee the presence of these *Stygobromus* species in this study (Fig. 1), these species basically were not found in the absence of such substrate.

***STYGOBROMUS* HABITATS.**—*Stygobromus* were collected primarily from the hyporheic zone of study streams (Table 2), accounting for 75% of total numbers of *Stygobromus* collected during the study. Even when Bou-Rouch samples are compared between habitats, twice as many *Stygobromus* were collected in the hyporheic as in the shore zone. Jackson Creek is the exception: *Stygobromus* were collected only in the shore zone (Table 2). This apparent preference of *Stygobromus* for hyporheic habitats differs markedly from collections of Pennak and Ward (1986) in which *Stygobromus* were found predominantly in the shore zone.

EFFECTIVENESS OF SAMPLING METHODS.—Results of the present study also point to the importance of using a variety of collection techniques. While the Bou-Rouch pump is efficient at collecting interstitial organisms (Pennak and Ward 1986, Ward and Voelz 1990, 1994), it has been shown to be less effective than the Karaman-Chappuis technique in certain situations (Strayer 1988). In the present study we used a wide-mouth net and the Karaman-Chappuis technique in addition to the Bou-Rouch pump. In fact, at 5 sites 1 or both *Stygobromus* species were found only in the wide-mesh net and/or Karaman-Chappuis samples (Table 2). These additional methods provided important distribution information that would have been unavailable had only the Bou-Rouch pump been used.

NOTES ON THE INTERSTITIAL COMMUNITY.—A diverse interstitial faunal assemblage was collected at all 30 sampling sites (Table 3). These interstitial communities were composed of many of the same groups found by Pennak and Ward (1986) at their site on the South Platte River, including both harpacticoid and cyclopoid copepods, ostracods, bathynellids, archiannelid worms, and mites. In addition, other interstitial organisms not found by Pennak and Ward (1986), but reported in later studies (Ward and Voelz 1990, 1994), such as

TABLE 2. Distribution of *Stygobromus* spp. in central Colorado by location, habitat type, and sampling method, spring 1988 (see also Fig. 1).

Sampling site	Hyporheic		Shore zone		Total collected
	Bou-Rouch (no. 10 L ⁻¹)	Surface net (no. sample ⁻¹)	Bou-Rouch (no. 10 L ⁻¹)	Karaman-Chappuis (no. 10 L ⁻¹)	
PLUM CREEK DRAINAGE					
Cook Creek					
<i>Stygobromus pennaki</i>	0	42	NA	NA	42
<i>Stygobromus coloradensis</i>	0	18	NA	NA	18
Bear Creek					
<i>S. pennaki</i>	0	3	NA	NA	3
<i>S. coloradensis</i>	6	1	NA	NA	7
Jackson Creek					
<i>S. pennaki</i>	0	0	1	0	1
FOUNTAIN/MONUMENT CREEK DRAINAGE					
Monument Creek-2					
<i>Stygobromus</i> n.sp.?	0	1	0	0	1
SOUTH PLATTE RIVER DRAINAGE					
South Platte River-2					
<i>S. pennaki</i>	4	19	0	0	23
<i>S. coloradensis</i>	6	9	1	0	16
South Platte River-3					
<i>S. coloradensis</i>	1	0	0	0	1
South Platte River-4					
<i>S. pennaki</i>	9	3	4	4	20
<i>S. coloradensis</i>	1	1	1	0	3
Twin Creek					
<i>S. pennaki</i>	0	0	0	2	2
<i>S. coloradensis</i>	0	0	0	2	2
<i>Stygobromus</i> n.sp.?	0	1	0	0	1
Trout Creek-2					
<i>S. pennaki</i>	0	0	1	2	3
<i>S. coloradensis</i>	1	0	4	4	9
Trail Creek					
<i>S. coloradensis</i>	1	0	NA	NA	1
Sugar Creek					
<i>S. pennaki</i>	5	0	0	0	5
<i>S. coloradensis</i>	2	0	2	0	4
NORTH FORK SOUTH PLATTE RIVER DRAINAGE					
North Fork South Platte River-1					
<i>S. pennaki</i>	0	0	0	5	5
<i>S. coloradensis</i>	0	0	0	7	7
North Fork South Platte River-2					
<i>S. pennaki</i>	1	0	2	0	3
North Fork South Platte River-3					
<i>S. pennaki</i>	0	0	3	1	4
<i>S. coloradensis</i>	1	0	1	1	3
Buffalo Creek					
<i>S. pennaki</i>	3	0	0	0	3
Kennedy Gulch					
<i>S. pennaki</i>	2	0	NA	NA	2
<i>S. coloradensis</i>	3	0	NA	NA	3
Total collected					
<i>S. pennaki</i>	24	67	11	14	116
<i>S. coloradensis</i>	22	29	9	14	74
<i>Stygobromus</i> n.sp.?	0	2	0	0	2
All <i>Stygobromus</i> spp.	46	98	20	28	192

TABLE 3. Preliminary distribution of interstitial organisms in central Colorado streams, 1988 (+ = present).

Site	<i>Stygobromus</i> spp.	Harpacticoid/cyclopoid copepods	Ostracods	Bathynellids	Cladocera	Tardigrades	Archannelids	Mites	Nematodes
PLUM CREEK DRAINAGE									
Cook Creek	+	+	+						
West Plum Creek	+	+	+	+				+	+
Bear Creek	+	+	+					+	
Jackson Creek	+	+	+						
FOUNTAIN/MONUMENT CREEK DRAINAGE									
Monument Creek-1	+	+	+	+	+				
Monument Creek-2	+	+	+						
Beaver Creek	+	+	+						
Fountain Creek	+	+	+						
SOUTH PLATTE RIVER DRAINAGE									
S. Platte River-1	+	+	+		+	+	+		+
S. Platte River-2	+	+	+		+	+			+
S. Platte River-3	+	+	+	+	+	+			+
S. Platte River-4	+	+	+	+	+	+	+		+
Middle Fork S. Platte	+	+	+	+	+	+	+		
Twin Creek	+	+	+	+	+				
Tarryall Creek		+	+	+					
Goose Creek		+	+	+					
Trout Creek-1		+	+						
Trout Creek-2	+	+	+		+				
West Creek		+	+						+
Trail Creek	+	+	+						
Sugar Creek	+	+	+	+		+		+	
Deer Creek		+	+		+				
NORTH FORK SOUTH PLATTE DRAINAGE									
N. Fork S. Platte-1	+	+	+						
N. Fork S. Platte-2	+	+	+						
N. Fork S. Platte-3	+	+	+	+					
Elk Creek		+	+	+					
Craig Creek		+	+						
Deer Creek		+	+	+	+				
Buffalo Creek	+	+	+			+			
Kennedy Gulch	+	+	+						
Frequency of occurrence (%)	53	100	90	47	40	17	10	10	17

cladocerans and tardigrades, were also collected at a number of sites (Table 3). These organisms have also been reported to be common members of the interstitial community in other studies (Strayer 1988, Danielopol 1989). Copepods were the most common interstitial organism, being found at all 30 sites, with ostracods present at 90% of sites (Table 3). Other crustaceans (amphipods, bathynellids, and cladocerans) were also common, being present at roughly 40–50% of sites. Non-crustacean organisms were encountered much less frequently, often at only 10% of sites.

CONCLUSIONS

Prior to the present study, the known range of *S. pennaki* and *S. coloradensis* was basically restricted to 2 adjacent stream reaches in the South Platte River drainage near the confluence of the mainstem and North Fork of the South Platte River (Ward 1977, Pennak and Ward 1986). Other *Stygobromus* species have been reported from springs and small interrupted streams west of Fort Collins, Colorado (Ward and Holsinger 1981), a saline spring in the Piceance Basin in western Colorado (Ward and Holsinger 1981), and the Fraser River near Winter Park (unpublished data). These last 2 are the only records of *Stygobromus* on the west slope of Colorado.

The present study provides 10 new locations for *Stygobromus* in Colorado (Fig. 1), increasing the known range of this genus in the West (Ward and Holsinger 1981, Holsinger 1986). There appeared to be a close association of *S. pennaki* and *S. coloradensis* with alluvial gravels derived from decomposed Pikes Peak granite common to the middle South Platte River basin and adjacent drainages. Results of this study also support findings of Ward and Voelz (1990, 1994) that interstitial communities are widespread in Colorado streams.

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DIET SWITCHING AND FOOD DELIVERY BY SHRUBSTEPPE PASSERINES IN RESPONSE TO AN EXPERIMENTAL REDUCTION IN FOOD

Frank P. Howe^{1,2}, Richard L. Knight¹, Lowell C. McEwen¹, and T. Luke George^{1,3}

ABSTRACT.—We experimentally reduced the food base of nesting Brewer's Sparrows (*Spizella breweri*) and Sage Thrashers (*Oreoscoptes montanus*) in a shrubsteppe region of south central Idaho in 1989 and 1990. Frequency and mass of "birdfood" arthropods in pitfall, sweep net, and stickyboard samples were generally lower on sites treated with a broad-spectrum insecticide (malathion) than on untreated sites though the effect varied among taxa. In 1990 *O. montanus* switched nestling diets to prey taxa not affected by the treatment. Time between nestling food deliveries was greater for *S. breweri* on the treated than untreated site in 1989. In 1990 there were no between-site differences, but there was an increase in delivery time on the treated plot after treatment; this difference was within the range of delivery times recorded on the untreated plot. Malathion applications did reduce the food base, but plasticity in passerine behavior and emergence characteristics of some prey taxa ameliorated indirect effects of food reduction to birds.

Key words: Brewer's Sparrow, Sage Thrasher, *Spizella breweri*, *Oreoscoptes montanus*, food reduction, diet switching, food delivery, malathion, insecticide.

Few investigators have experimentally reduced prey abundance in the field to determine indirect effects to birds (but see Cooper et al. 1990, Rodenhouse and Holmes 1992, Pascual 1994). Our objective was to experimentally reduce prey of nesting migratory passerines through application of malathion, a broad-spectrum insecticide, and determine what effects this perturbation would have on prey abundance, food delivery intervals, and nestling diets.

We predicted that the number (frequency) and/or mass of "birdfood" arthropods sampled with 3 different methods would decrease on the treated plot after insecticide application. Where food was reduced, time between food deliveries was predicted to increase. Furthermore, we predicted that some arthropod taxa would be reduced more than others after the application (Pfadt et al. 1985) and that adults would switch to more abundant prey types (Rotenberry 1980).

Wiens (1974, 1977, 1984) and Wiens and Rotenberry (1980) suggested that arthropod food in shrubsteppe ecosystems is "superabundant" during most years, but birds may experience an ecological crunch in those years

when food is scarce. Howe et al. (1996) found no effect of food reduction on nestling survivorship but some effects on nestling size on our study site. If food were reduced but not to crunch levels during our study, we would expect to observe behavioral responses, such as diet switching and increased feeding times, as adults attempt to cope with food reduction. Changes in behavioral and physical characteristics might be expected even when no effects on adult density or productivity are evident from food reduction.

STUDY AREA AND METHODS

The study area is located in the shrubsteppe region of south central Idaho approximately 72 km north of Twin Falls at an elevation of 1450–1500 m. A single untreated plot (unsprayed) was randomly chosen for the 2-yr study, and 2 different treatment plots were chosen for 1989 and 1990. Each plot consisted of a 49-ha core area wherein all data were collected. On the treated plots we sprayed the core areas and an additional 0.8-km-wide strip around the core areas. A standard grasshopper control rate of malathion was applied on 3

¹Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, CO 80523.

²Present address: Utah Division of Wildlife Resources, 1594 W. North Temple, Suite 2110, Box 146301, Salt Lake City, UT 84114-6301.

³Present address: Department of Wildlife, Humboldt State University, Arcata, CA 95521.

June 1989 and 8 June 1990. Detailed site and treatment application descriptions can be found in Howe et al. (1996).

Spizella breweri (Brewer's Sparrows) and *Oreoscoptes montanus* (Sage Thrashers) are found throughout the shrubsteppe region of western North America (Wiens and Rotenberry 1981). Both species are primarily insectivorous during the breeding season (Wiens and Rotenberry 1979, Rotenberry 1980) and feed their young almost exclusively arthropods (Petersen and Best 1986, Petersen et al. 1986, Rotenberry and Wiens unpublished data). On our study sites *S. breweri* began hatching in late May, with peak hatching during the first 2–3 wk of June. *Oreoscoptes montanus* began hatching in early May, with 1 hatching peak during late May and another in late June.

Spizella breweri nests were observed with binoculars from elevated (1.2–2.5 m) platforms placed within 50 m of nests. Nest observations were made between ~0800 and 1200 h and 1600 h until sunset to avoid the coolest and warmest parts of the day. We conducted 2-h observations twice at each nest when nestlings were 1–3 d old (early) and 4–6 d old (late). Feeding intervals, i.e., time elapsed between consecutive feedings, were calculated and averaged for each nest over the observation period. *Oreoscoptes montanus* feeding interval data could not be obtained; if observers were within 150 m, the birds would not approach their nests.

We used the ligature method (Kuligin 1981, Henry 1982) to sample food items brought to nestlings. Ligatures were placed on each nestling in a nest for 1 h during midmorning or late afternoon. The entire amount of food brought to all nestlings within the 1-h period was considered to be a single sample. Nestling diet samples were taken from 5- and 8-d-old *O. montanus* and 5-d-old *S. breweri*. Ligature samples were not taken during food delivery observations to avoid excess disturbance. All diet samples were stored in 70% alcohol.

Arthropods were collected twice before and 3 times after treatment applications on untreated and treated plots. Timing of arthropod collections in relation to treatment varied because we avoided cold, rainy conditions. In 1989 collections were taken 13 and 2 d pretreatment and 7, 21, and 35 d posttreatment. Collections in 1990 were taken 14 and 2 d pretreatment and 11, 17, and 27 d posttreatment.

We employed 3 arthropod capture techniques: (1) pitfall traps—16-oz plastic cups buried flush with the surface with approximately 1 oz of ethylene glycol as a killing fluid; (2) sweep nets; and (3) stickyboards—pre-manufactured glue traps with approximately 190 cm² area per board. Twenty arthropod collection stations were selected at random on each plot. Pitfalls (2 beneath sage and 2 in the open) and stickyboards (2 high in the sage canopy and 2 near the ground) were placed at each station for 24 h during each of the 5 sampling periods. Sweep nets (50 each in shrubs and grass) were used during midmorning at each station. Pitfall and sweep net samples were also stored in 70% alcohol; while this may cause some shrinkage of samples, samples from both plots were treated identically to avoid any bias.

Arthropods from all samples were counted, measured (length), and identified to family (some families were divided into adult and larval forms). Arthropod taxa not detected in diet samples were omitted from environmental samples before analysis. Environmental samples were also truncated to reflect maximum prey size, but not minimum size (Johnson et al. 1980), found in nestling diets. Arthropod taxa found in diet samples and truncated for maximum length were considered birdfood taxa.

Mass was estimated for each arthropod using length/weight regressions (Rogers et al. 1976, 1977). Mass per sample was calculated by multiplying mass of each individual by number of individuals in each taxon.

Analysis

Our experimental design included measurement of treated and untreated subjects before and after pesticide application. We randomly assigned plots to untreated or treated groups before the 2-yr experiment and standardized measurement procedures during the experiment to control for procedure effects and experimenter bias. While it was not possible to replicate treatments within years, we were able to replicate the experiment in 2 yr. Also, we restricted our inference to the plots studied, thus avoiding pseudoreplication (Hurlbert 1984).

Unless otherwise stated, we used analysis of variance (ANOVA; SAS 1988); 1- or 2-tailed tests of significance were used depending on the comparison. Before the treatment,

between-plot comparisons (untreated vs. treated) were made with 2-tailed tests; post-treatment between-plot comparisons used 1-tailed tests. For pretreatment vs. posttreatment comparisons within plots, we used 1-tailed tests. Other between-period, within-plot comparisons used 2-tailed tests. To normalize data from both environmental and diet samples, we transformed frequency (square root) and mass (natural log) of arthropods. The alpha level for all statistical tests was 0.05.

Environmental samples from each of the 3 arthropod collection techniques were analyzed separately. We analyzed these samples first considering all birdfood taxa. A subsequent analysis was done on each arthropod taxon constituting >10% (by mass or frequency) of nestling diets; taxa making up <10% of nestling diets were lumped into an additional group—"other birdfood" (see Tables 1, 2).

We tested for differences in food delivery intervals for three 10-d periods following the

TABLE 1. Arthropods (percent of total mass and percent of total frequency) in nestling *Spizella breweri* diets.

Arthropod taxa ^a	1989			1990		
	N ^b	Mass ^c (%)	Freq ^d (%)	N	Mass (%)	Freq (%)
Araneida	13	8.5	11.5	9	18.5	11.5
Coleoptera larvae	3	0.5	2.0	7	15.0	53.5
Diptera	6	7.5	4.0	4	18.5	3.5
Hemiptera	6	0.5	5.0	5	6.5	7.5
Homoptera						
Cicadidae	13	53.0	11.5	—	—	—
Other	6	1.5	9.5	7	2.0	12.5
Hymenoptera	5	1.5	3.5	1	2.0	1.0
Lepidoptera						
Adults	8	3.5	7.0	1	10.5	1.0
Larvae	14	15.0	33.0	3	4.5	5.5
Neuroptera	8	2.5	8.5	—	—	—
Orthoptera	3	6.5	2.0	3	23.0	5.5

^aValues represent total for all families within order unless specified.

^bNumber of ligature samples containing arthropod taxa, not number of individual arthropods; total number of ligature samples = 52.

^cPercent of total diet (mass) made up of individual arthropod taxa; mass estimated using length/weight regressions (Rogers et al. 1976, 1977).

^dPercent of total diet (frequency) made up of individual arthropod taxa.

TABLE 2. Arthropods (percent of total mass and percent of total frequency) in nestling *Oreoscoptes montanus* diets.

Arthropod taxa ^a	1989			1990		
	N ^b	Mass ^c (%)	Freq ^d (%)	N	Mass (%)	Freq (%)
Araneida	1	<0.5	2.0	6	3.5	4.5
Coleoptera	6	1.0	11.5	4	0.5	3.0
Diptera	—	—	—	3	1.5	3.0
Hemiptera	1	1.0	3.5	1	<0.5	0.5
Homoptera						
Cicadidae	11	55.0	26.0	4	11.0	5.0
Other	—	—	—	1	<0.5	0.5
Hymenoptera	2	1.5	7.5	8	1.0	8.0
Lepidoptera						
Adults	2	3.5	3.5	—	—	—
Larvae	9	13.5	28.0	7	1.5	5.0
Orthoptera						
Acrididae	5	15.5	13.0	12	12.5	11.0
Gryllidae	2	9.0	3.5	26	69.0	58.5

^aValues represent total for all families within order unless specified.

^bNumber of ligature samples containing arthropod taxa, not number of individual arthropods; total number of ligature samples = 51.

^cPercent of total diet (mass) made up of individual arthropod taxa; mass estimated using length/weight regressions (Rogers et al. 1976, 1977).

^dPercent of total diet (frequency) made up of individual arthropod taxa.

1989 treatment (insufficient data were collected to make a valid pretreatment comparison). In 1990, 1 pretreatment and 2 posttreatment periods were used. We also analyzed all between-period (within-plot) combinations in both years.

Diet samples were categorized as pre- or posttreatment. *Oreoscoptes montanus* diet samples were compared on both plots before and after treatment. Since the treatment application preceded the peak of *Spizella breweri* hatching, we made only posttreatment comparisons of their diet samples.

We calculated a posteriori power for feeding interval and arthropod frequency and mass tests which were not significant. Actual mean values were used for the untreated plot; values for the treated plot were arbitrarily set at 5 min more than the untreated plot. Power to detect 5-min differences among sampling periods within untreated and treated plots was also determined. Power to detect a 50% difference on the treated plot, compared to the actual measured value from the untreated plot, was determined (K. Burnham and G. White, Colorado State University, personal communication). We defined power as good (≥ 0.70), moderate (> 0.30 and < 0.70), or poor (≤ 0.30). Power calculations with an alpha level of 0.05 were based on 1- or 2-tailed tests of significance depending on the comparison as described above.

RESULTS

Overall Prey Reductions

Since malathion is a broad-spectrum insecticide, we expected substantial prey taxa reductions posttreatment. And, as predicted, frequency and/or mass of birdfood arthropods from pitfall, sweep net, and stickyboard samples were lower on treated than untreated plots in most posttreatment samples in 1989 and 1990. This pattern, while variable, was evident for both *S. breweri* and *O. montanus* prey in both years of the study from all 3 sampling techniques (Figs. 1, 2). Where prey was affected, the most common posttreatment pattern observed was a lower arthropod frequency and mass on the treated plot (e.g., Fig. 2, 1990A). In a few cases (1989 sweep net samples) pretreatment differences were evident immediately before treatment; thus, posttreatment differences may have been influenced by factors other than treatment alone.

Mass and frequency of arthropods were different ($P < 0.01$) on stickyboards placed high and low in the sage canopy and were analyzed separately. Differences between microhabitats sampled by pitfall traps (open or under sage) and sweep nets (grass or sage) were not significant and did not require separate analyses.

Power to detect a 50% change in arthropod frequency and mass was consistently good for tests using pitfall and sweep net samples. Power varied more widely for tests using stickyboard samples but was generally moderate to good (Appendix A).

Spizella breweri Prey Taxa

Maximum size of prey items in *S. breweri* diets was 27 mm for Lepidoptera larvae and 23 mm for all other taxa. Prey taxa of *S. breweri* typically showed lower frequency and/or mass on the treated than untreated plot during 1 or more sampling periods after insecticide application. This pattern was evident both in 1989 and 1990. Another posttreatment pattern was also evident in 1990: a lower frequency but no detectable difference in mass (Fig. 1, 1990D). This resulted from fewer but larger prey on the treated plot.

In 1989 birdfood arthropod taxa analyzed for *S. breweri* included Araneida (arachnids), Homoptera, Lepidoptera, and "other" (a combination of taxa which individually made up $< 10\%$ of nestling diet; see Table 1); these taxa were not equally affected by the insecticide (Appendix B). After treatment significantly smaller prey frequency and/or mass values were detected on the treated plot for all birdfood taxa: Araneida (both variables in pitfalls and stickyboards), Homoptera (both variables in pitfalls, frequency in sweep nets, mass in stickyboards), Lepidoptera (both variables in stickyboards), and other (mass in pitfalls). The only differences detected in these taxa immediately before treatment were in Homoptera (frequency in stickyboards) and other (both variables in sweep nets and stickyboards).

In 1990 Coleoptera and Orthoptera (mass tests only) were added to the prey taxa list for *S. breweri* (see Table 1). Significantly lower posttreatment values for prey frequency and/or mass were again detected on the treated plot for all prey taxa: Araneida (mass in stickyboards), Coleoptera (frequency in pitfalls), Homoptera (frequency in pitfalls and stickyboards), Lepidoptera (mass in pitfalls and

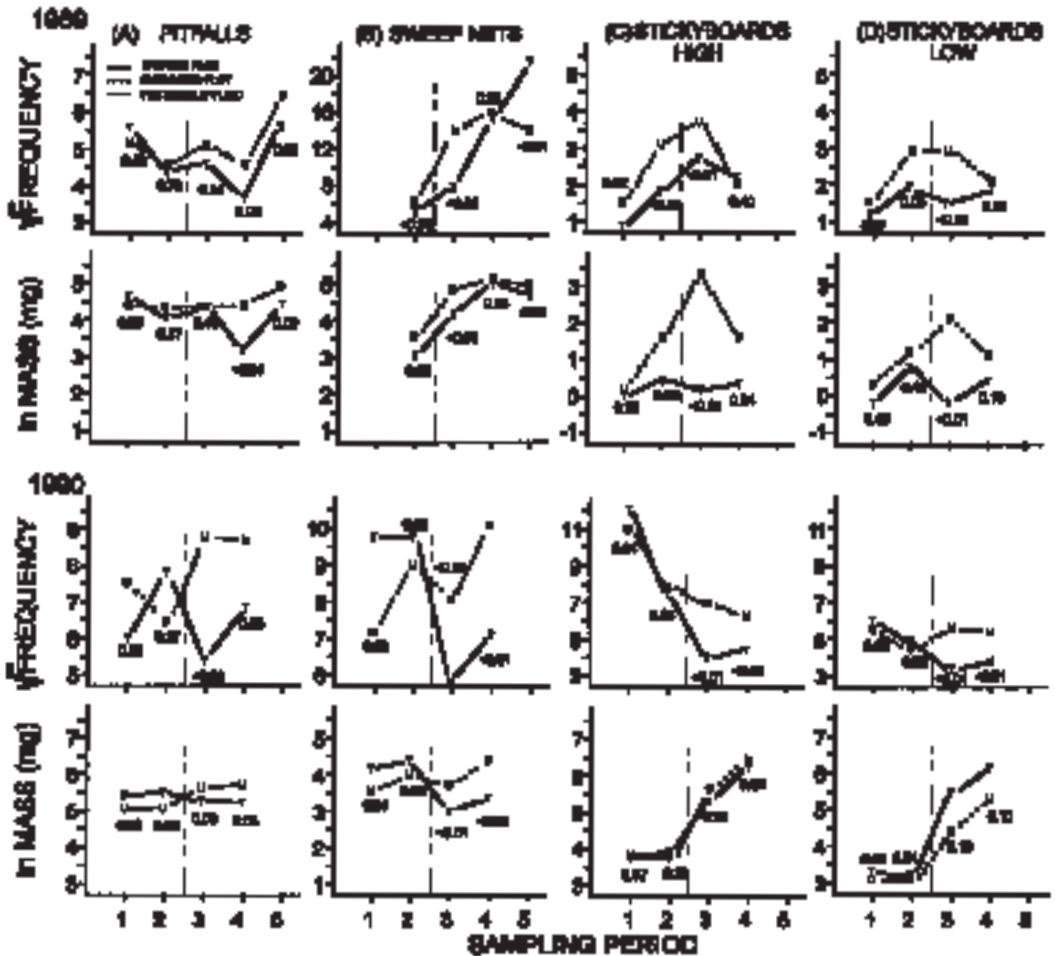


Fig. 1. *Spizella breweri* food abundance (frequency and mass of arthropods) before and after insecticide treatment in 1989 and 1990. Arthropod families were combined and represent only those taxa actually consumed by nestlings. Within figures, letters (T = treated, U = untreated) indicate means and numbers indicate probability (ANOVA) of between-plot differences occurring by chance. In 1989 sampling periods 1 and 2 were 13 and 2 d pretreatment, respectively; periods 3, 4, and 5 were 7, 21, and 35 d posttreatment, respectively. In 1990 sampling periods 1 and 2 were 14 and 2 d pretreatment; periods 3, 4, and 5 were 11, 17, and 27 d posttreatment.

stickyboards), Orthoptera (mass in pitfalls and sweep nets), and other (both variables in all 3 samples). Before treatment only Coleoptera (frequency in stickyboards) were less frequent on the treated than untreated plot; all other taxa showed either no difference or greater treatment plot values (Appendix B).

Oreoscoptes montanus Prey Taxa

Maximum size of prey in *O. montanus* diets was 32 mm for Lepidoptera larvae and 27 mm for all other taxa. Frequency and mass of *O. montanus* birdfood arthropods were generally significantly reduced on the treated but not

untreated site after treatment was applied. Again, responses differed depending on taxa involved (Appendix B). In 1989 and 1990 *O. montanus* prey taxa used in analyses included Coleoptera (frequency only), Homoptera, Lepidoptera, Orthoptera, and other (Table 2).

In 1989 Coleoptera (frequency in sweep nets), Homoptera (frequency in sweep nets), Lepidoptera (mass in pitfalls, both variables in stickyboards), and other (both variables in sweep nets, frequency in stickyboards) had lower values on the treated plot after malathion application. Immediately before treatment, Coleoptera (frequency in sweep nets),

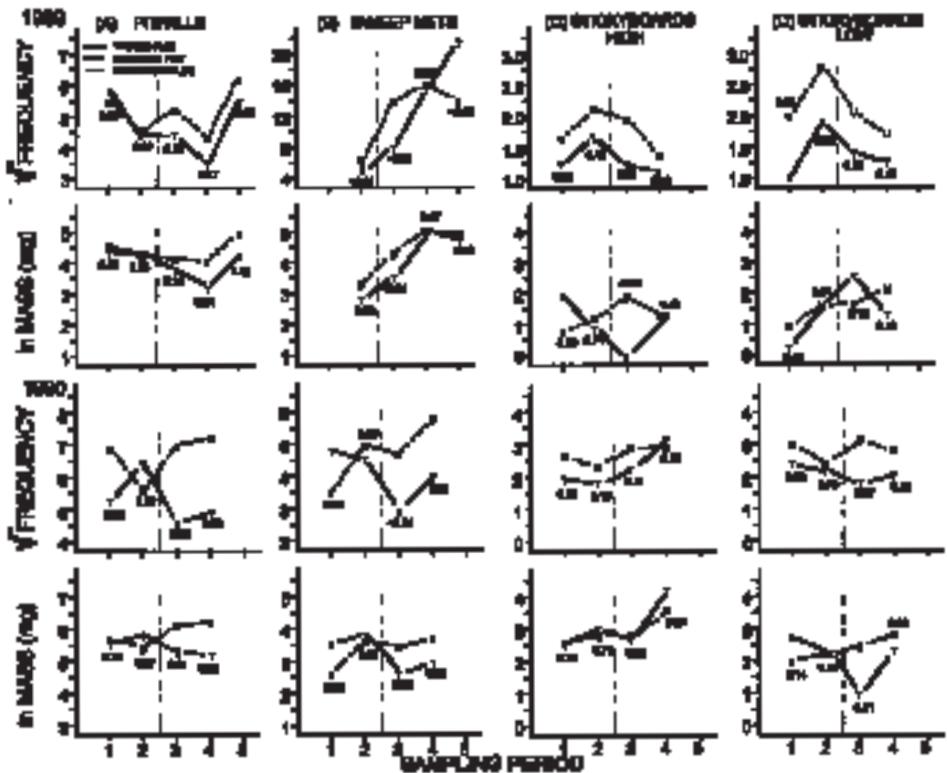


Fig. 2. *Oreoscoptes montanus* food abundance (frequency and mass of arthropods) before and after insecticide treatment in 1989 and 1990. Arthropod families were combined and represent only those taxa actually consumed by nestlings. Within figures, letters (T = treated, U = untreated) indicate means and numbers indicate probability (ANOVA) of between-plot differences occurring by chance. In 1989 sampling periods 1 and 2 were 13 and 2 d pretreatment, respectively; periods 3, 4, and 5 were 7, 21, and 35 d posttreatment, respectively. In 1990 sampling periods 1 and 2 were 14 and 2 d pretreatment; periods 3, 4, and 5 were 11, 17, and 27 d posttreatment.

Homoptera (frequency in sweep nets), and other (both variables in sweep nets and frequency in stickyboards) showed significantly greater values on the treated plot.

After treatment in 1990 Coleoptera (frequency in pitfalls and stickyboards), Orthoptera (both variables in pitfalls and stickyboards), Homoptera (frequency in sweep nets), and other (both variables in sweep nets) were lower on the treated plot. Before treatment all taxa except Coleoptera (frequency in pitfalls) showed either no difference or greater treatment plot values (Appendix B).

Food Delivery

Food reduction was expected to cause birds on the treated plot to forage longer for prey and thus have greater intervals between food deliveries to nestlings. Figure 3 illustrates differences in food delivery intervals for *S. brew-*

eri in 1989. Because there were significant differences between delivery intervals for early and late nests, they were analyzed separately. We found no between-plot differences in food delivery intervals during any posttreatment periods for the 1- to 3-d-old (early) nestlings. However, a significant increase was detected in the food delivery interval between the 1st (1–10 d) and 3rd (>20 d) posttreatment periods on the treated ($P = 0.02$) but not untreated ($P = 0.57$) plot. No other between-period differences for the early age group were found.

We found no between-plot differences in the 1st posttreatment period for the late (4- to 6-d-old) nestling group in 1989. However, during the 2nd posttreatment period (11–20 d), feeding intervals on the treated plot were over 3 min longer ($P = 0.07$) than on the untreated plot. This was followed by a significant decline ($P = 0.04$) in the food delivery

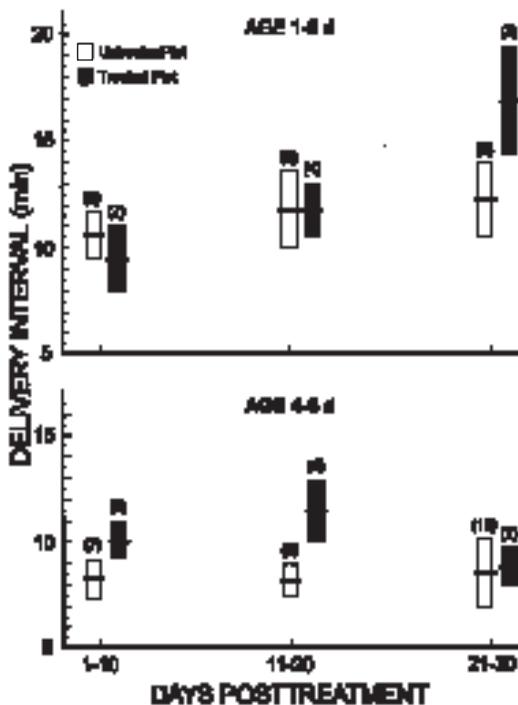


Fig. 3. Food delivery intervals for 1- to 3-d-old and 4- to 6-d-old *Spizella breweri* from an untreated and insecticide-treated site in 1989. Delivery intervals for each nest were averaged over a 2-h observation; horizontal lines represent mean of all nests observed $\pm s_{\bar{x}}$ (vertical bars); number of nests is in parentheses.

interval on the treated plot from the 2nd to 3rd posttreatment periods, with no between-plot difference during the 3rd period. No other significant differences were detected (Fig. 3). Power to detect a 5-min difference in delivery intervals between plots and between periods was good for all tests in 1989.

Because we detected no differences between early and late nests in 1990, these data were pooled for analysis. Before treatment, intervals on the untreated site were longer ($P = 0.01$) than on the treated plot. Feeding interval length on the untreated plot declined ($P = 0.04$) between the pretreatment and 1st posttreatment period. We detected no between-plot differences during either posttreatment period (1–10 d and >10 d).

On the treated plot *S. breweri* adults took more than 5 min longer per trip to feed their young during the 2nd posttreatment period than before malathion application ($P = 0.03$); however, this was within the range of feeding

intervals measured on the untreated plot (Fig. 4). Power for all tests was moderate.

Arthropod Use and Prey Switching

Diets of nestling *S. breweri* were more diverse than those of nestling *O. montanus*, though Araneida, Coleoptera, Homoptera, Lepidoptera, and Orthoptera occurred in nestling diets of both species (Tables 1, 2). We found no significant between-plot differences in frequency (number hr^{-1}) of birdfood arthropods from *S. breweri* nestling diets following the treatment application in either study year. Pretreatment comparisons were not made for *S. breweri*.

The mass (mg hr^{-1}) of ligature samples from nestling *S. breweri* did not differ significantly between untreated and treated plots. In 1989 mass was almost identical ($P = 0.49$, $N = 32$) on untreated ($\bar{x} \pm s_{\bar{x}} = 42.95 \pm 1.2 \text{ mg hr}^{-1}$) and treated (43.38 ± 1.3) plots; in 1990 mass on the treated plot (45.15 ± 1.3) was marginally smaller ($P = 0.07$) than on the untreated plot (83.93 ± 1.2), but sample size was low ($N = 10$).

No between-plot differences in birdfood frequency or mass were detected in *O. montanus* diet samples in 1989. Also, arthropod frequency and mass did not decrease on the treated plot after the 1989 treatment as predicted. Furthermore, the plot \times period interaction was not significant. In 1990 we detected a significant plot \times period interaction in frequency of arthropods from *O. montanus* nestling diets ($P = 0.05$). However, the number of arthropods in *O. montanus* diets was significantly higher on the treated than untreated plot before ($P = 0.03$) malathion was applied. Frequency declined marginally ($P = 0.08$) on the treated site and rose slightly on the untreated site between periods and was not different between plots ($P = 0.29$) after pesticide application.

Prey switching was evident for *O. montanus* in 1990 (Fig. 5). *Oreoscoptes montanus* fed their young primarily Orthoptera (mostly crickets; family Gryllidae) on both untreated and treated plots before the treatment. After treatment, *O. montanus* switched to Homoptera (primarily Cicadas) on the treated plot but continued to feed Orthoptera on the untreated plot. Cicadas made up only a small fraction of *O. montanus* nestling diets on either plot before treatment. Despite the change in primary

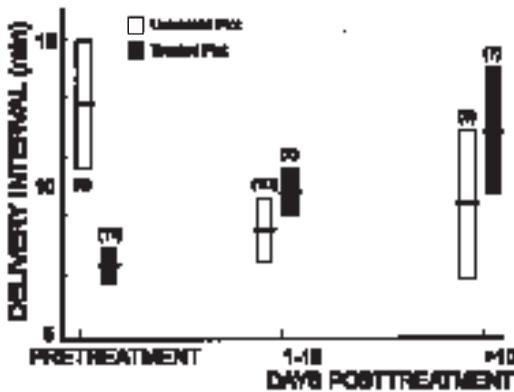


Fig. 4. Food delivery intervals for 1- to 6-d-old *Spizella breweri* from an untreated and insecticide-treated site in 1990. Delivery intervals for each nest were averaged over a 2-h observation; horizontal lines represent mean of all nests observed $\pm s_x$ (vertical bars); number of nests is in parentheses.

prey taxa on the treated plot, mass of arthropods in posttreatment diet samples ($\bar{x} \pm s_x$, 357.13 ± 1.36 mg hr⁻¹, $N = 5$) did not appear to change significantly ($P = 0.28$) from pretreatment samples (448.05 ± 1.25 , $N = 9$), although sample size was small.

Prey switching in *O. montanus* in 1989 appeared to occur but was not as evident as in 1990. The proportion of Orthoptera in nestling *O. montanus* diets began and remained low on the treated plot, but began low and increased marginally between periods on the untreated plot (plot \times period interaction, $P = 0.08$). After treatment there were more Orthoptera in nestling diets on the untreated than treated site ($P = 0.02$). Homopteran proportions on the treated site increased from 25% to >50% of the diet between periods, but neither this increase ($P = 0.38$) nor any between-plot comparisons were significant (Fig. 5).

Spizella breweri were not feeding nestlings before treatment applications, so we were not able to determine if they switched their diets in response to the treatment. However, post-treatment between-plot comparisons of nestling *S. breweri* diets could be made. In 1989 a greater proportion (by frequency) of Homoptera were fed to nestlings on the treated than untreated plot ($P = 0.03$). This does not appear to be a treatment effect since Homoptera abundance was lowered by the treatment. There were no significant between-plot differences in frequency or mass of any other prey

taxa measured. Additionally, none of the dietary proportions of arthropod taxa were significantly different between plots in 1990 (Fig. 6).

DISCUSSION

Food is usually "superabundant" during the breeding season in shrubsteppe ecosystems (Wiens 1984). However, in some years food abundance may be unusually low, leading to changes in avian productivity. This has been referred to as an ecological crunch (Wiens 1974, 1977, Wiens and Rotenberry 1980). In this scenario the food limitation threshold, i.e., the level of abundance below which food scarcity begins to influence productivity (Rodenhous and Holmes 1992), is met or exceeded only rarely.

Food reductions may not affect productivity if birds are able to compensate for lost resources through changes in behavior. Thus, indirect effects of food reductions might be reflected in behavioral changes, e.g., diet switching or increased foraging time, even when reductions in productivity are not evident.

Overall Prey Reductions

We expected applications of malathion to significantly reduce both frequency and mass of birdfood arthropods (see Jepson 1989). And, results from our pitfall, stickyboard, and sweep net samples indicate that abundance of ground-dwelling, aerial, and cover-dwelling birdfood arthropods was generally reduced by insecticide treatment. However, effects of the treatment varied among families of arthropods such that some prey taxa were more abundant than others after treatment.

Malathion is a nonpersistent, broad-spectrum, contact insecticide (Smith 1987) that does not affect all arthropod families equally (Pfadt et al. 1985, Swain 1986). Those arthropod taxa whose behavior or life history characteristics (Pascual 1994) allowed them to avoid contacting malathion would have been less susceptible to our treatments. Cicadas (order Homoptera, family Cicadidae), for example, did not emerge before the treatment in either year of study and were thus not affected by it. In contrast, crickets (order Orthoptera, family Gryllidae) emerged before the treatment and spent much of their time on the ground in relatively open areas that received greater insecticide coverage. The order Orthoptera, including

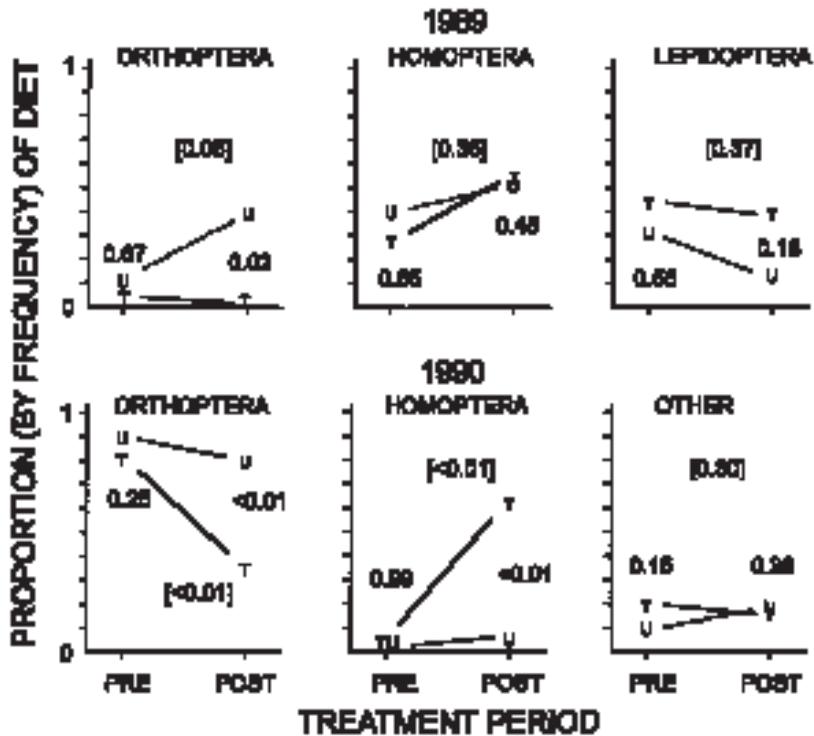


Fig. 5. Proportion of arthropods (by frequency) in nestling *Oreoscoptes montanus* diets before and after an insecticide treatment in 1989 ($N = 20$ samples) and 1990 ($N = 32$ samples). Items collected from different nestlings in the same nest were combined for each sample; nests may have been sampled more than once, and so samples may represent the same nest on different dates. Letters (T = treated, U = untreated) indicate means, bracketed [] numbers are ANOVA plot \times period interactions, and unbracketed numbers are ANOVA between-plot test results.

crickets, was significantly reduced on the treated but not untreated site after the 1990 malathion application. Also, crickets, more than any other arthropod, were found dead after the 1990 treatment.

Food Reduction Effects on Birds

Pesticide-induced reduction of food has been shown to affect a variety of physical and behavioral factors in birds. Food reductions decreased passerine reneesting (Rodenhous and Holmes 1992), lowered fat reserves (Whitmore et al. 1993), increased foraging area (Cooper et al. 1990), and led to diet shifts (Sample et al. 1993) in eastern deciduous forest studies. Food reductions lessened nestling size in a western shrubsteppe study (Howe et al. 1996). Such effects appear to be evident even when reductions in factors such as density (Howe et al. 1996) and productivity (Rodenhous and Holmes 1992, Howe et al. 1996) are small or undetectable.

Bird densities were not significantly reduced on our treatment plots after the malathion-induced food reduction in either year (T.L. George, Humboldt State University, unpublished data). Similarly, George et al. (1992) found no declines in density of 10 common grassland birds in plots where a carbaryl bran bait treatment reduced birdfood arthropods. George et al. (1995) also found no effects on avian density, richness, diversity, or evenness from malathion, sevin-4 oil, carbaryl bait, and *Nosema locustae* applications in 5 western states.

Rodenhous and Holmes (1992) lowered Lepidoptera abundance with 2 annual applications of a bacterial larvicide (*Bacillus thuringiensis*) and found a reduction of reneests, but not overall productivity, of Black-throated Blue Warblers (*Dendroica caerulescens*). However, they also found significant reductions in fledging, nestling growth, nestling survival, and number of nest attempts during natural

declines in food abundance. They concluded that during most years in their eastern U.S. temperate forest study areas, food was probably a limiting factor for *D. caerulescens* productivity.

In another study of eastern deciduous forests, researchers found that a gypsy moth insecticide (diflubenzuron) reduced Lepidoptera and nontarget insects (Martinat et al. 1988). This food reduction did not affect abundance of 21 bird species but resulted in decreased Lepidoptera larvae consumption (Cooper et al. 1990) and diet shifting (Sample et al. 1993) in 5 bird species as well as lower fat reserves in 7 species (Whitmore et al. 1993) on treated plots. Foraging areas of male Red-eyed Vireos (*Vireo olivaceus*) were also found to be larger on these treated sites (Cooper et al. 1990). Only adult birds were sampled during these studies, and reproductive variables were not measured.

Pascual (1994) found a greater than 4-fold decline in density of Lepidoptera larvae after spraying a plot with malathion. Despite this decline, Lepidoptera densities were not lower on the treated than untreated plot during any of 3 posttreatment sample periods. This was because while 1 Lepidoptera species was nearly depleted, another species with different emergence characteristics was relatively unaffected. Also, Lepidoptera densities were significantly higher on the treatment plot before malathion application. The author did not measure bird abundance, behavior, or foraging, but found no detectable differences between untreated and treated plots in nestling mass, hatching success, number fledged per nest, daily survival rate, or nestling mass of Blue Tits (*Parus caeruleus*), whose primary food source is Lepidoptera larvae.

Diet switching allows individuals to cope with unpredictable food supplies and alleviate the effects of selective food reductions. In response to a reduction in crickets, *Oreoscoptes montanus* on the 1990 treated site switched from feeding primarily crickets to primarily cicadas. On the untreated site, however, they fed crickets almost exclusively to their young during both the pre- and posttreatment periods. The switch in *O. montanus* diets was not accompanied by a detectable reduction in mass of food items delivered to nestlings. So, if food quality of cicadas was comparable to that of crickets, *O. montanus* were able to compensate

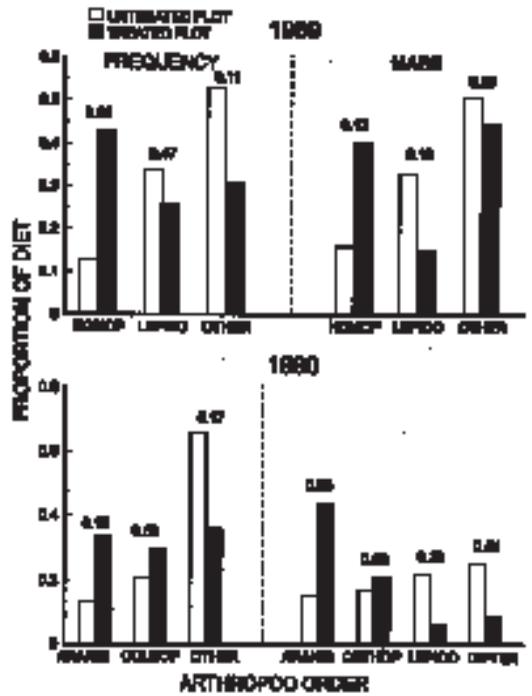


Fig. 6. Proportion of arthropods (by frequency and mass) in nestling *Spizella breweri* diets after an insecticide treatment in 1989 ($N = 32$, 1-h samples) and 1990 ($N = 10$). Items collected from different nestlings in the same nest were combined for each sample; each nest was sampled only once. Between-plot ANOVA probability values appear above histograms.

for the food reduction in our experiment by shifting their diets.

Sample et al. (1993) also found diet shifts in response to an insecticide-induced food reduction of Lepidoptera larvae. They found that adults of 5 eastern deciduous forest birds shifted diets from Lepidoptera larvae to a variety of other prey taxa.

One would expect that a reduction in food would cause an increase in time taken by adults to deliver food to their young. This could, however, be compensated for by adults delivering a greater amount or mass of food to nestlings. Few studies have directly monitored feeding rates after food reduction, though several studies have noted effects of brood manipulation on feeding rates (review by Martin 1987).

Results from our experiment indicated a slight effect of food reduction on delivery times (we could not measure feeding rates per se) of adult *S. breweri* in both years of the

study. However, delivery intervals on the treated plot posttreatment were not greater than intervals measured on the untreated plot, and no effective between-plot difference in food mass delivered to nestlings was detected.

In a related study Howe et al. (1996) found that food reduction on the treated plot resulted in smaller nestling sizes for *O. montanus* in 1989 (but not 1990) and *S. breweri* in 1990 (but not in 1989). They also found that fewer *O. montanus* fledged per nest attempt in 1989 (but not 1990). The number of *S. breweri* fledged was not affected, and neither species showed lower Mayfield nest survivorship in either year. Stochastic factors, such as weather (Howe 1991, Rotenberry and Wiens 1991) and ectoparasitism (Howe 1991), may act to confound effects of prey reduction on behavior and productivity of shrubsteppe birds. Such factors may partially account for the inconsistent results between years in Howe et al. (1996) and this study.

Thus, it appears that food reduction did, under the conditions of this study and Howe et al. (1996), affect physical and behavioral responses in shrubsteppe birds without greatly affecting adult density or productivity. Since treatment did not significantly affect all measured factors in both years, it appears that both *S. breweri* and *O. montanus* were able to at least partially compensate for the malathion-induced reduction in birdfood arthropods in this study.

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APPENDIX A. Power to detect a 50% change or difference in arthropod abundance to *Spizella breweri* and *Oreoscoptes montanus* based on pitfall, sweep net, and stickyboard samples.

P ^a	Pitfall		Sweep net		Stickyboard high ^d		Stickyboard low ^e							
	Frequency ^b	Mass ^c	Frequency	Mass	Frequency	Mass	Frequency	Mass						
	1989	1990	1989	1990	1989	1990	1989	1990						
<i>Spizella breweri</i>														
1	0.81	0.69	—	0.52	—	0.76	*	1.00	0.187	0.38	0.44	0.81	0.21	0.26
2	0.67	0.59	*	0.71	*	0.76	*	0.91	*	0.38	0.78+	0.61	0.23	0.26
3	0.88	*	*	0.74	*	0.84	*	*	*	0.50	*	*	*	0.37
4	0.77+	0.87+	*	0.96	0.89	0.84	0.76	*	*	0.50	0.63	*	0.34	0.37
5	0.97+	—	*	0.90	—	—	—	—	—	—	—	—	—	—
<i>Oreoscoptes montanus</i>														
1	0.85	0.54	—	0.44	—	—	0.56	0.48	0.18	0.38	0.34	0.30	0.28	0.27
2	0.72	0.39	*	0.66	*	0.47	0.90	0.41	0.26	0.37	0.47	0.21	0.33	0.27
3	0.89+	*	*	*	*	*	*	0.75	*	0.52	0.40	0.41+	0.94	*
4	0.76	*	*	0.95	*	0.85	0.59+	0.74	0.29	0.53	0.29+	0.39	0.34+	0.38
5	0.97+	—	*	0.89	—	0.85	—	—	—	—	—	—	—	—

^aPower estimations were based on 2-tailed tests in pretreatment periods (Pd) 1 and 2 and 1-tailed tests in posttreatment periods 3-5.

^bAll frequency data were normalized with square-root transformations.

^cAll mass data were normalized with logarithmic transformations.

^dStickyboards placed at height of sagebrush canopy.

^eStickyboards placed near the ground.

*Test result significant at $P \leq 0.05$, power not calculated.

+Test result significant at $0.05 < P \leq 0.10$, power calculated.

—Not tested

APPENDIX B. Probability values by sampling period resulting from ANOVA tests on the abundance (frequency and mass) of arthropod orders fed to nestling *Spizella breweri* and *Oreoscoptes montanus* in 1989 and 1990. Probability estimates were based on 2-tailed tests for periods 1 and 2 (pretreatment) and 1-tailed tests for periods 3-5 (posttreatment). Italicized values were significant differences in the direction opposite our predictions.

Taxa ^c	Pitfalls																	
	Frequency ^a							Mass ^b										
	1989			1990				1989			1990							
ARAN	0.07	0.46	0.18	0.04	0.17	0.74	<0.01	0.19	0.27	<0.01	0.19	0.15	0.02	0.20	0.72	0.03	0.12	0.33
COLE	*	*	*	*	*	0.56	0.07	<0.01	0.03	*	*	*	*	*	*	*	*	*
HOMO	—	—	0.03	0.24	<0.01	0.21	0.18	<0.01	0.02	—	—	<0.01	0.30	<0.01	*	*	*	*
LEPI	0.72	0.71	0.08	0.20	0.29	0.45	0.32	0.31	0.06	0.32	0.76	0.44	0.04	0.10	0.32	0.56	0.40	0.04
ORTH	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	—	0.03
OTHER	0.28	0.99	0.06	0.06	0.07	0.31	0.57	0.04	0.01	0.85	0.98	0.07	0.02	0.18	0.53	0.05	0.01	0.15

Taxa	Sweep nets																	
	Frequency							Mass										
	1989			1990				1989			1990							
ARAN	0.41	0.17	0.39	0.23	0.10	0.87	0.43	0.39	0.88	0.28	0.50	0.48	0.42	0.96	0.20	0.08	0.08	
COLE	*	*	*	*	0.33	<0.01	0.09	0.39	*	*	*	*	*	*	*	*	*	*
HOMO	0.44	<0.01	0.24	<0.01	0.01	0.06	0.48	0.11	0.16	0.12	0.35	0.41	*	*	*	*	*	
LEPI	0.74	0.14	0.08	0.29	0.31	0.33	0.12	0.23	0.68	0.12	0.12	0.23	0.79	0.91	0.33	0.06	0.06	
ORTH	*	*	*	*	*	*	*	*	*	*	*	*	0.20	0.81	0.41	0.02	0.02	
OTHER	<0.01	<0.01	<0.01	<0.01	0.97	0.82	<0.01	<0.01	0.05	<0.01	<0.01	0.05	0.03	0.11	<0.01	<0.01	<0.01	

APPENDIX B. Continued.

Taxa	Stickyboards															
	Frequency						Mass									
	1989			1990			1989			1990						
1	2	3	4	1	2	3	4	1	2	3	4					
ARAN	0.99	0.91	0.03	0.15	0.42	0.27	0.20	0.27	0.41	0.99	0.03	0.23	0.72	0.73	<0.01	0.45
COLE	*	*	*	*	0.02	0.01	<0.01	<0.01	*	*	*	*	*	*	*	*
HOMO	0.08	<0.01	0.31	0.02	0.03	0.85	<0.01	<0.01	0.28	0.19	0.34	0.01	*	*	*	*
LEPI	0.08	0.79	<0.01	0.09	0.30	0.28	0.19	0.50	0.88	0.61	<0.01	0.12	0.79	0.22	0.17	0.07
ORTH	*	*	*	*	*	*	*	*	*	*	*	*	0.10	0.48	0.10	0.03
OTHER	0.07	<0.01	<0.01	0.13	0.15	0.23	<0.01	0.02	0.66	0.02	<0.01	0.17	0.61	0.45	<0.01	0.06

Taxa	Pitfalls															
	Frequency						Mass									
	1989			1990			1989			1990						
1	2	3	4	5	1	2	3	4	1	2	3	4				
COLE	0.11	0.27	0.28	0.32	0.07	0.26	0.02	0.03	0.49	*	*	*	*	*	*	*
HOMO	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
LEPI	0.71	0.40	0.07	0.20	0.20	*	*	*	*	0.50	0.39	0.47	0.04	0.04	*	*
ORTH	—	0.22	0.40	—	—	0.38	0.58	<0.01	<0.01	—	0.39	0.29	—	—	0.61	<0.01
OTHER	0.41	0.90	0.20	0.11	0.08	0.91	<0.01	0.12	0.26	<0.01	0.15	0.36	0.12	0.35	0.66	0.08
																0.88
																0.06
																0.10

Oreoscoptes montanus

APPENDIX B. Continued.

		Sweep nets															
		Frequency				Mass				Frequency				Mass			
		1989				1990				1989				1990			
Taxa		2	3	4	5	1	2	3	4	2	3	4	5	1	2	3	4
COLE	0.93	<0.01	<0.01	0.02	*	*	*	*	*	*	*	*	*	*	*	*	*
HOMO	0.44	<0.01	0.24	<0.01	<0.01	0.31	0.11	<0.01	<0.01	0.16	0.12	0.30	0.41	0.97	0.61	0.03	0.07
LEPI	0.74	0.13	0.08	0.29	0.14	0.86	0.09	0.34	0.34	0.68	0.34	0.12	0.23	0.24	0.32	0.15	0.25
ORTH	—	—	0.17	0.17	0.63	0.84	0.48	0.04	0.04	—	—	0.26	0.23	0.20	0.81	0.41	0.02
OTHER	<0.01	<0.01	<0.01	<0.01	<0.01	0.37	0.42	<0.01	0.03	<0.01	<0.01	<0.01	0.03	0.32	0.86	<0.01	0.02

		Stickyboards															
		Frequency				Mass				Frequency				Mass			
		1989				1990				1989				1990			
Taxa		1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
COLE	*	*	*	*	0.09	0.88	0.31	0.01	0.01	*	*	*	*	*	*	*	*
HOMO	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
LEPI	0.08	0.79	<0.01	0.09	0.38	0.62	0.17	—	0.86	0.61	<0.01	0.12	0.01	0.85	0.45	—	—
ORTH	*	*	*	*	0.09	0.39	0.03	0.01	0.01	*	*	*	*	0.09	0.32	0.11	0.01
OTHER	0.02	0.01	<0.01	0.01	0.36	0.91	0.39	0.22	0.74	0.43	0.06	0.31	0.37	0.42	0.13	0.02	0.02

^aAll frequency data were normalized with square-root transformations.
^bAll mass data were normalized with logarithmic transformations.
^cArthropod taxa: ARAN = Araneida, COLE = Coleoptera, HOMO = Homoptera, LEPI = Lepidoptera, ORTH = Orthoptera, OTHER = Diptera, Hemiptera, Hymenoptera, Neuroptera (*Spizella breweri* only).
^dSample not sufficient to analyze separately; included in OTHER.
^eSample not sufficient to analyze; not included in OTHER.

EFFECTS OF CATTLE GRAZING ON NORTH AMERICAN ARID ECOSYSTEMS: A QUANTITATIVE REVIEW

Allison Jones¹

ABSTRACT.—A quantitative review was conducted of the effects of cattle grazing in arid systems on 16 response variables ranging from soil bulk density to total vegetative cover to rodent species diversity. Various studies from North American arid environments that used similar measures for assessing grazing effects on the same response variables were used for the review; each study was assigned to serve as a single data point in paired comparisons of grazed versus ungrazed sites. All analyses tested the 1-tailed null hypothesis that grazing has no effect on the measured variable. Eleven of 16 analyses (69%) revealed significant detrimental effects of cattle grazing, suggesting that cattle can have a negative impact on North American xeric ecosystems. Soil-related variables were most negatively impacted by grazing (3 of 4 categories tested were significantly impacted), followed by litter cover and biomass (2 of 2 categories tested), and rodent diversity and richness (2 of 2 categories tested). Vegetative variables showed more variability in terms of quantifiable grazing effects, with 4 of 8 categories testing significantly. Overall, these findings could shed light on which suites of variables may be effectively used by land managers to measure ecosystem integrity and rangeland health in grazed systems.

Key words: grazing, grazing effects, arid ecosystems, meta-analysis, rangeland conservation.

The debate regarding ecological effects of domestic livestock grazing on arid rangelands of the western U.S. is far from over, and many conservation biologists have become sufficiently concerned about the issue to join the debate (Brussard et al. 1994, Noss 1994). One can observe abundant examples of apparent overgrazing in North American arid systems (Fleischner 1994). Conservation biologists, however, may be skeptical of grazing literature, especially those studies conducted in the past. Nonetheless, I suggest that there is valuable information available in this abundant body of literature on effects of cattle grazing.

To those familiar with grazing literature, it is clear that there is still no scientific consensus regarding potentially detrimental effects of livestock grazing on arid rangelands (Brussard et al. 1994, Fleischner 1994, Noss 1994). The lack of consensus probably stems in part from inconsistencies in the grazing literature. Results of studies done in different plant communities, or at different sites representing the same community, often contradict one another. For example, a grazing study conducted in an arid shrub/bunchgrass community in central

Utah found that total vegetation cover was greater in grazed areas (Brotherson and Brotherson 1981), whereas another study in shrub/bunchgrass habitat in the adjacent valley reported that total vegetative cover was greater in ungrazed areas (Johansen and St. Clair 1986).

Traditional qualitative literature reviews do little to resolve such controversial issues, as they are subject to biases of the reviewer. For example, Fleischner's (1994) review of effects of grazing in western North America almost exclusively cites prior studies demonstrating detrimental effects of grazing. A range scientist with a contrary bias could easily cite as many studies demonstrating insignificant, and beneficial, effects of grazing. Though Fleischner's study sought to make the case against grazing rather than present a comprehensive review of grazing literature, I cite this example to illustrate that literature reviews can sometimes be a front for specific agendas. A more recent, more comprehensive grazing review completed by Belsky et al. (1999) qualitatively summarizes major effects of livestock grazing on stream and riparian systems in the West.

¹Department of Biology, University of Nevada—Reno, Reno, NV 89557. Present address: the Wild Utah Project, 165 S. Main St., Suite 1, Salt Lake City, UT 84111.

This review was less biased than Fleischner's in that it used a more systematic approach in searching the literature.

The purpose of this paper is to present results of a quantitative synthesis of effects of cattle grazing on arid western rangelands. Quantitative reviews provide an alternative to traditional literature reviews and can take many forms. One of the more widely used methods is meta-analysis, which utilizes statistics to synthesize research results and draw general interpretations from a collection of original studies on a common topic (Hedges and Olkin 1985, Gurevitch and Hedges 1993).

A formal meta-analysis in this case would require means and variances of paired grazed and ungrazed sites from a set of similar studies. From these means and variances, one could calculate an effect size for each study, which is a standardized measure of the effect of grazing. However, of 112 studies screened for inclusion in the analyses, only 26 (23%) presented either a measure of variation along with means or data that would allow calculation of variability; thus, it was impossible to use formal meta-analysis for this quantitative review. Furthermore, other methods for quantitative review such as combined probability tests (i.e., Fisher 1932) were inappropriate because most studies screened failed to report exact *P*-values.

Because of these limitations, I grouped papers that used similar measures for assessing effects of grazing on the same response variables, and each study was used as a single data point in paired comparisons of grazed versus ungrazed sites. A similar approach was used by Milchunas and Lauenroth (1993) to assess relative roles of different environmental factors in determining differences between grazed and ungrazed sites worldwide. In yet another similar approach, Milchunas et al. (1998) synthesized published and unpublished data on various guilds of organisms from grazing studies performed at an experimental range in Colorado. While these 2 examples focused on community-level functional responses at first the global and then local level, this paper aims to shed light on the more basic issue of general effects of cattle grazing on arid western rangelands.

The objective of this study was to quantitatively synthesize effects of cattle grazing on

arid western rangelands. This was accomplished by grouping individual grazing studies into different categories, based on similarities in response variables measured, and using outcomes of these studies as single data points in paired comparisons of grazed versus ungrazed sites.

METHODS

Various databases were searched for primary research articles in journals, symposia volumes, and technical government publications concerning effects of livestock grazing on arid rangelands of the western U.S. AGRICOLA and BIOSIS were the primary databases used. Searches were done for the years 1945–1996. The literature was searched using the terms *grazing*, *cattle grazing*, or *livestock grazing* as primary key words and *effect* or *effects* as secondary key words. Studies were rejected that included grazers other than cattle. In addition, only studies that simultaneously compared grazed areas with nearby ungrazed controls were included. This eliminated all studies that compared only different intensities or levels of grazing (i.e., that lacked an ungrazed control) and studies that made temporal comparisons of the same sites before and after grazing.

Only studies conducted in arid environments of the western U.S. and with site descriptions that included xeric vegetation types were included in the analyses. Most studies used were conducted west of the Rocky Mountains, but a few occurred in arid shrub/grasslands of the western Great Plains or the Southwest. Studies pooled for analysis included sites from Oregon to Kansas and from Montana to Texas, and covered an elevational gradient from alpine to desert ecosystems. Vegetation types in these study areas ranged from forest ecosystems to grasslands. It was necessary to combine data from seemingly disparate study areas in order to achieve pooled sample sizes large enough to analyze. Again, any overall effects revealed through combining these data, despite differences in community type, would constitute general evidence of grazing effects in arid landscapes.

Similarly, it was necessary to lump studies that used different systems of grazing (independent from stocking rates, which are discussed below). Some studies used in my analysis

utilized a spring, summer, or winter grazing regime, or even a combination of these seasons. Others used a deferred-rotation system. Some studies reported multiple years of different grazing systems over time, while others did not report the grazing regime at all. With such a wide range of systems used among studies considered for inclusion in my analysis, it was necessary to combine different types to achieve pooled categories of sufficient size for analysis. Again, any overall effects seen through combining data from many different studies would constitute considerable evidence of grazing effects in western North America.

One hundred twelve studies were initially located on effects of grazing on fauna, flora, and soil properties, but after applying the above criteria for inclusion of studies, 54 were selected for the analyses. Several papers included appropriate data for more than a single analysis, such as articles with data on both vegetation and wildlife in grazed versus ungrazed sites (e.g., Bock et al. 1984, Medin and Clary 1989, 1990). Some papers also contributed 2 or more observations to a given analysis. Examples include those that assessed effects of grazing using the same vegetation variables measured independently in distinctly different community types or sites (e.g., Pieper 1968, Wheeler et al. 1980, Roundy and Jordan 1988). However, when non-independent observations were reported, such as a certain response variable being measured in the same grazed and ungrazed locations at different times or subsampling within the same grazed and ungrazed experimental units, these were reduced to single observations by calculating mean values. In some papers investigators compared ungrazed sites with 2 or more sites that were grazed at different intensities. In such cases the lower intensity grazing data were used to represent grazing effects when 2 levels of grazing were used (i.e., "lightly grazed" rather than "heavily grazed" data were used for comparison with an ungrazed control); data for the intermediate grazing intensity were used when 3 levels of grazing were used (i.e., "moderately grazed" was used rather than "lightly grazed" or "heavily grazed" for comparison with an ungrazed control).² I was unable to analyze grazing intensity categories (i.e., heavily and lightly grazed categories) separately because the analysis would have resulted in data pools too small for analysis.

The following response variables were separately analyzed: rodent species diversity, rodent species richness, vegetation diversity, total vegetation cover, shrub cover, grass cover, forb cover, total vegetation biomass, tree seedling survival, non-tree seedling survival, cryptogamic crust cover, litter cover, litter biomass, soil bulk density, infiltration rate, and soil erosion. Rodent species diversity measurements used the standard H' index. Rodent species richness was measured as total number of rodent species present per site. Vegetation diversity values were standard diversity indices (H') calculated according to percent cover of the 3 broad vegetation types (shrubs, grasses, and forbs) within the study areas. Total vegetation biomass was measured using various methods but always reported as weight per unit area.

Quantitative analysis for these 16 categories included data from several papers grouped by similar response variables and measures that were used to assess effects of grazing on these response variables. Each analysis included 4–18 data points (i.e., paired comparisons of grazed vs. ungrazed areas) taken from 3–16 different studies. Several response variables from the literature review were not analyzed because I did not find sufficient comparable data (i.e., I found <4 data points), or because data from too many papers did not meet the above criteria for inclusion.

Data to be included in each analysis were first tested for normality using the Shapiro-Wilks statistic (SAS 1987). Statistics designed for paired comparisons were used in all analyses of grazing effects. In all cases treatment means for each study were treated as fixed quantities, with no consideration of within-site variation (which generally was not reported in the individual studies). Raw data sets that were normally distributed (12 of 16 analyses) were tested using t tests for paired comparisons. Of the remaining 4 data sets, 3 (seedling survival for non-tree plant species, and litter cover and biomass) were normalized by standardizing differences between ungrazed and grazed measures by dividing by the ungrazed measures (i.e., [ungrazed – grazed] / ungrazed).

²Studies that defined "heavy," "moderate," and "light" grazing described heavy grazing as 0.5–2 ac AUM⁻¹ (or 50–80% herbage utilization), moderate grazing as 1.5–2.5 ac AUM⁻¹ (or 30–45% herbage utilization), and light grazing as 2–4 ac AUM⁻¹ (or <30% herbage utilization).

These transformed data sets, which reflect the relative reduction due to grazing of the 3 standardized measures, were also analyzed with paired-comparisons *t* tests. Neither raw nor transformed data were normally distributed from 1 data set (infiltration rates), so a non-parametric Wilcoxon matched-pairs signed-ranks test was applied to this analysis (Siegel 1956).

In all analyses the null hypothesis that grazing has no effect on the measured variables was tested against the 1-tailed alternative. This entailed testing for significant positive or negative deviations from 0 in ungrazed-grazed paired comparisons. For example, grazing would generally be considered detrimental if it caused reduced plant or animal diversity, reduced cover or biomass of plant litter or cryptogamic crusts, reduced seedling survival, or reduced infiltration rates of water into soil. However, for 2 variables analyzed, soil bulk density and erosion, grazing-induced increases would instead be considered detrimental effects, while grazing-induced decreases would be considered positive effects of grazing.

RESULTS

For each of 16 response variables analyzed, Table 1 shows numbers of papers and data points included in the analysis, identity of each paper included, and statistical results of the analysis. Table 2 shows treatment and control means (grazed versus ungrazed) and difference of the means for each analysis category. Eleven of 16 analyses (69%) revealed significant detrimental effects of livestock grazing on arid rangelands. With a type I error rate of 0.05, only 1 test would be expected to yield significance by chance (i.e., $16 \times 0.05 = 0.80$); the actual number of statistically significant analyses (11/16) was significantly greater than this ($\chi^2 = 130.1$, $df = 1$, $P \ll 0.001$). In addition, many of the other 5 analyses were quite close to being significant (i.e., the largest *P*-value for the null hypothesis of no grazing effect was 0.111). Furthermore, if a 2-tailed test that grazing had no detrimental effect on the various categories had been used instead, 7 of 16 analyses (44%) would have been significant, and none of these would have indicated beneficial effects.

Overall, the 3 broad categories of variables (soil-related, vegetation-related, and animal-related variables) showed a varied response to

grazing influences. Soil-related variables in particular seemed to reflect detrimental effects of grazing. Among paired grazed and ungrazed areas, the former had significantly reduced cryptogamic crust cover ($P = 0.021$) and infiltration rates (Wilcoxon: $P = 0.002$) and significantly greater soil loss to erosion ($P = 0.007$). Analysis of vegetation variables indicated that grazed areas had significantly reduced litter biomass ($P = 0.009$) and cover ($P = 0.046$), seedling survival (non-trees, $P = 0.028$), total vegetation biomass ($P = 0.005$), and grass and shrub cover ($P = 0.016$ and 0.013 , respectively) than paired ungrazed areas. Rodent categories, the only vertebrate categories for which I was able to gather sufficient data, indicated reduced species diversity ($P = 0.039$) and richness ($P = 0.034$) in response to grazing.

DISCUSSION

My analyses of data gleaned from the literature suggest that livestock grazing may have detrimental effects on North American arid ecosystems. Because the data are drawn from various studies conducted at different times and in different environments, these effects may be applicable to North American xeric systems in general, rather than to specific locations and/or study periods. Of course, this does not preclude the likely possibility that spatial and temporal heterogeneity in these arid environments play a role either in further exacerbating or in ameliorating these detrimental effects. Moreover, the analyses did not take into account certain details of individual studies, such as stocking rates and intensity and timing of grazing, that could affect measured impacts.

This later issue may be considered problematic because different kinds of grazing systems can result in differential impacts to the land. For example, a particular rotational system developed with great ecological sensitivity may work better in arid lands than perhaps systems that have been "transplanted" from the Midwest. In fact, some range management textbooks (i.e., Heady and Child 1994, Holecheck 1998) give sound evidence of this. However, to effectively take this particular variable into account in this analysis would have required locating many more studies that use the same system and stocking rate and that address the same response variables. Only then would further analysis be feasible.

TABLE 1. Results of tests for detrimental effects of livestock grazing on arid ecosystems.

Category	N		Test ^a	P	Observations with a decrease in dependent variable ^b	Literature sources ^c
	Source	Observations				
Rodent species diversity (H')	8	15	t	0.039	13(87%)	3, 18(7), 19, 25, 29, 30, 33(2), 45
Rodent species richness	8	17	t	0.034	10(59%)	3, 16(3), 18(7), 25, 29, 30, 33(2), 45
Vegetation diversity (shrubs, grasses, forbs)	13	15	t	0.086	7(47%)	3, 4, 11, 15, 20, 22, 29, 30, 38(3), 40, 45, 49, 50
Shrub cover (%)	16	18	t	0.013	10(56%)	3, 4, 7, 11, 15, 20, 21, 22, 29, 30, 38(2) 40, 45, 46(2), 49, 50
Grass cover (%)	15	17	t	0.016	12(71%)	3, 4, 7, 11, 15, 20, 22, 29, 30, 31, 38(3), 40, 45, 49, 50
Forb cover (%)	15	17	t	0.111	9(53%)	3, 4, 7, 11, 12, 20, 22, 29, 30, 31, 38(3), 40, 45, 49, 50
Total vegetation cover (%)	14	16	t	0.051	8(50%)	1, 4, 6, 7, 11, 20, 21, 23, 27, 38(3), 40, 43, 44, 49
Total vegetation biomass (kg ha ⁻¹)	7	11	t	0.005	10(91%)	8, 14, 16(2), 24, 31(2), 37, 38(3)
Seedling survival, trees (%)	5	8	t	0.098	6(75%)	10, 17, 26, 48, 52(4)
Seedling survival, non-trees (%)	3	4	ts	0.028	4(100%)	32(2), 35, 47
Cryptogamic crust cover (%)	6	6	t	0.021	5(83%)	1, 2, 7, 21, 23, 40
Litter cover (%)	9	12	ts	0.046	6(50%)	2, 7, 12, 14, 23, 34, 38(3), 40, 46(2)
Litter biomass (kg ha ⁻¹)	6	7	ts	0.009	6(86%)	5, 12, 16(2), 27, 41, 42
Soil bulk density (g cm ⁻³)	7	9	t	0.094	2(22%)	8, 27, 28(2), 31(2), 34, 42, 51
Soil/water infiltration rate (cm hr ⁻¹)	12	15	Wilcoxon	0.002	12(80%)	5(2), 8, 9, 13, 14, 27, 31(2), 36(2), 39, 42, 51, 53
Soil erosion (kg ha ⁻¹)	7	9	ts	0.007	0(0%)	13, 14, 31(2), 36(2), 39, 51, 54

^aStatistical tests employed were paired-comparisons *t* tests on actual data (t), paired-comparisons *t* tests on data standardized by ungrazed means (ts), or Wilcoxon matched-pairs signed ranks test.

^bPercentages of observations (usually individual studies) that experienced a decrease in dependent variable due to grazing treatment.

^cNumbers within parentheses indicate numbers of observations or data points utilized per literature source; no parentheses indicate only 1 observation was utilized. All other numbers identify literature sources utilized as follows: (1) Anderson et al. 1982, (2) Beymer and Klopatek 1992, (3) Bock et al. 1984, (4) Brady et al. 1989, (5) Branson et al. 1962, (6) Brotherson and Brotherson 1981, (7) Brotherson et al. 1983, (8) Brown and Schuster 1969, (9) Buckhouse and Gifford 1976, (10) Conroy and Svejcar 1991, (11) Cottam and Evans 1945, (12) Dady et al. 1998, (13) Dunford 1954, (14) Gamougoun et al. 1984, (15) Gardner 1950, (16) Grant et al. 1982, (17) Hall et al. 1992, (18) Hanley and Page 1981, (19) Heske and Campbell 1991, (20) Holecheck and Stephenson 1983, (21) Jeffries and Klopatek 1987, (22) Jepson-Innes and Bock 1989, (23) Johansen and St. Clair 1986, (24) Johnson 1956, (25) Johnson 1982, (26) Kingery and Graham 1991, (27) Knoll and Hopkins 1959, (28) Laycock and Conrad 1967, (29) Medin and Clary 1989, (30) Medin and Clary 1990, (31) Meeuwig 1965, (32) Milchunas et al. 1992, (33) Oldemeyer and Allen-Johnson 1988, (34) Orodho et al. 1990, (35) Owens and Norton 1992, (36) Packer 1953, (37) Pearson 1965, (38) Pieper 1968, (39) Pluhar et al. 1987, (40) Rasmussen and Brotherson 1986, (41) Reardon and Merrill 1976, (42) Rhoades et al. 1964, (43) Rich and Reynolds 1963, (44) Robertson 1971, (45) Rosenstock 1996, (46) Roundy and Jordan 1988, (47) Salihi and Norton 1987, (48) Schmidt and Stubbendieck 1993, (49) Schuster 1964, (50) Smith and Schmutz 1975, (51) Thompson 1968, (52) Wheeler 1980, (53) Wood 1982, (54) Wood and Blackburn 1981.

TABLE 2. Treatment and control means by category, with difference of means.

	Means (M)		$M_{\text{ugr}} - M_{\text{gr}}$
	Ungrazed (M_{ugr})	Grazed (M_{gr})	
Rodent species diversity (H')	0.564	0.438	0.126
Rodent species richness	5.94	4.70	1.24
Vegetation diversity	0.284	0.261	0.023
Shrub cover (%)	11.01	9.56	1.45
Grass cover (%)	25.33	20.19	5.14
Forb cover (%)	8.77	8.23	0.54
Total vegetation cover (%)	32.06	27.48	4.58
Total vegetation biomass (kg ha ⁻¹)	1935.8	1478.7	457.1
Seedling survival, trees (%)	41.6	36.0	5.6
Seedling survival, non-trees (%)	24.78	11.67	13.11
Cryptogamic crust cover (%)	34.46	19.29	15.17
Litter cover (%)	30.36	28.0	2.36
Litter biomass (kg ha ⁻¹)	2573.3	1034.0	1539.3
Soil bulk density (g cm ⁻³)	1.17	1.22	-0.05
Soil/water infiltration rate (cm hr ⁻¹)	9.85	6.0	3.85
Soil erosion (kg ha ⁻¹)	288.74	525.91	-237.17

Furthermore, nearly 54 studies analyzed were found to be *quasi-experiments* (no randomization, but other experimental qualifications are met) rather than strict experiments in which experimental units are randomly assigned to control and treatment. Because of this, I do not infer causation between results presented in this review and western rangelands in general. I view these results as a basis for understanding which features of North American arid environments are most likely to suffer general impacts of grazing rather than as evidence relevant to the issue of the sustainability (or lack of it) of livestock grazing on western rangelands.

Various features of xeric soils appear to be sensitive to effects of cattle grazing (Table 1). Of those variables reflecting potential changes in soils that are generally attributed to trampling and compaction by cattle (Fleischner 1994), such as physical structure (bulk density) and functional properties (erosion, infiltration, cryptogamic crusts), there was statistical evidence for an effect of grazing on all 3 of the latter.

Although there may be some correlation between increase in erosion in grazed areas and a significant decrease in vegetation cover in grazed areas, the analyses, nevertheless, did appear to detect potential impacts of grazing on plant communities. Livestock grazing had significant effects on vascular plants for 4 of 8 vegetation response variables analyzed. Cover of grasses and shrubs, as well as total vegetation biomass, was reduced significantly by

grazing. The indication that shrub cover may be reduced by grazing contradicts other studies (Archer 1989, Schlesinger et al. 1990). However, many of these studies cite grazing as part of a complex of factors (i.e., fire suppression and climate change) that lead to increased shrub abundance.

Because many studies included in the analyses provided data only for vegetation categories such as shrubs, forbs, or grasses, analyses were necessarily limited to such broad categories. Although forb cover and vegetation diversity were statistically similar between grazed and ungrazed areas, much of this apparent lack of response to grazing may simply be an artifact of lumping plant species into broad vegetation categories. For example, lack of a grazing effect on forbs might occur even though palatable species of these plants are depleted by grazing, if this depletion is compensated by increases in unpalatable species or grazing-adapted, exotic weeds. The vegetation diversity category would have had more useful implications for range scientists and managers if it had been possible to include grazing studies that reported vegetation diversity in terms of numbers of native and nonnative species. I urge future investigators of grazing effects to collect and present vegetation data on a species-specific basis.

Rodents also seemed to react negatively to grazing influences. While in rare cases rodent diversity increased in grazed systems (i.e., Grant et al. 1982, Bock et al. 1984), the fact that meta-analysis of published literature

revealed negative overall impacts on rodents suggests that grazing is generally unfavorable for rodent communities on arid rangelands. Effects of domestic grazers on rodents are probably manifested indirectly through associated effects on soils and/or vegetation. For example, some desert rodent species specialize in foraging for seeds in certain soils and thus prefer particular soil properties (Price and Waser 1985, Price and Longland 1989). Grazing-induced changes in physical properties of soils could thus lead to loss of such specialized species or their replacement by a species more suited to the new edaphic conditions. Similarly, reduction in organic litter due to grazing may explain the loss of some species; western harvest mice (*Reithrodontomys megalotis*), for example, exhibit a strong affinity for grass litter (Clark and Kaufman 1991). Moreover, analyses indicated that grazing in these arid ecosystems reduces total vegetation biomass as well as shrub and grass cover (Table 1). Both natural ecotonal transitions from grass- to shrub-dominated habitats (Schroder and Rosenzweig 1975) and experimentally imposed changes in grass, shrub, and/or total vegetation cover (Rosenzweig 1973, Price 1978, Longland 1994) can have profound effects on desert rodent densities and species composition. Thus, it is quite possible that reduced vegetation cover in grazed areas drives the responses of the local rodent community.

The tentative conclusion that North American arid systems may be sensitive to livestock grazing is perhaps unsurprising. Whereas large herbivores that might be considered ecological counterparts to domestic livestock are native to many other arid regions of the world, there is a paucity of large, native grazers in contemporary North American xeric environments. American bison (*Bison bison*), for example, occurred very rarely in the arid West (Mack and Thompson 1982, Berger and Cunningham 1994, Kay 1994). In a worldwide review of effects of grazing by large herbivores, Milchunas and Lauenroth (1993) concluded that an evolutionary history involving grazing animals and the local environment was the most important factor in determining negative impacts of grazing on productivity. North American arid rangelands lack such an evolutionary history. Until Europeans introduced cattle and other grazers to our arid rangelands, the western range was relatively free of large grazing mammals

for 10,000 years (Berger 1986, Berger and Cunningham 1994). Arguments that these plant communities are adapted to grazing because they supported a diverse herbivore fauna during the Pleistocene (Burkhardt 1996) are probably irrelevant to this issue, as plant communities have most certainly changed in the intervening time and there have been few selective agents favoring retention of grazing tolerance.

Certainly, distinguishing effects of herbivory by native species versus livestock grazing is a concern to range scientists. However, it is notable that native grazers such as jackrabbits (*Lepus* spp.) and native browsers such as mule deer (*Odocoileus hemionus*) and pronghorn (*Antilocapra americana*) are usually allowed access to grazing enclosures such as those used in studies compiled in this review. Hence, the absence of grazing and browsing by native herbivores should rarely confound assessments of cattle grazing effects.

When biologists are faced with an abundance of very disparate studies or individual studies that yield no significant effects (as often found in the grazing literature), quantitative analysis allows detection of broad patterns due to a consistent direction of differences among those disparate studies. I used this tool to glean more objective information from the grazing literature than has been revealed in the past. It seems that soil-related variables and vegetative cover variables are most sensitive to grazing in arid systems. These findings may prove useful to rangeland managers, who traditionally have used only 1 or 2 metrics to assess rangeland health, with the most common criterion being soil condition. Perhaps investigation of a whole suite of connected variables, such as cryptogamic crust cover, soil infiltration rates, and litter cover, will give managers a more complete picture of ecosystem integrity in grazed landscapes.

It is imperative that conservation biologists work more closely with range managers and scientists. Livestock grazing is the most widespread land management practice in western North America. Seventy percent of the western U.S. is grazed, including wildlife refuges, wilderness areas, and part of our National Park System. The influence of grazing on arid ecosystems is just beginning to be realized. Conservation biologists could do much toward identifying potential impacts of grazing on biodiversity and ecosystem function by executing

more sophisticated grazing studies. A more traditional meta-analysis was unsuitable for this review because most studies used in this analysis were quasi-experiments, and many failed to present any measure of variability. This suggests that, although the literature is rich in studies of grazing effects, there is much room for improved experimental design and data presentation in this area of research.

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STATUS OF WHITE PINE BLISTER RUST IN THE INTERMOUNTAIN WEST

Jonathan P. Smith¹ and James T. Hoffman²

ABSTRACT.—During 1995–1997 we conducted a white pine blister rust (WPBR) disease survey in white pines of the Intermountain West. Incidence of WPBR in white pines was 59% overall, 73% in the northern Rocky Mountains, 55% in the middle Rocky Mountains, and 67% in the Sierra Nevada sample stands. Intensity within infected stands averaged 35% and ranged from 2% to 100%. Southward spread of the disease along the western slopes of the Rocky Mountains appears to have slowed or stopped, and the disease was found at the northern and western edges of, but not within, the Great Basin region. Smaller-diameter trees infected with WPBR sustained more severe damage than larger-diameter trees. Mortality and top kill caused by WPBR were very low across the entire study area, but incidence and intensity of the disease appear to have increased substantially in the northern and middle Rocky Mountains since the 1960s.

Key words: white pine, white pine blister rust, *Cronartium ribicola*, tree diseases, Great Basin forests, Rocky Mountain forests, subalpine forests.

Most, if not all, white pines (genus *Pinus* L., subgenus *Strobus* Lemm., section *Strobus* subsections *Cembrae* Loud. and *Strobi* Loud., and section *Parrya* Mayr subsection *Balfouriana* Engelm.) are susceptible to white pine blister rust disease (WPBR) caused by the introduced fungus *Cronartium ribicola* J.C. Fisch. ex Rabenh (Hoff et al. 1980, Keane and Arno 1993). *Cronartium ribicola* causes only minimal damage to its primary *Ribes* spp. (ribes) host but can produce cankers that girdle and kill its alternate white pine host, or destroy the reproductive potential of white pines by killing the uppermost, cone-bearing branches (Keane et al. 1994, Krebill and Hoff 1995).

Within 30 yr of its 1910 introduction into Vancouver, British Columbia, the fungus had spread throughout most of the range of mid-elevation white pine forests, which contain *Pinus monticola* Dougl. ex D. Don. (western white pine) and *P. lambertiana* Dougl. (sugar pine; Mielke 1943). By 1960 it had spread throughout much of the range of the subalpine white pine species, *P. albicaulis* Engelm. (whitebark pine), concentrated in areas where its distribution coincides with that of *P. lambertiana* and *P. monticola* (Hoff et al. 1994).

Recent studies have shown that the WPBR epidemic is devastating *P. albicaulis* in the northern Rocky Mountains (Keane and Arno

1993, Keane and Morgan 1994, Kendall et al. 1996). In western Montana, for example, Keane et al. (1994) reported that of a sample of 2503 *P. albicaulis* trees, 83% were infected with WPBR. Estimates of *P. albicaulis* mortality are as high as 90% for portions of the Selkirk Range in northern Idaho and for the east side of Glacier National Park (Kendall and Arno 1990).

Less is known about the status of WPBR in the area we refer to here as the Intermountain West. A formal WPBR survey has not been conducted in this area since 1967 (Brown and Graham 1969). From that survey and other recorded observations, it appears that the disease was present at low levels throughout much of the area in the late 1960s (Krebill 1964, Brown and Graham 1969).

There is a growing body of evidence to suggest that WPBR has the capacity to intensify in subalpine white pine forests and spread to new, uninfected areas in the western United States. Results of a recent study in Grand Teton National Park suggest that WPBR incidence is increasing in *P. albicaulis* and *P. flexilis* of the middle Rocky Mountain region (Kendall et al. 1996). Relatively recent infections have been reported in southeastern Wyoming (Brown 1978) and South Dakota (Lundquist and Geils 1992), and in 1990 WPBR was discovered in *P. strobiformis* Engelm. (southwestern white pine)

¹Northern Arizona University, School of Forestry, Box 15018, Flagstaff, AZ 86011.

²USDA Forest Service, Forest Health Protection, 1249 S. Vinnell Way, Boise, ID 83709.

in the Sacramento and adjoining White Mountains of New Mexico (Hawksworth 1990, Conklin 1994). The New Mexico infection center lies over 900 km away from any other known WPBR infections. It is not known whether the disease spread to this location via a corridor of infected pines and *Ribes*, by long-distance spore dispersal, or by the accidental introduction of infected nursery stock (Conklin 1994).

This recent intensification and spread of WPBR prompted us to question whether the disease would become better established in the Intermountain West. Thus, a disease survey was conducted in 1995–1997 to document WPBR epidemic characteristics (incidence, intensity, damage, and mortality) in the Intermountain West, and to use these characteristics to investigate whether WPBR has increased, intensified, or spread since the 1960s.

METHODS

Study Area

The study area encompasses the Great Basin physiographic province and adjoining areas of the Colorado Plateau and Sierra Nevada, and portions of the middle Rocky Mountain and northern Rocky Mountain provinces (Fennemans 1931). We surveyed the portion of the middle Rocky Mountains that lies south of the Yellowstone Plateau and the portion of the northern Rocky Mountains that lies south of the westward course of the Salmon River at approximately 45°N latitude (Fig. 1). Physiographic regions were subdivided into sections based on geology, geomorphology, and climate (Steele et al. 1981, 1983).

Throughout the study area the white pine species, *P. albicaulis*, *P. flexilis*, *P. monticola*, and *P. longaeva* D.K. Bailey [= *P. aristata* var. *longaeva* (D.K. Bailey) Little] (Great Basin bristlecone pine), occur in high-elevation subalpine forests up to the highest elevations of tree growth at the boundary with the alpine zone. *Pinus flexilis*, however, has the unique capability of occupying lower, dry treeline sites as well as upper, cold treeline sites (Arno and Hammerly 1984), especially in the northern and eastern portions of the study area. Along the western boundary of the Great Basin and Sierra Nevada provinces, *P. flexilis* is less common at lower treeline, but *P. lambertiana* occasionally occupies mid-elevation forests. *Pinus monticola* occurs in subalpine

forests in the Sierra Nevada and, therefore, is referred to here as a subalpine white pine species. In the Rocky Mountains *P. monticola* tends to occupy mid-elevation forests but does not grow south of the Salmon River in Idaho, the approximate northern boundary of the study area.

Survey Procedures

During the summers from 1995 through 1997, we inspected white pines for WPBR in 100 subalpine locations throughout the study area. Sample locations were randomly chosen from a list of areas identified by local forest managers as having white pine species present. In each white pine area, the 1st patch, or stand, of trees encountered that appeared to have at least 50 white pines >1.37 m (4.5 ft) tall was sampled. During the 1995 field season we installed 10 rectangular plots according to methods specified by the Whitebark Pine Monitoring Network (Kendall 1995). For the 1996 and 1997 field seasons, 90 strip transects were used to delineate sample trees. We switched to transects because white pine species in the Intermountain West tend to grow as dispersed woodlands or as infrequent seral components in subalpine forests. Obtaining 50 white pines in a rectangular plot of a reasonable size was often impossible. Once established in the stand, both rectangular plots and strip transects precluded a biased tree selection by imposing bounds on which trees were inspected. Location criteria and data collection procedures were identical for plots and transects, and so the data were combined for our analysis.

Strip transects were 4.6 m wide and oriented along the contour of the slope or perpendicular to the contour from an arbitrary point on the edge of the stand. We traversed the transect until at least 50 white pines (at least 30 live or recently killed trees) >1.37 m tall had been inspected, or until we reached the edge of the stand. In open woodland stands, or where white pines were minor seral components, the edge of the stand was defined as a change in habitat type or phase (Steele et al. 1981, 1983), horizontal canopy structure, aspect (>10°), slope (>10%), elevation (>100 m), or topographic position. If the edge of the stand was encountered before 50 trees had been inspected, a 2nd segment of the transect was initiated 2.3 m to the left or right of the

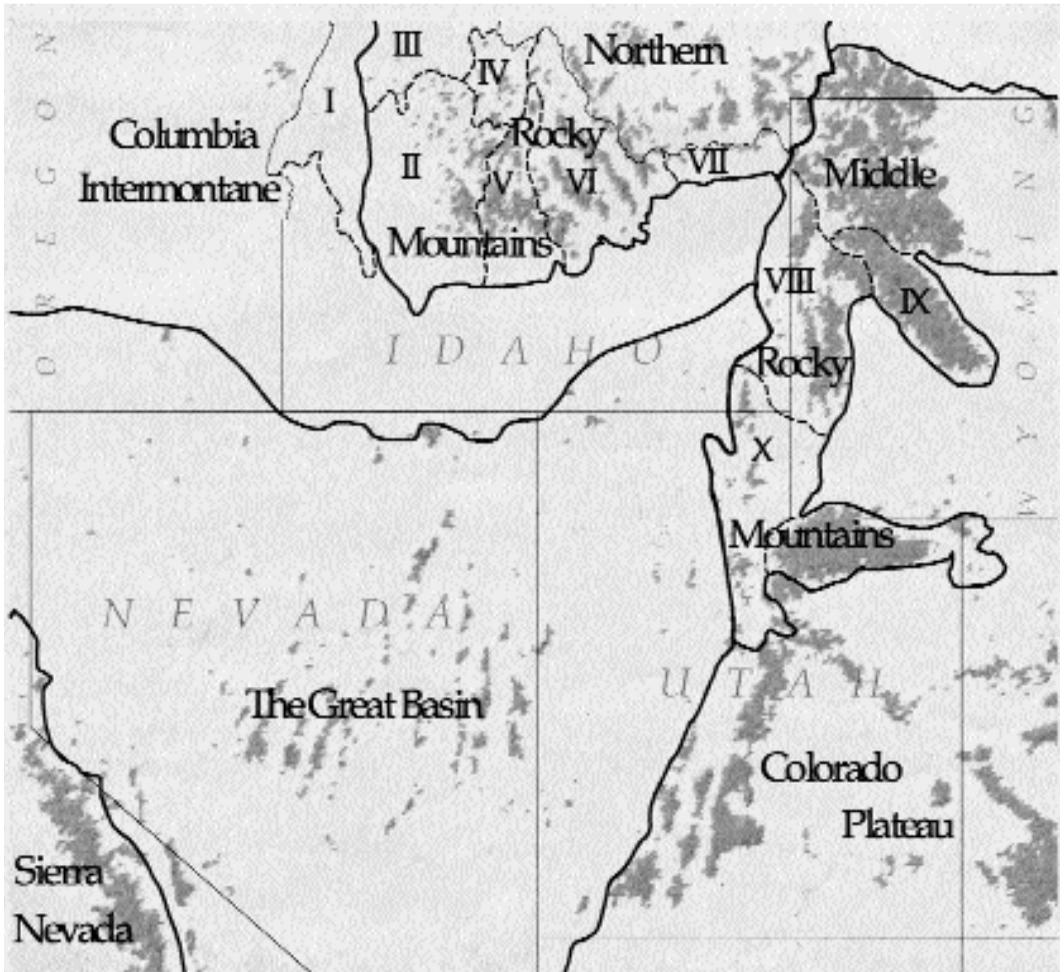


Fig. 1. Physiographic regions and sections of the Intermountain West adapted from Steele et al. (1981, 1983). Sections of the northern and middle Rocky Mountains: I, Wallowa–Seven Devils; II, Idaho Batholith; III, western Salmon Uplands; IV, eastern Salmon Uplands; V, Challis; VI, open Rocky Mountains; VII, mountains of the upper Snake River headwaters; VIII, Wyoming Ranges; IX, Wind River; X, Wasatch. Shaded areas are elevations >2440 m above sea level.

1st segment (toward the center of the stand) and traversed in the opposite direction of the 1st segment. Thus, the left edge of the 2nd segment corresponded with the left edge of the 1st segment, but care was taken not to inspect the same tree twice. Sampling continued in this manner until 50 trees had been inspected.

Using binoculars for foliar and stem disease signs and symptoms, we inspected each white pine within the strip transect or plot boundaries. Tree diameter at breast height (DBH) was measured at 1.37 m aboveground in 5-cm-diameter classes. Stems that forked below 1.37 m were considered individual trees. For infected

trees the distance from the main stem to the closest (most proximal) branch canker was estimated and used to assign each tree to 1 of 5 damage classes.

An additional 27 transects were established where white pines were encountered en route to predetermined sample areas. Most of these incidental samples were located in lower tree-line rather than subalpine white pine stands. We treated them separately because they were often located near roads or trails and usually did not meet the sampling criterion of at least 50 trees. Sampling methods were identical to the methods described above except that damage and mortality data were not collected.

Since 11 of these samples contained <30 trees, and 8 of those had <15 trees, intensity estimates are probably less accurate than the transect and plot estimates. Nevertheless, data from these samples were deemed useful for describing the geographic extent of WPBR throughout the study area and for generating hypotheses about the spread and intensification of the disease. We clearly distinguish how these supplemental data are used throughout the paper.

Analyses

Our definitions of incidence, intensity, and damage are as follows: WPBR *incidence* refers to presence or absence of WPBR in a sample stand. *Intensity* is the percentage of live trees in infected sample stands that were infected with WPBR. Incidence and intensity were calculated only for live trees, and since most stands had at least some dead trees, these calculations were usually based on <50 trees. Thirteen samples had <40 live trees, but only 1 had <30 live trees. *Damage* is based on the location of a permanent infection, or canker, within a tree crown (minor damage = branch canker >60 cm from stem; moderate damage = branch canker 15–60 cm from stem; severe damage = branch canker within 15 cm or on the main stem; top kill = foliage dead above stem canker; mortality = no live foliage visible). Cankers within 15 cm of the main stem, or on the main stem, were considered potentially lethal.

We used contingency table analysis as an omnibus test to investigate whether WPBR incidence is independent of the physiographic region in which stands were surveyed. Analysis of variance (ANOVA) and Fisher's Least Significant Difference test (Fisher's LSD) were employed to test for a relationship between physiographic region and WPBR intensity. Means of proportions were normalized with an arcsine square root transformation (Zar 1996).

Differences between WPBR incidence in 1967 and 1995–1997 were analyzed using contingency table analysis. The 1967 survey encompassed 4 national forests within our much broader study area. Therefore, we used only the 1995–1997 samples that corresponded with these same 4 national forests. The Mantel-Haenszel test was used to perform a contingency table test of independence between

WPBR incidence and survey year, stratified by national forest (Systat 1992). Coincidentally, because many of our incidental stands were sampled in these national forests, we performed a second Mantel-Haenszel test with a 1995–1997 data set that included 20 of our incidental samples.

RESULTS

Southward Spread of White Pine Blister Rust

MIDDLE ROCKY MOUNTAINS.—The most southerly location of WPBR in the middle Rocky Mountains that we found was at 42.5°N latitude in the Gannett Hills of Wyoming, near the Idaho border (Fig. 2). The 4 *P. flexilis* inspected at this lower treeline location had numerous WPBR cankers. The site, at the entrance to Allred Flat campground, is only about 45 km farther south of the southern WPBR limit reported by Brown and Graham (1969). The disease may have spread further south. Our only sample location south of the Allred site, however, was >40 km away, on Commissary Ridge (Fig. 2), the southernmost stand of *P. albicaulis* in western Wyoming (R. Lanner personal communication). We found no WPBR at this location.

NORTHERN AND EASTERN GREAT BASIN.—No WPBR was found south of Skinner Canyon at approximately 42.5°N latitude, the southernmost location in Idaho reported by Krebill (1964; see Fig. 2). We also found no evidence of WPBR infection in any of our Utah sample locations.

GREAT BASIN.—WPBR was found in no forest islands associated with the Basin and Range geomorphology that occurs throughout most of Nevada. However, WPBR was found in *P. monticola* and *P. albicaulis* at 2 locations in the Carson Range (Fig. 3). This was the 1st report of WPBR in Nevada (Smith et al. 2000). However, the Carson Range is not typical of isolated forests elsewhere in the state because it is linked by nearly continuous forest cover to the Sierra Nevada ecosystem.

EASTERN SLOPES OF THE SOUTHERN SIERRA NEVADA.—WPBR has been present in *P. lambertiana* in the southern Sierra Nevada since at least the 1960s and now extends throughout almost the entire range of that species (Kliejunas 1996). Southward spread of WPBR in *P. monticola* and *P. albicaulis* has been somewhat

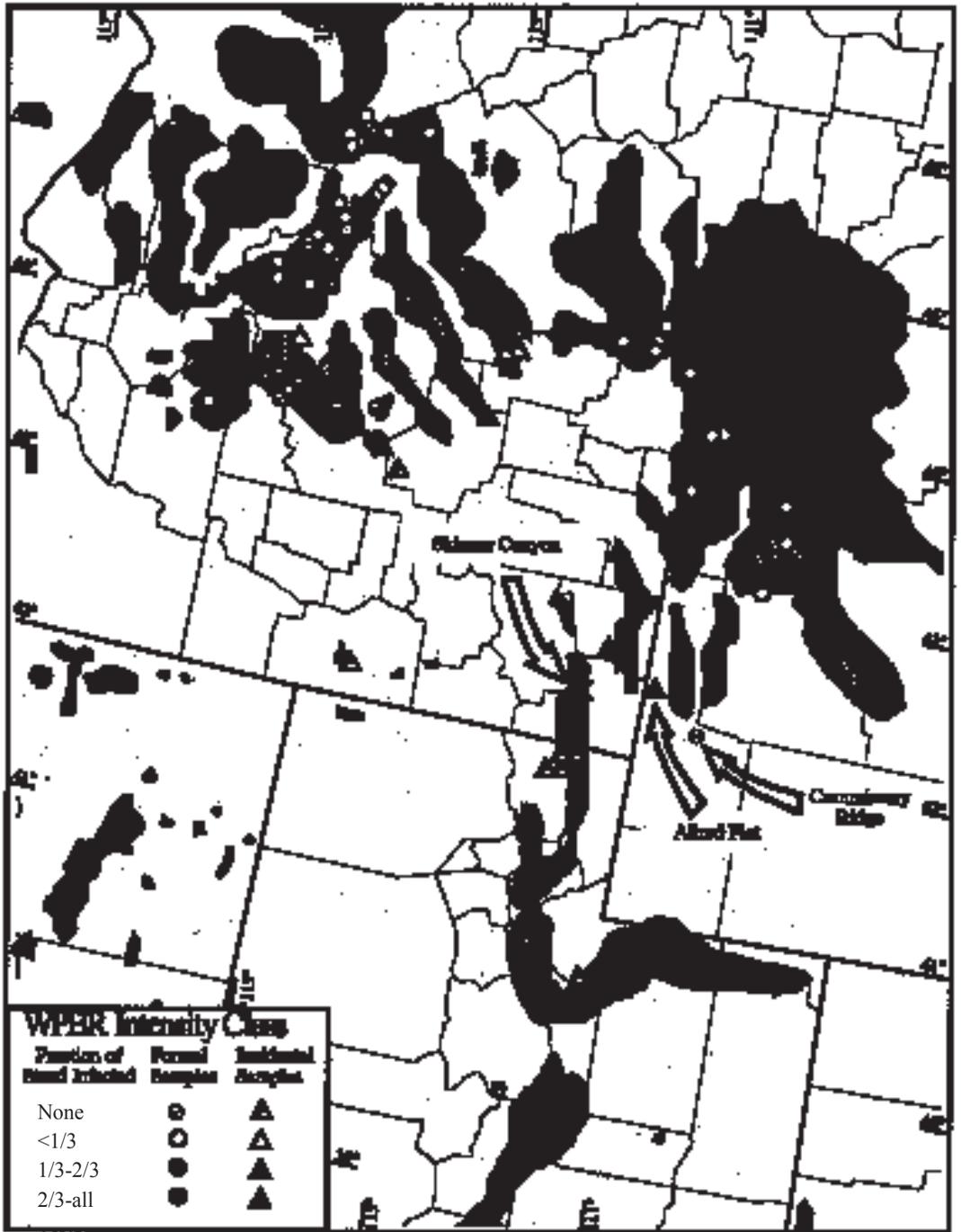


Fig. 2. Northern and middle Rocky Mountain sample locations and WPBR intensity for 100 formal samples and 27 incidental samples. X marks the location of Skinner Canyon, the southernmost WPBR pine infection location in the Rocky Mountains reported by Krebill (1964). Distribution of white pine species (shaded areas) derived from Little (1971).

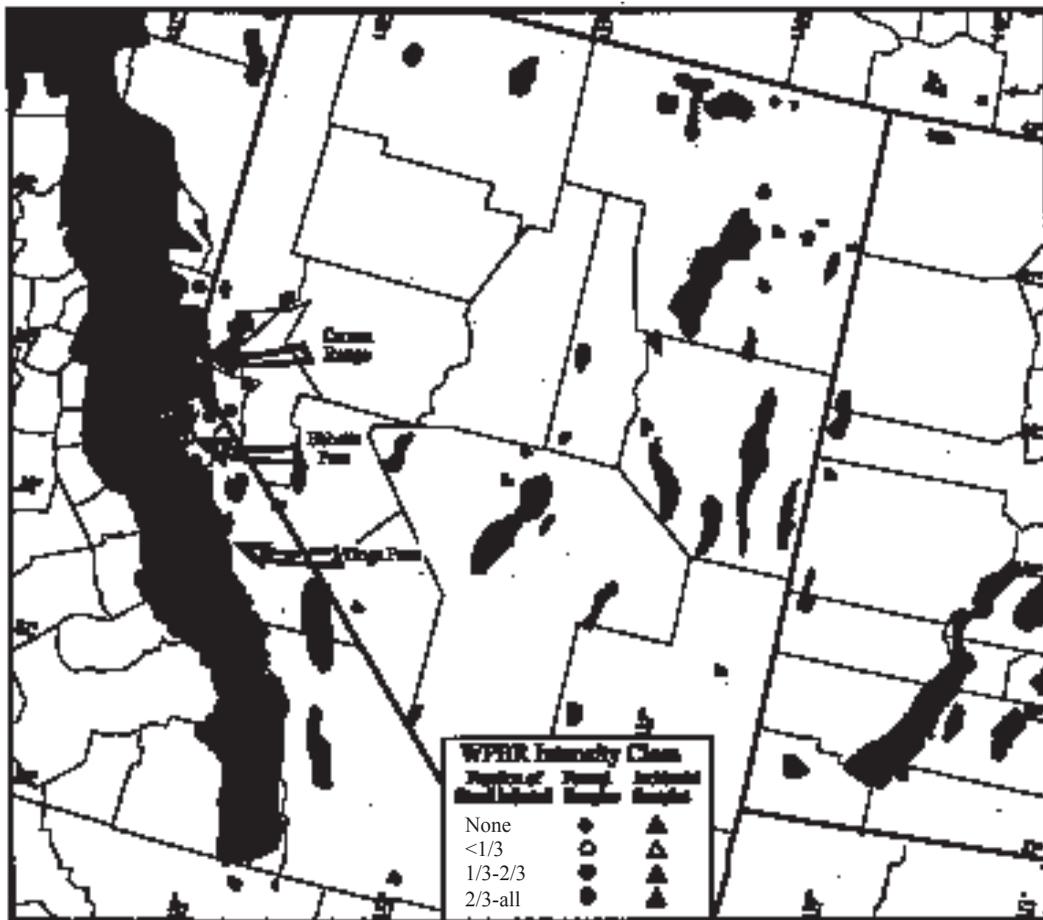


Fig. 3. Sierra Nevada and Great Basin sample locations and WPBR intensity for formal and incidental samples. Distribution of white pine species (shaded areas) derived from Little (1971).

slower. The southernmost location of WPBR in *P. albicaulis* that we observed was in the Sierra Nevada at Ebbetts Pass, at about 38°N latitude (Fig. 3). We know of no other reports of WPBR in *P. albicaulis* south of this location in the Sierra Nevada. However, *P. monticola* infected with WPBR have been observed much farther south, in the Sequoia National Forest, in recent years (J. Pronos personal communication). We did not find WPBR in *P. albicaulis* and *P. monticola* at our Carson-Iceberg Wilderness sample site, which was our southernmost sample location in the Sierra Nevada at a latitude approximately 7 km south of Ebbetts Pass (see Fig. 3). The disease also was not found during informal inspections of *P. albicaulis* and *P. flexilis* near Mammoth Lakes, California, and along the

North Fork of Big Pine Creek, near the town of Big Pine, California (J.J. Smith, August 1997, personal observation). Both locations are farther south than Tioga Pass, in Yosemite National Park, where Hoff et al. (1994) reported that no WPBR was observed in *P. albicaulis* in 1992 (see Fig. 3).

White Pine Blister Rust Incidence and Intensity

Region-wide incidence of WPBR in sub-alpine white pine samples was 59% (59 of 100 sampled stands). Average intensity in infected stands was approximately 36%. Addition of 27 incidental samples does not substantially change these overall infection values (Table 1); however, only the 100 formal samples were used in the statistical analysis.

TABLE 1. Incidence of white pine blister rust cankers, potentially lethal cankers, and intensity in formal white pine sample stands and in all sample stands during 1995–1997 in the Intermountain West.

Physiographic region/ Section ^c	Formal sample stands ^a				All sample stands ^b		
	Stands sampled (<i>N</i>)	Stands infected (%)	Average intensity (%)	Average incidence of potentially lethal cankers (%)	Stands sampled (<i>N</i>)	Stands infected (%)	Average intensity (%)
Northern Rocky Mountains	60	73.3	34.9	9.8	73	74.0	38.4
I. Wallowa–Seven Devils	3	100	59.0	20.9	3	100	59.0
II. Idaho Batholith	12	75.0	25.6	6.4	14	71.4	24.7
III. Western Salmon Uplands	4	100	52.9	19.1	5	100	52.3
IV. Eastern Salmon Uplands	14	85.7	16.6	6.3	14	85.7	16.6
V. Challis	6	0	0	0	9	22.2	52.0
VI. Open Rocky Mountains	8	25.0	21.1	1.4	14	50.0	51.0
VII. Mtns. of the upper Snake River hdwtrs.	13	100	52.0	21.0	14	100	51.9
Middle Rocky Mountains	22	54.5	38.8	6.8	34	50.0	51.8
VIII. Wyommide Ranges	10	90	48.4	16.2	17	82.3	60.8
IX. Wind River	8	37.5	9.9	0.3	8	37.5	9.9
X. Wasatch	4	0	0	0	9	0	0
Great Basin ^d	12	0	0	0	14	0	0
Slopes and associated ranges of the Sierra Nevada	6	66.7	32.6	9.4	6	66.7	32.6
TOTALS	100	59.0	36.1	8.1	127	58.3	41.7

^a*n* = 100 transect and plot samples only.

^b*n* = 100 transect and plot samples plus 27 incidental samples.

^cPhysiographic regions and sections adapted from Steele et al. (1981, 1983).

^dIncludes 2 samples from the western edge of the Colorado Plateau physiographic province in Utah.

Results of the contingency table analysis suggested that WPBR incidence is not independent of physiographic region (chi square = 21.57, $P < 0.001$). Using Fisher's LSD, we found a significant pairwise comparison between the Great Basin, where no WPBR was found, and the other 3 regions: northern Rocky Mountains ($P < 0.001$), middle Rocky Mountains ($P = 0.001$), and Sierra Nevada ($P = 0.003$). Significant differences in disease incidence among these latter 3 regions were not detected. Observed levels of significance ranged from 0.126 to 0.793 for pairwise comparisons among these regions.

We found no evidence to suggest a difference in WPBR intensity among any of the infected regions. Analysis of variance showed no significant relationship between the arcsine square root transformed mean of the proportion of trees infected and the physiographic

region in which the sample originated ($P = 0.970$).

Damage and Mortality Caused by White Pine Blister Rust

Severe damage or potentially lethal infections were found in 61% (630 of 1029) of WPBR-infected trees. Incidence of potentially lethal canker infections was highest in the Wallawa–Seven Devils Mountains of the upper Snake River headwaters and Wyommide sections (Table 1). Most potentially lethal Wyommide infections were in the Teton Mountains.

Of 5209 trees sampled, 452 (8.7%) were standing dead trees, and 154 of these had died recently (i.e., their bark and fine limbs were still present). We did not attempt to diagnose the cause of death of the 298 "old dead" trees (those with no bark or fine limbs remaining). Of the new dead trees, 34 (22%) had definite

signs of WPBR canker girdling on the main stem, such as residual aecial peridia, pycnial (spermagonial) scars, swollen, cracked bark, and evidence of rodent feeding on spermagonial exudate. The other 120 trees appeared to have died from physical damage, other diseases, and unknown causes. Twelve (35%) of 34 trees killed by WPBR were in the 5-cm-DBH class, and all trees killed by WPBR were <30 cm DBH (see Fig. 4). Severe damage, top kill, and mortality were proportionally more prevalent in smaller-diameter trees, while minor damage was more common in larger-diameter trees. The overall mortality attributable to WPBR, calculated as the 34 WPBR-killed trees divided by the total number of live and new dead (diagnosable) trees, was 0.7%.

Comparison with 1967 Disease Levels

In the 1967 survey of Intermountain West white pines in eastern Idaho and western Wyoming, 9 of 31 sample locations had WPBR in either white pines or *Ribes* (Brown and Graham 1969). From the data in that report, we calculated an overall incidence of WPBR in pines to be about 12% (3 of 26 white pine sample locations; Table 2). Results of the Mantel-Haenszel test suggest that WPBR incidence is independent of the survey year (chi square = 3.09, $P = 0.079$). However, incorporating our 20 incidental samples into the analysis resulted in a significant test of independence result (chi square = 8.42, $P = 0.0004$).

We did not statistically analyze WPBR intensity between survey years because of the prohibitively small number of sample locations in the 1967 data. However, we inferred that the average intensity of WPBR in pines was approximately 38% in the 1967 survey, compared to 51% in 1995–1997. Overall, slightly more than 1% (14 of 1078) of white pines inspected in the 1967 survey had WPBR. In comparison, 31% (785 of 2546) of white pines had WPBR in our survey of the same area.

DISCUSSION

Increase in White Pine Blister Rust Incidence and Intensity

Results of the initial statistical analysis of WPBR incidence in the 1967 and 1995–1997

surveys were somewhat inconclusive. When only the formal 1995–1997 sample data were used, we rejected the hypothesis that WPBR incidence has changed significantly between the 2 periods. However, when the 20 incidental plot data points were added, we found evidence to indicate an increase in WPBR incidence. We feel that the test of independence using only formal sample data was underpowered, and that the addition of more samples in the Caribou and Sawtooth National Forests increased the ability of the test to detect a significant change in WPBR incidence. Additionally, the 1 high-intensity sample in the 1967 survey consisted of only 6 white pines, which were all infected. This sample is probably not representative of overall WPBR intensity in the 1967 study area. The other 2 infected samples from that survey, with 5% and 10% intensities, had sample sizes of 20 and 30 trees, respectively.

Our analysis and anecdotal observations indicate an increase in incidence and intensity of WPBR in the middle and northern Rocky Mountain portions of our study area over the past 30 yr. Results from our WPBR damage assessment support this hypothesis. We found that the vast majority of infected trees had cankers close to branch tips, near points of initial infection, the needles. Had WPBR levels remained constant since the 1960s, we presumably would have found cankers more evenly distributed throughout the canopy and main stem of infected trees. Furthermore, we found that smaller-diameter (and usually younger) white pines suffered more serious damage, including top kill and mortality, than larger-diameter trees. This DBH–damage class relationship is very likely related to distance between foliage (the point of infection) and main stem, and the amount of cambium circumference that must be girdled in order to kill the top of the tree, or cause mortality. Assuming cankers progress at a roughly similar rate in smaller- and larger-diameter trees, if the rate of infection had remained constant over the past several decades, we should have seen more serious infections in larger-diameter trees.

Implications of an Increase in Damage Caused by White Pine Blister Rust

In some heavily infected stands most, if not all, small-diameter trees are infected. It is

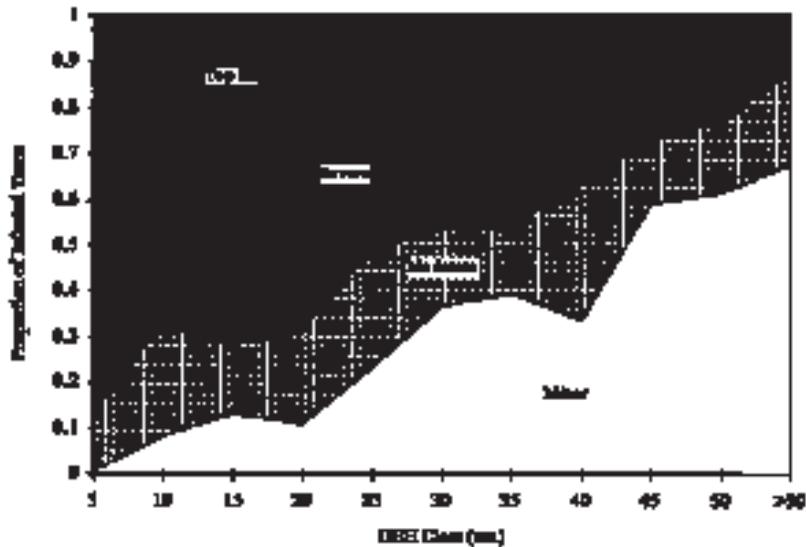


Fig. 4. WPBR damage on infected white pines by DBH (diameter at breast height) class. White pines were surveyed during 1995–1997 in the Intermountain West.

difficult to say with certainty whether any of these trees will live long enough to reproduce. Estimates of canker growth rates and natural inactivation of cankers are derived from *P. monticola* and *P. lambertiana* studies (Harvey 1967, Kimmey 1969, Hungerford 1977). Relatively little is known about the inactivation rate and growth rate of cankers in subalpine white pine species. Thus, infections far out on the end of a limb are also potentially lethal. We should note that the number of cankers on each tree affects the probability of a single canker reaching the main stem (Slipp 1953), and we did not collect data on this disease characteristic. Yet, regardless of the severity of infection, we rarely found inactive cankers and have no reason to believe that trees will escape serious damage even if they have only a few cankers. Research has shown that genetic resistance to infection or canker growth is rare in many subalpine white pine species (Hoff et al. 1980, 1994). Thus, damage from WPBR infection will likely increase in most currently infected trees, and smaller trees will succumb to top kill and mortality more quickly than larger trees. In high-intensity areas it is likely that only those few trees genetically resistant to WPBR will survive to maturity. Furthermore, we observed WPBR cankers high in the crowns of trees at most sites. Cones of at least 1 white pine species, *P. albicaulis*, are pro-

duced primarily in the upper 1/3 of the crown (Keane et al. 1994). Nonresistant trees that do survive to maturity in high-intensity areas may lose their reproductive capability long before they die.

Of immediate concern to forest managers is the area in the northeastern portion of the study area where WPBR incidence is high, intensity is high on many sites, and mortality is beginning to occur. Increased mortality in the western and southern portions of the Greater Yellowstone Ecosystem is of particular concern. This area is home to the threatened grizzly bear (*Ursus arctos horribilis*) that uses *P. albicaulis* seeds as an autumn food source. Abundance of *P. albicaulis* seeds is linked to grizzly bear cub production and to frequency of bear-human conflicts (Kendall and Arno 1990, Mattson and Reinhart 1994). The west slope of the Teton Range, where we found very high WPBR incidence and intensity, is also of particular concern. Loss of *P. albicaulis* in this prime grizzly bear habitat would be severely detrimental to future grizzly bear conservation efforts (D. Mattson personal communication).

Other areas of high WPBR incidence and intensity include the Idaho Batholith, eastern Salmon River Mountains, and Seven Devils Mountains in the northwestern part of the study area. We associated recent mortality of

TABLE 2. Comparison of 1967 and 1995–1997 white pine blister rust surveys in 4 Idaho and Wyoming national forests.

National forest	1995–1997 survey ^a			1967 survey ^b		
	Stands sampled (N)	Stands infected (%)	Average intensity ^c (%)	Stands sampled (N)	Stands infected (%)	Average intensity (%)
Bridger-Teton	12	50.0	34.5	16	18.8	38.3
Caribou ^d	3	33.3	78.1	4	0	0
Sawtooth	13	23.1	43.8	5	0	0
Targhee	30	96.7	55.3	1	0	0
TOTALS	58	67.2	51.5	26	11.5	38.3

^aTransect data ($n = 35$) and supplemental transect data ($n = 20$)

^bBrown and Graham (1969)

^cSum of percentage of trees infected with WPBR in infected samples divided by number of infected samples.

^dIncludes the Idaho portion of the Cache National Forest surveyed by Brown and Graham (1969).

P. albicaulis with *Dendroctonus ponderosae* (mountain pine beetle) and root pathogens (unidentified). The interaction of these opportunistic parasites and WPBR may accelerate white pine mortality in this area.

Further Spread of White Pine Blister Rust

Whether WPBR will cause problems for white pines in areas that are now free of the disease is unknown. The southward spread of WPBR in the southern portion of the middle Rocky Mountains and along the northern boundary of the Great Basin has proceeded very slowly, if at all, since the 1960s. Furthermore, we found no evidence of WPBR in any of the isolated Great Basin forests closest to infected regions, even those that are only a few kilometers from moderately high infection centers in the Sierra Nevada. Isolation from *Ribes* populations, or infected pine populations, may be a primary factor in the absence of WPBR in the Great Basin.

Lack of climatic conditions conducive to WPBR spread and intensification may also be an important factor in explaining the absence of WPBR in the Great Basin. Climates of the Great Basin and central Utah are generally more arid than elsewhere within the range of WPBR. In Great Basin mountain ranges, it is unknown whether moisture events necessary for infection by WPBR, such as fog, rain, and dew (Mielke 1943), occur frequently enough for WPBR to persist or intensify.

The apparent absence of WPBR in the Great Basin and the Rocky Mountains in Utah suggests that there is not a continuous, or even broken, corridor of infected pines between

infection centers in the Sierra Nevada or northern and middle Rocky Mountains to the New Mexico infection site described by Hawksworth (1990). We did not investigate the eastern Rocky Mountain ranges; however, our review of WPBR survey literature documents a long-known WPBR infection in the southern end of the Laramie Range in southeastern Wyoming (Brown 1978). This range is the northwestern extension of the Colorado Front Range (Lageson and Spearing 1988). Limber pines grow in both ranges, indicating a possible route for spread of the disease. The mountains in New Mexico receive relatively abundant moisture during late summer due to a monsoonal climate (Baker 1944). The disease also may have spread via long-distance spore dispersal and become established only where climatic conditions and alternate host distribution were favorable.

We hypothesize that the combination of isolation from reservoirs of infected pines and environmental conditions which are relatively unfavorable to initial WPBR infection has thus far been a barrier to WPBR establishment in the Great Basin. But, the potential for spread and subsequent intensification of WPBR should not be underestimated. During our survey we observed that, at some sites, most WPBR cankers were located at a similar distance from the main tree stem. Since we recorded only the most proximal canker found on each tree, we could not perform a statistical analysis of this apparent clustering of canker distances. However, the observation alone suggests that infections occurred during the same time period. This type of pattern is indicative of a wave year phenomenon wherein

most WPBR infections occur only during years when environmental conditions are favorable for infection (Mielke 1943, Peterson 1971). The probability of a wave year may be lower in the relatively arid Intermountain West than in the maritime provinces and might help explain the slow spread of WPBR in our study area. However, we observed several sites in which distances of cankers from the main stem were more evenly distributed, indicating a higher frequency of years in which environmental conditions are favorable enough for at least some infections to occur.

A recent climate analysis of the Greater Yellowstone Ecosystem suggests that years during which the climate is favorable to WPBR infection are common in the subalpine zone. If montane climates in other portions of the Intermountain West yield frequent wave years, factors such as the timing of *Ribes* leaf emergence and distribution of white pine and susceptible *Ribes* may be more important in explaining the spread of WPBR in the Intermountain West. Additional research to age cankers and to clarify the roles of climate, site conditions, and the distribution of host species will help researchers more accurately predict where WPBR is likely to occur and intensify in the immediate future, and under long-term climate change scenarios.

Management Implications

Training land managers to identify WPBR and establishing a frequent, regular monitoring regime would help in the early detection of new infection centers. If, as we presume, years in which the climate is conducive to infection are rare in the Great Basin, early detection and implementation of control measures, such as canker removal or selective tree removal, might slow or even stop a small infection center in the isolated white pine populations of the region. In heavily infected areas of the Intermountain West, silvicultural or prescribed fire treatments could be used to reduce inoculum potential or to promote natural reproduction of phenotypically resistant white pines by removing infected white pines or other competing tree species. Identifying and collecting seed from resistant trees could provide stock for breeding programs and for reintroduction of native resistant stock. In any situation, management of white pine ecosystems should be based not only on WPBR

epidemiology, but also on preservation of white pine genetic diversity and local disturbance ecology.

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APPENDIX. White pine species sampled, incidence of white pine blister rust, mortality, and geographic location of stands sampled during 1995–1997 in the Intermountain West.

Sample ^a	Species sampled ^b	Live trees (N)	Infected trees (N)	WPBR mortality ^c (%)	Coordinates		Sample location
					Latitude	Longitude	
BOI01	A	39	3	0	43.61235	115.44104	Near Trinity Mountain, ID
BOI02	A	49	20	2.0	43.99066	115.32479	N of Shepherd Peak, ID
BOI03	A	47	30	1.9	44.17672	115.75901	E of Scott Mtn. Lookout, ID
BOI04	A	57	31	0	44.41286	116.12706	Snowbank Mountain, ID
BRI01	A	48	17	0	43.16663	110.18464	Spring Creek near The Rim, WY
BRI02	A	52	0	0	43.39252	110.08593	Bacon Ridge, W of Mosquito Lake, WY
BRI03	A	50	3	0	43.46214	109.93764	Near Fish Creek Work Center, WY
BRI04	A	50	9	0	43.75610	110.07015	Togwotee Pass, WY
BRI05	A	51	22	0	42.84406	110.58272	McDougal Gap, WY
BRI06	A	53	0	0	42.07242	110.57198	Commissary Ridge, WY
GRO01	A	53	3	0	43.44329	110.06318	Buffalo Meadow, WY
WIN01	A	51	0	0	42.69115	109.23433	Upper S Temple Creek, WY
WIN02	A	53	0	0	42.67272	109.25683	Big Sandy Opening, WY
WIN03	A	37	0	0	43.45941	109.94090	Near Fish Creek, WY
WIN04	A	39	0	0	43.29536	109.93423	Near Gypsum Creek, WY
LIM18	F	4	4	—	42.49976	110.91625	Allred Flat, WY
LIM05	F	15	0	—	43.36980	111.49372	Fall Creek, ID
LIM11	F	30	0	—	42.65791	111.62572	Soda Springs, ID
LIM12	F	32	25	—	43.20678	111.21272	Jensen Pass, ID
CED01	F, L	50	0	0	37.56362	112.84558	Cedar Canyon, UT
BRY01	F, L	38	0	0	37.78900	112.14900	Church Garden, UT
HUM01	A	38	0	0	41.83000	115.46200	Jarbidge Mountain, NV
PFR01	A, F	50	0	0	41.68096	118.74585	Pine Forest Range, NV
SAN01	F	47	0	0	41.78800	117.55075	Santa Rosa Mountains, NV
RUB01	A, F	36	0	0	40.63174	115.40645	Ruby Mountains, NV
SNA01	F	41	0	0	39.00517	114.30749	Wheeler Peak, NV
SNA02	F	34	0	0	38.96481	114.27636	Baker Creek, NV
CAR01	A	49	24	0	39.31264	119.89728	Mt. Rose Summit, NV
CAR02	M	50	6	0	39.06936	119.89367	Spooner Summit, NV
SIE01	A, M	49	0	0	38.51056	119.56856	Carson-Iceberg Wilderness, CA
SIE02	A, M	45	7	0	38.54268	119.81133	Ebbetts Pass, CA
SIE03	M	50	0	0	38.67728	119.59634	Monitor Pass, CA
PNM01	M	51	0	0	38.81221	119.51499	Pine Nut Mountains, NV
BAL01	M	50	27	0	39.60208	120.10436	Bald Mtn. Range, CA
SWE01	A	52	0	0	38.41627	119.26680	Sweetwater Range, CA
WHI01	L	47	0	0	37.39044	118.17978	Schullman Grove, CA
VIR01	M	6	0	—	39.33252	119.63949	Virginia Range, NV
SAL15	A	51	27	0	45.37411	115.86560	Marshall Lake, ID
SAL16	A	50	30	2.0	45.34305	115.84562	Near California Lake, ID
SAL17	A	46	30	0	45.31940	115.79160	War Eagle Peak, ID
SAL18	A	44	35	0	44.87426	115.94709	Boulder Peak, ID
SAL19	A	15	5	0	45.01326	116.11976	Brundage Mountain, ID
SEV01	A	45	38	0	45.35110	116.50976	Seven Devils, ID
SEV02	A	42	16	16.0	45.34903	116.49246	Heaven's Gate, ID
WBP04	A	50	25	—	45.18590	116.13010	Hazard Lake, ID
BIT01	A	49	1	0	45.46384	114.32236	Continental Divide–Spring Creek, ID
BIT02	A	48	0	2.0	45.47249	114.35710	Blue Nose Lookout, ID
BIT03	A	50	7	3.8	45.55438	114.51407	East of Reynolds Lake, ID
BIT04	A	48	7	0	45.51721	119.83699	Morgan Mountain, ID
BIT05	A	51	0	0	44.78314	113.35547	Grizzly Hill, ID
BIT06	A	52	21	0	45.08084	113.54208	Headwaters of Kenney Creek, ID
CLE01	A	47	15	4.1	45.39577	114.61340	Corn Lake, ID
CLE02	A	52	10	0	45.38938	114.55931	Long Tom Ridge/Swamp Creek, ID
CLE03	A	50	10	1.9	45.35919	114.57914	Long Tom Ridge/Bear Camp Spring, ID
LEM02	A	44	0	0	44.43026	113.32289	W of Meadow Lake Campground, ID
LEM03	A	49	0	0	44.44096	113.31661	N of Meadow Lake Campground, ID
LEM04	A	31	0	0	44.65323	113.65154	Mill Lake, ID

APPENDIX. Continued.

Sample ^a	Species sampled ^b	Live trees (N)	Infected trees (N)	WPBR mortality ^c (%)	Coordinates		Sample location
					Latitude	Longitude	
SAL01	A	49	6	0	45.25773	114.01104	Salmon R. Mountain/Wallace Lk., ID
SAL02	A	48	8	0	45.19917	114.04678	Salmon R. Mountain/Turner Gulch, ID
SAL03	A	53	21	0	45.13484	114.06392	Salmon R. Mountain/Phelan Mtn., ID
SAL04	A	51	6	0	45.00075	114.42997	Red Rock Peak, ID
SAL05	A	52	6	0	45.06037	114.44690	Quartzite Mountain, ID
SAL06	A	52	3	0	45.09697	114.51502	Crags Campground, ID
SAL07	A	50	0	0	45.08478	114.52858	S of Crags Campground, ID
LOS01	F	31	0	0	44.13672	113.81795	W Slope, Mt. Borah, ID
BOU01	A	42	0	0	43.91627	114.36801	North Fork of Lost River Headwaters, ID
MAC01	A	52	1	0	43.88511	113.68992	White Knob Mountains, ID
SAL08	A	51	1	0	44.46408	114.73555	Loon Creek Summit, ID
SAL09	A	52	0	0	44.47163	114.48829	Mill Creek Summit, ID
SAL10	A	34	2	0	44.75359	114.67964	Sleeping Deer Lookout, ID
SAL11	A	52	1	0	44.67445	114.55989	Fly Creek Point, ID
SAL12	A	52	0	0	44.60336	114.47234	Twin Peak, ID
SAL13	A	52	4	0	44.58764	115.00826	Sheep Mountain, ID
SAL14	A	47	10	2.1	44.56863	115.01072	Fonzez Creek, ID
SAW01	A	71	0	0	43.96262	114.69275	Pole Creek, ID
SAW02	A	62	0	0	43.88052	114.71073	Galena Summit, ID
SAW03	A	49	0	0	43.59235	114.68143	Dollarhide Summit, ID
SAW04	A	52	0	0	44.02695	114.65040	Phyllis Lake, ID
SAW05	A	89	0	0	43.81082	114.80664	Frenchman Creek, ID
SAW06	A	46	0	0	43.84080	114.50401	Boulder City, ID
WBP01	A	30	5	—	43.32808	114.61948	Boulder View, ID
WBP02	A	50	2	—	44.17230	114.57488	Railroad Ridge, ID
WBP03	A	20	0	—	43.85551	114.88476	Beaver Creek, ID
LIM01	F	15	0	—	43.82085	114.25056	Trail Creek, ID
LIM03	F	50	50	—	43.80094	114.41991	Murdock Creek, ID
LIM02	F	50	0	—	43.42440	113.54859	Craters of the Moon, ID
LIM19	F	50	0	—	42.31617	113.64109	Mt. Harrison, ID
CEN01	A	48	32	4.0	44.41939	112.34467	Pleasant Creek Summit, W, ID
CEN02	A	51	33	0	44.41944	112.34460	Pleasant Creek Summit, E, ID
CEN03	A	38	8	0	44.55312	111.42022	Sawtelle Creek, ID
CEN04	A	42	5	0	44.56013	111.44394	Sawtelle Krumholtz site, ID
CEN05	A	49	45	2.0	44.53543	112.05843	Big Table Mountain, W, ID
CEN06	A	48	45	0	44.53213	112.03794	Big Table Mountain, E, ID
CEN07	A	33	10	0	44.41944	112.34460	Sawtelle Peak, ID
CEN08	A	41	33	2.3	44.56038	111.58557	Blair Lake, ID
CEN09	A	50	11	0	44.53138	111.85361	Hancock Lake, ID
HEN01	A	33	32	15.2	44.68883	111.29229	Targhee Pass/Avalanche Gulch, ID
HEN02	A	42	31	6.0	44.62466	111.25966	Mt. Two Top, ID
HEN03	A	52	11	0	44.69912	111.39685	Black Mountain, ID
LEM01	A	42	0	0	44.34804	113.26162	Spring Mountain Canyon, ID
MCP01	A	52	1	0	44.51267	111.15442	Moose Creek Plateau/Black Canyon, ID
TET01	A	52	9	0	44.11943	110.89848	Flagg Ranch Road, WY
TET02	A	46	34	2.1	43.49712	110.95485	Teton Pass-East, WY
TET03	A, F	49	20	0	43.88905	110.96675	Badger Creek, WY
TET04	F	49	43	0	43.49131	110.95602	Teton Pass-West, WY
TET06	A	53	16	0	44.12063	110.85708	Camp Loll, WY
TET07	A	51	27	1.9	44.03884	110.90426	Hominy Peak, WY
WBP05	A	9	7	—	44.04221	110.94600	Hominy Peak, W, WY
WBP06	A	40	20	—	44.51400	111.86200	Alduous Lake, ID
WBP07	A	10	8	—	44.07353	110.97240	Jackass Loop, WY
LIM04	F	50	40	—	44.37300	112.70800	Webber Creek, ID
LIM06	F	30	24	—	43.52364	111.25986	Mike Spencer Canyon, ID
LIM07	F	15	4	—	44.27560	112.75000	Crooked Creek, ID
LIM08	F	50	4	—	44.30068	112.92534	Nicholia Canyon, ID
LIM09	F	20	20	—	43.93972	112.92534	Deer Canyon, ID
LIM10	F	30	30	—	44.24532	112.80766	Buckhorn Canyon, ID

APPENDIX. Continued.

Sample ^a	Species sampled ^b	Live trees (N)	Infected trees (N)	WPBR mortality ^c (%)	Coordinates		Sample location
					Latitude	Longitude	
WAS03	F	44	0	0	39.86788	111.74625	Mt. Nebo, UT
WAS01	F	40	0	0	40.60006	111.59843	Solitude Ski Area, UT
WAS02	F	41	0	0	40.65176	111.59385	Silver Peak, UT
WAS04	F	52	0	0	40.56368	111.65012	Snowbird Ski Area, UT
STA01	F	52	0	0	40.48520	112.62066	Stansbury Range, UT
LIM13	F	4	0	—	37.49200	111.17500	Yellow Pine, UT
LIM14	F	10	0	—	41.77800	111.63200	Logan Cave, UT
LIM15	F	5	0	—	41.82700	111.59500	Ricks Spring, UT
LIM16	F	10	0	—	41.93900	111.54900	Beaver Mtn., UT
LIM17	F	30	0	—	41.90900	111.45200	Old Limber Trail, UT

^aSamples with LIM or WBP prefixes are incidental samples of *Pinus flexilis* (limber pine) and *P. albicaulis* (whitebark pine).

^bF = *P. flexilis*, A = *P. albicaulis*, M = *P. monticola*, L = *P. longaeva*.

^cMortality data not collected in incidental plots.

DISTRIBUTION, MOVEMENTS, AND HABITAT USE OF RAZORBACK SUCKER (*XYRAUCHEN TEXANUS*) IN A LOWER COLORADO RIVER RESERVOIR, ARIZONA-NEVADA

Gordon Mueller¹, Paul C. Marsh², Glen Knowles³, and Ty Wolters⁴

ABSTRACT.—Distribution, movements, and habitat use of 10 wild adult razorback suckers (*Xyrauchen texanus*) were examined in Lake Mohave, Arizona-Nevada, from November 1994 through July 1997. Movement rates (0.00–17.35 km d⁻¹) and ranges (\bar{x} = 39 km) were similar to those for riverine populations. All study fish returned to spawning sites used in previous years, but they also visited other spawning areas. Spawning females were significantly ($P = 0.031$) more active than males (480 vs. 87 m d⁻¹) and moved substantial distances between spawning sites during peak reproduction (1–28 February). Fish became most active (m d⁻¹, km month⁻¹) after spawning and moved to areas known to support higher algal production. Fish were typically within 50 m ($P < 0.001$) of shore and at average depths between 3.1 and 16.8 m (range 0.2 to >30.0 m). Adults were detected throughout the available thermal gradient (12°–30°C), but during summer typically had body temperatures between 18° and 22°C. Vertical movements within the water column showed no correlation with depth or time of day, but seasonal shifts suggest fish may regulate body temperature by seeking specific temperatures during reservoir stratification.

Key words: *Xyrauchen texanus*, razorback sucker, reservoir, spawning, habitat, movements, telemetry.

Xyrauchen texanus, the razorback sucker, is the largest catostomid in North America and is endemic to the Colorado River basin. Historically common, this riverine species now is reduced to relic and fragmented populations; 3 of 4 known populations (>100 fish) are in reservoirs (Minckley et al. 1991, Modde et al. 1996, Holden et al. 1997), the largest located in Lake Mohave, Arizona-Nevada. It was listed by the U.S. Fish and Wildlife Service as an endangered species in 1991 (USFWS 1991).

Telemetric research has focused primarily on rivers where adults have been found to use backwater and other lentic type habitats (Tyus 1987, Marsh and Minckley 1989, Modde and Wick 1997). However, riverine monitoring has been hampered by problems associated with working in large, remote systems, a scarcity of wild fish, and a short (2–3 wk) spawning season that occurs on the ascending limb of spring runoff (Tyus 1987, Minckley et al. 1991). Published reports specific to lentic environments are limited to McAda and Wydoski's (1980) description of *X. texanus* use of a gravel pit adjacent to the Colorado River in Colorado and Medel-Ulmer's (1983) abstract describing

X. texanus movement in Senator Wash Reservoir in California. While information is scarce, backwater and floodplain habitat is viewed as critical for species restoration (Valdez and Wick 1981, Wydoski and Wick 1998). The following report presents telemetry data describing *X. texanus* distribution, movements, and habitat use in a Colorado River mainstem reservoir and provides new information on spawner movements and female use of multiple spawning sites.

STUDY AREA

Lake Mohave is a mainstem Colorado River reservoir created with the construction and closure of Davis Dam located 5 km upstream of Laughlin, Nevada. The reservoir borders both Arizona and Nevada and extends 100 km upstream to the tailrace of Hoover Dam. When full (surface elevation 197 m/msl) the reservoir has a surface area of 11,655 ha. The reservoir inundates Black Canyon, located immediately downstream of Hoover Dam, and Pyramid Canyon where Davis Dam was constructed. Between these canyons the reservoir broadens, forming Cottonwood Basin, which

¹United States Geological Survey, Box 25007, D-8220, Denver, CO 80225.

²Department of Biology, Arizona State University, Tempe, AZ 85287-1501.

³United States Fish and Wildlife Service, Carlsbad, CA.

⁴Bureau of Reclamation, Boulder City, NV 89006.

has a maximum width of 6 km (Fig. 1). Lake Mohave has no tributaries other than the Colorado River, which enters as cold, hypolimnetic releases (Lake Mead) from Hoover Dam. Flows are discernible for the first 20–30 km, at which point the river exits Black Canyon and the reservoir broadens and depth increases. Maximum depth at Davis Dam is 35 m.

Construction of Davis Dam in 1954 represented the last mainstem reservoir built on the lower Colorado River. It is believed the reservoir population of *X. texanus* originated from an initially high period of recruitment from individuals trapped upstream during the closure of Davis Dam (Minckley 1983, Marsh 1994).

METHODS

Collections

A trammel net (2 m × 3.7 cm × 50 m) was used to capture wild adult *X. texanus* on 6–7

November 1994 from Lake Mohave at Yuma and Tequila coves. Each fish was measured for total length (mm), weighed (g), anesthetized with tricaine methanesulfate (125 mg L⁻¹), and surgically implanted (after Tyus 1987) with a sonic transmitter. A 30- to 40-mm medio-lateral incision was made slightly anterior and dorsal to the left pelvic fin, and the transmitter was inserted into the abdominal cavity so that it rested on the pelvic girdle. The incision was sutured with 4–5 knots using 3-0 Ethilon black monofilament nylon and an FS-1 cutting needle. We allowed the fish to recover 1–10 min after surgery and then released them at capture sites. Transmitters weighed 6 g, measured 16 × 55 mm, had a 14-month life expectancy, and were individually coded. Transmitters had an average detection range of 1 km and logged the transmitter (fish) temperature ($\pm 0.25^\circ\text{C}$) that was compared with water temperature profile data to determine fish depth.

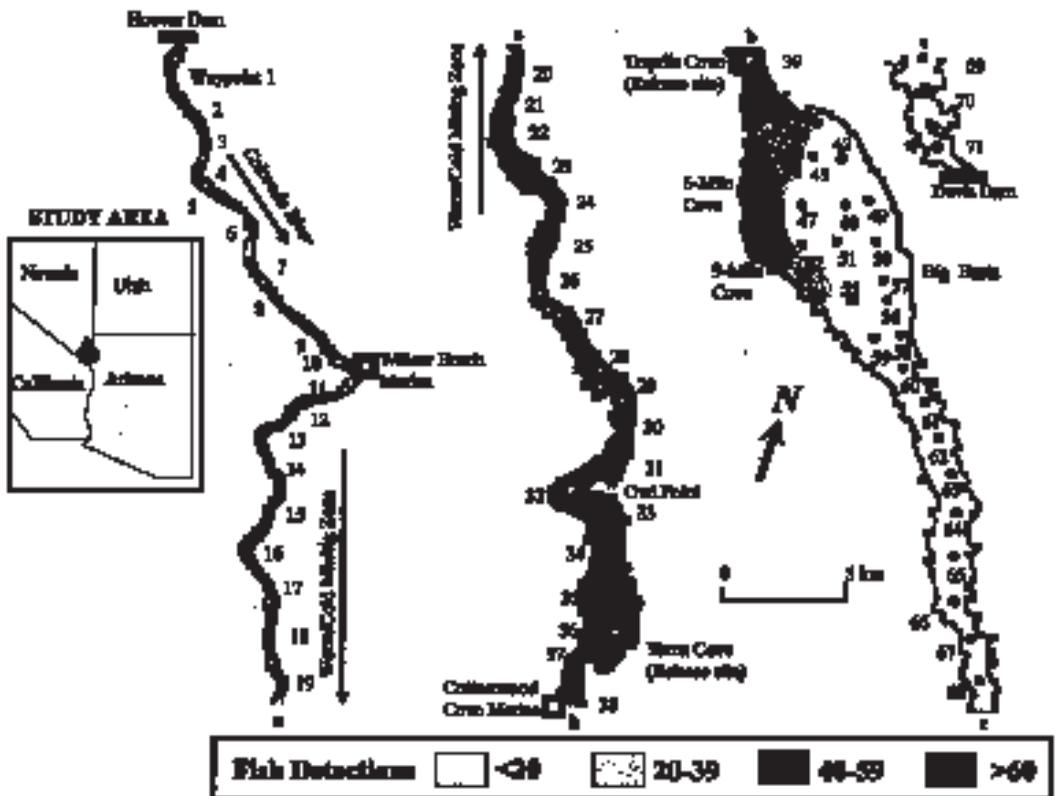


Fig. 1. Segmented map of Lake Mohave, Arizona-Nevada, showing numbered GPS way-point locations and place names mentioned in the text. Shaded areas reflect total number of fish detections per way-point from November 1994 through July 1997.

Survey Design

We conducted weekly surveys by boat using a global positioning system (GPS) and a preestablished survey grid composed of 71 way-points or "listening stations" programed into a GPS navigational system (Fig. 1). Sites were at <1600-m intervals to standardize search effort and ensure systematic coverage of the reservoir. Transmitter signals were detected using a DH-2 hand-held, directional hydrophone, a USR-5W ultrasonic receiver, and headphones. When signals were detected from way-points, we searched out the exact location and further triangulated using the hydrophone and GPS. A digital readout provided time interval measurements between signals that correlated to tag (fish) temperature. Recorded data included fish location (latitude and longitude), body temperature, and estimated distance (<10 m, 10–50 m, 50–100 m, >100 m) from shore. Vertical water temperature profiles were measured using a Hydro-lab™ temperature profiler between May and October 1995.

Surveys were scheduled biweekly for the 14-month transmitter life and were conducted in 2 shifts: 0200–1000 h and 1400–2200 h. Transmitter life greatly exceeded manufacturer estimates, allowing us to collect additional intermittent information between April and August 1996 and from April through July 1997.

Data Analysis

Using digitized shoreline profile maps of Lake Mohave and the geographical information system (GIS) program ARCINFO™, we created movement maps and calculated distances (m) and movement rates (m d^{-1}) between detection locations. Rate measurements and distances from shore were transformed into single classification frequency distributions, and observed data were summarized by classes. Shoreline use was examined by comparing percentiles of available surface habitat to the percentile of fish use within specific zones via a chi square test ($P < 0.001$; Sokal and Rohlf 1981). Comparisons of shoreline habitat utilization, movement rates, and area affinity were divided into spawning (November–April) and nonspawning (May–October) periods as defined by reports for *X. texanus* in Lake Mohave (Minckley 1983, Bozek et al. 1990, Minckley et al. 1991). Active spawning

was determined through observations and the collection of newly emergent larval *X. texanus* by an independent program (Mueller 1995). Movement rates (m d^{-1}) during active spawning (31 January–15 March 1995, 1996) for both sexes were examined for differences in movement patterns and distances using an analysis of variance ($P < 0.05$; Sokal and Rohlf 1981). To compare male and female movement patterns when spawning observations and larval sucker densities were most prevalent, we mapped individual fish movement during peak spawning (1–28 February).

RESULTS

A total of 20 *X. texanus* (10 males and 10 females) were surgically implanted with sonic transmitters. Six females and 4 males were tracked during the entire 14-month study period and were used in this analysis (Table 1; see Mueller et al. 1998). Remaining fish were excluded from analysis because either we lost contact during the study period or transmitters became immobile (shed tag or mortality). An expanded description can be found in Mueller et al. (1998). Study fish averaged 609 mm (555–680 mm) total length and 2.78 kg (1.75–4.21 kg). More than 1000 contacts were recorded representing 580 daily fish sightings, 300 hourly sightings, 800 body temperatures, and 100 vertical water temperature profiles.

Distribution

Fish distribution was distinctly seasonal. Some areas of the reservoir were occupied year-round, while other locations were used specifically for spawning or as summer sanctuaries. Big Basin and Owl Point areas (Fig. 1) were used year-round; Tequila and Yuma coves and the warm/cold mixing zone were used seasonally. Fish were seldom detected in up- or down-reservoir canyon habitats. Detection numbers were highest between way-point (WP) 30 and WP 37. Fish found in Big Basin typically were along the Nevada shoreline between Nine Mile and Six Mile coves (Fig. 2). This area was used by 3 fish during spawning and by 5 during summer. Tequila Cove (WP 39) was visited by all but 1 fish during spawning.

Owl Point (WP 32) was visited by all spawners and by 4 fish during summer and autumn. Following spawning, 7 suckers moved into the area between WP 12 and WP 24

TABLE 1. Individual tracking summaries for sonic telemetry of 10 wild adult *Xyrauchen texanus* in Lake Mohave, Arizona and Nevada, November 1994 to July 1997. Fish are individually identified by tag code; number of observations, average and total distance (m d⁻¹) traveled, days tracked, and range (km) of each fish are presented.

Fish ID	TL (mm)	Weight (kg)	No. of obs.	Distance traveled			s	Total distance traveled (km)	Days tracked	Range (WP ^a)
				Min.	Max.	Avg.				
				----- (m d ⁻¹) -----						
FEMALES										
88	615	2.70	65	0	6,703	603	1322	250.4	974	32-66
276	654	3.61	71	21	3,502	606	708	352.5	953	24-67
339	665	3.33	62	9	10,108	767	1413	417.4	981	27-99
375	680	3.35	54	4	2,368	417	544	249.7	540	16-64
384	631	2.76	36	0	6,886	614	1133	183.0	466	26-65
465	614	2.94	65	9	6,558	485	851	264.3	969	5-34
\bar{x}	643	3.12	59	7	6,021	582	996	286.2	814	
MALES										
2228	558	2.40	51	3	15,607	788	2280	231.5	540	39-90
366	588	2.29	57	0	1,986	243	509	167.7	974	31-62
348	526	1.75	65	0	17,353	509	2154	181.7	960	32-71
258	595	2.26	57	0	1,635	242	334	120.9	540	29-47
\bar{x}	567	2.18	58	1	9,145	446	1319	175.5	754	

^aWP = way-point

where cold Hoover Dam releases mix with warmer Lake Mohave waters. We observed 9 *X. texanus* (nontagged) near the surface at the mixing zone on 8 June 1997 (9 fish per 1.5 km).

Movements

Fish movements were variable and distinctive by sex and among individuals. Both males (>17.4 km d⁻¹) and females (10.1 km d⁻¹) traveled substantial distances in short periods of time, while some fish remained sedentary for days. Fish on average moved 527 m d⁻¹ (\bar{x} = 242-788 m d⁻¹), and while there was no statistical difference between sexes, females tended to be slightly more active (\bar{x} = 582 m d⁻¹) than males (\bar{x} = 446 m d⁻¹; Table 1). Hourly movement rates were statistically examined, and although no significant trends were identified, apparently fish might be slightly more active during summer at midmorning hours (0900-1000 h), supporting previous observations (McAda and Wydoski 1980).

Movement rates were examined both for nondirectional (m d⁻¹) and directional (linear km month⁻¹) activities. Monthly averages near the end of, or shortly after, spawning (March, April, May) exceeded 1000 m d⁻¹ for 1995, 1996, and 1997 (Table 2). Linear distances traveled (km month⁻¹) peaked following spawning for all 3 yr (March 1995, May 1996, April 1997 [Table 2]). Linear ranges for indi-

viduals ($N = 10$) averaged 39 km (18-72 km) during the course of the study. Females on average ranged 42 km (29-72 km) compared to 35 km (18-51 km) for males.

All study fish returned to spawning sites used in previous years, but they also visited other spawning sites. Spawning (31 January-15 March 1995, 1996) females were significantly (ANOVA/ $F_{1,8} = 6.79$, $P = 0.0314$) more active (460 vs. 87 m d⁻¹) than males. During peak spawning (1-28 February 1995, 1996), the majority of females crossed the reservoir to visit other spawning sites while males typically remained at a single site (Fig. 2).

Habitat Use

Xyrauchen texanus exhibited a significant association with inshore (<50 m of shore) habitats ($P < 0.001$, chi square test). This affinity was most pronounced during spawning when distance from shore averaged <30 m. Fish moved offshore during summer (July-November), possibly to avoid warmer water temperatures (Fig. 3).

During warmer months the reservoir presented fish a wide range of thermally stratified habitats. Temperatures up-reservoir were cold (12°-16°C), regardless of season or depth, due to hypolimnetic releases from Lake Mead. During summer the reservoir thermally stratifies further downstream presenting temperatures ranging from 30°C (surface) to 15°C

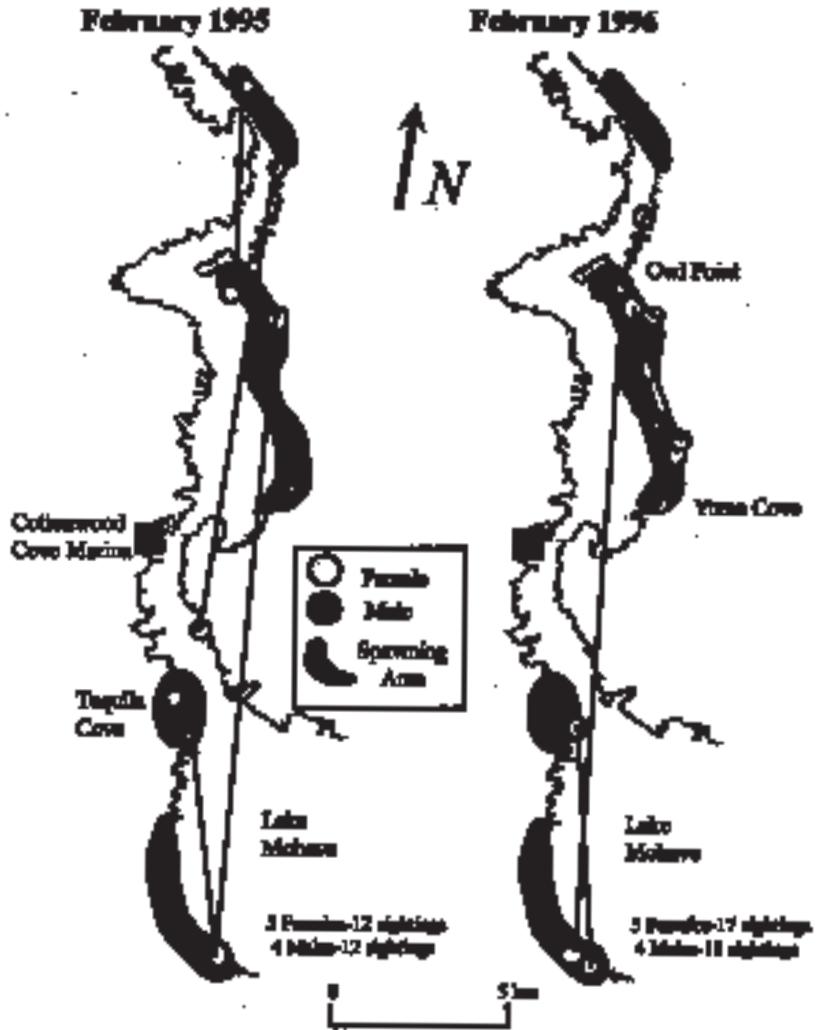


Fig. 2. Location and movements of male and female *Xyrauchen texanus* in association with major spawning areas during peak spawning (1–28 February 1995, 1996) in Lake Mohave, Arizona-Nevada.

(depths >30 m). Fish body temperatures ranged between 12° and 28°C, with summer averages ranging from 18° to 22°C, which was similar to thermal preferences reported by Bulkley and Pimentel (1983). Hourly data indicated fish moved vertically in the water column, but we found no correlations for depth with time of day.

Vertical temperature profiles ($n = 107$) were taken from May through November 1995 to correlate body temperature with depth. Fish ranged to depths >30 m but typically were found near 9 m ($\bar{x} = 9.1$ m; Fig. 3). Average fish depths changed with season, suggesting

fish may regulate body temperature during reservoir stratification (Fig. 3). Fish were found nearer the surface during spring and autumn and deeper during midsummer.

DISCUSSION

Lake Mohave scarcely represents what many would consider pristine *X. texanus* habitat. However, it is noteworthy that 3 of 4 remaining wild populations (>100 individuals) are found in reservoirs (Minckley et al. 1991, Holden et al. 1997, Modde and Wick 1997). Investigators who have conducted research in riverine environments have been challenged

TABLE 2. Monthly tracking summaries for sonic telemetry of 10 wild adult *Xyrauchen texanus* in Lake Mohave, Arizona and Nevada, from November 1994 to July 1997. The average monthly distance traveled is an average of individual monthly movements (total m month⁻¹).

Month	Julian day	Average	s	No. observations
November 1994	34639	1216 ^a	1658	16
December	34669	488	563	25
January 1995	34700	350	431	32
February	34731	345	525	25
March	34759	1100	2703	35
April	34790	309	515	33
May	34820	445	770	24
June	34851	463	593	28
July	34881	679	1256	27
August	34912	686	2030	23
September	34943	157	214	24
October	34973	307	541	24
November	35004	333	380	21
December	35034	521	773	21
January 1996	35065	199	261	17
February	35096	262	390	10
March	35125	247	335	30
April	35156	479	1407	18
May	35186	1730	2179	6
June	35217	475	453	40
July	35247	533	641	33
April 1997	35521	2338	5017	11
May	35551	510	399	14
June	35582	576	806	17
July	35612	477	685	6

^aBoldface numbers, $P < 0.05$.

by fish scarcity, logistics associated with river hydraulics, sampling in remote areas, and poor water visibility (Tyus 1987, Tyus and Karp 1990, Modde and Irving 1998). On the other hand, researchers working in reservoir environments are presented with a broader and less fluctuating range of physical parameters not found in natural river settings. For instance, reservoir water visibility (>10–15 m) allowed direct observations, summer water temperatures presented a stable but wide thermal gradient (12°–30°C), flows ranged from 0 to 2 m sec⁻¹, depths exceeded 40 m, and fish could choose both littoral and pelagic habitats. Reservoir conditions allowed us to observe spawning and document reproduction through the collection of larval *X. texanus* (Mueller 1989, Minckley et al. 1991, Mueller 1995). River studies have not shared in this degree of documentation, and spawning typically has been inferred by transmitter movement and in a few cases by collection of ripe fish (Tyus 1987, Tyus and Karp 1990, Modde and Irving 1998).

It has been widely reported that *X. texanus* migrate to specific spawning areas (Tyus 1987,

Tyus and Karp 1990, Modde and Irving 1998), and while spawning site fidelity has been speculated, it has never been proven (Tyus and Karp 1990, Scholz et al. 1992, and Modde et al. 1996). Recently, Modde and Irving (1998) speculated *X. texanus* may use multiple spawning sites in the Green River; however, this was not documented by observation or collection of gametes or larvae.

Adult *X. texanus* in Lake Mohave typically used broad, shallow shoreline habitats and generally did not occupy deeper canyon habitat typical of the lower or upper reservoir. Fish were seldom found together except during spawning (McAda and Wydoski 1980) and exhibited movement rates and ranges similar to those in riverine habitats (Tyus 1987, Tyus and Karp 1990, Modde and Irving 1998). Individual fish exhibited various degrees of sedentary and roaming behavior similar to other stream fish (Funk 1955).

Xyrauchen texanus spawning in reservoirs occurs from January through March, which is earlier and typically 2–3 times longer than riverine spawning (Minckley 1983, Minckley et al. 1991). Highly social, these fish form

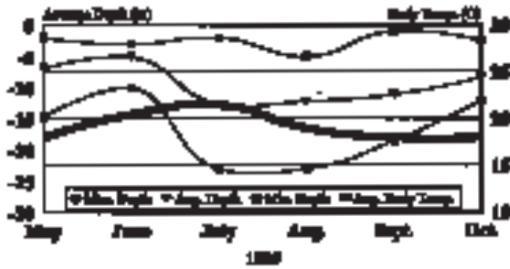


Fig. 3. Monthly comparison of average depth (m) and body temperature ($^{\circ}\text{C}$) of *Xyrauchen texanus* during thermal stratification (May–October) of Lake Mohave, Arizona-Nevada, in 1995.

spawning groups that can number in the hundreds. Males typically dominate (2:1) spawning sites (Minckley 1983). Females normally join males from adjacent deeper waters when ready to release their eggs (Minckley 1983, Mueller 1989), a behavior common with other catostomids (Moyle 1976).

Prolonged spawning combined with excellent observation and field conditions allowed us to more closely examine spawning and post-spawning movements. All study fish returned to spawning sites used the previous year, although they were also tracked to other spawning groups. In some cases the distance between spawning sites exceeded 50 km; 9 of 10 fish were found crossing the reservoir, participating in spawning groups on both the Arizona and Nevada shorelines. Fish movements during peak spawning (1–28 February 1995, 1996) suggested males typically remain on specific spawning sites while females roam substantial distances between spawning sites. We were unable to determine whether females spawned at multiple sites, but reports of females spawning over extended periods combined with the species known fecundity (>100,000 ova; Minckley 1983, Minckley et al. 1991) support the contention that multiple-site spawning occurs. Multiple-spawning-site behavior also helps explain the high genetic diversity of this population (Dowling et al. 1996).

Travel distances and movement rates peaked post-spawning as the majority (70%) of study fish moved immediately up-reservoir to the warm/cold water mixing zone where nutrient-rich hypolimnetic releases from Lake Mead stimulate algal production (Baker and Paulson 1980). Post-spawning movement supports earlier speculations that *X. texanus* historically

moved to more productive habitats following spawning (Valdez and Wick 1981, Tyus and Karp 1990, Modde and Wick 1997). Increased activity (Table 2) in shallower depths (Fig. 3) may indicate planktonic feeding (Marsh 1987). Wydoski and Wick (1998) suggested floodplain habitats and associated feeding activity are critical for fish to regain body condition after spawning.

Homing patterns of spawning and non-spawning populations were typical of those described by Gerking (1958): "Spawning migrations are directed toward a specific location . . . [while] the fish are usually scattered over a wide area during the non-reproductive portion of life." While fish used common areas during spawning, they typically dispersed after spawning, with some fish returning to specific locations in which they had been found the previous summer. The distance between spawning and summer use areas ranged from 20 km (4 fish) to 30 km (6 fish), with no correlations with sex or size. Fish exhibited a great deal of individuality, some being quite active while other were quite sedentary and remained in specific coves for weeks.

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EFFECT OF SALINITY AND PLANTING DENSITY ON PHYSIOLOGICAL RESPONSES OF *ALLENROLFEA OCCIDENTALIS*

Bilquees Gul¹, Darrell J. Weber², and M. Ajmal Khan¹

ABSTRACT.—Physiological responses of *Allenrolfea occidentalis* to salinity and seedling density were investigated. Effects of salinity (0, 200, 400, 600, 800, and 1000 mM NaCl) and 3 planting densities (2000, 4000, 6000 plants m⁻²) on the growth, survival, and ecophysiology of *A. occidentalis*, a stem succulent inland halophyte, were studied under controlled greenhouse conditions. Plants were grown in a sand culture using subirrigation. Dry mass of roots was highest at 600 mM NaCl at low density (2000 plants m⁻²), but declined as salinity increased. Tissue water content was highest at the 200 mM NaCl treatment and decreased with increased salinity. Water potential of the plants became more negative with increasing salinity due to the accumulation of NaCl in the leaves. Inorganic ions, especially Na⁺ and Cl⁻, contributed substantially to dry mass. Na⁺ and Cl⁻ concentration in shoots and roots increased when NaCl level was increased while K⁺, Ca⁺⁺, Mg⁺⁺, SO₄⁻⁻, and NO₃⁻ contents decreased. Net photosynthesis increased at low salinity (200 mM), but photosynthesis at other salinities was not significantly different from the control. While *A. occidentalis* is very salt tolerant and photosynthesis functioned reasonably well at high salinities, extremely high salinity did decrease dry mass of roots and shoots.

Key words: salinity, planting density, *Allenrolfea occidentalis*, halophyte, salt tolerance, pickleweed.

Halophytes are plants that complete their life cycle at high salinities (Flowers et al. 1977), and their survival in salt marshes depends on salt tolerance at different stages of their life cycle (Adam 1990). Dry mass of halophytes usually decreases with increases in salinity (Ungar 1991), although growth of several halophytes is stimulated at some levels of salinity (Flowers and Yeo 1986, Munns et al. 1983, Khan and Aziz 1998). Nevertheless, high NaCl concentration is probably not essential for optimal growth of most halophytes. There are several halophytes that show optimal growth at NaCl concentrations of 400 mM or higher, e.g., *Cress crinitic* (425 mM NaCl; Khan and Aziz 1998), *Suaeda fruticosa* (400 mM NaCl), *Haloxylon recurvum* (400 mM NaCl), and several cold-desert halophytic species like *Salicornia rubra*, *S. utahensis*, *Suaeda moquinii*, and *Kochia scoparia* (600 mM NaCl; Khan et al. unpublished data).

Intraspecific competition may influence survival, growth, and fecundity of annual populations in saline habitats (Ungar 1991). However, the role of competition in perennial populations appears to be limiting in reference to new recruitment (Khan and Aziz 1998, Gul and Khan 1999). Most perennial halophytes

usually do not recruit through seeds, and ramets are competitively superior to genets at the recruitment phase of the life cycle (Gul and Khan 1999). In a saline habitat dominated by perennials, drought, temperature, and salinity stress synergistically cause death of seedlings and depress growth of adult plants. Mortality in perennial halophytes occurs at the seedling stage due to high salinity, temperature, or severe drought, while adult plants enter into a phase of dormancy to avoid death (Khan and Aziz 1998).

Osmotic active adjustment under saline conditions may be achieved by ion uptake, synthesis of osmotica, or both (Cheesman 1988, Popp 1995). Halophytes differ widely in the extent to which they accumulate ions and overall degree of salt tolerance (Glenn et al. 1996). Stem- and leaf-succulent chenopods are commonly known as salt accumulators and have high Na⁺ and Cl⁻ content (Breckle 1975, Albert and Popp 1977, Gorham et al. 1980, Neumann 1997, Khan and Aziz 1998). Halophytes have adapted to highly saline conditions by their ability to adjust osmotically to increasing salinity levels (Reihl and Ungar 1982, Clipson et al. 1985). Tolerance of photosynthetic systems to salinity is associated with

¹Department of Botany, University of Karachi, Karachi-75270, Pakistan.

²Department of Botany and Range Science, Brigham Young University, Provo, UT 84602. Corresponding author.

the capacity of plant species to effectively compartmentalize ions in the vacuole, cytoplasm, and chloroplast (Reddy et al. 1997). Chlorophyll fluorescence, an analytical tool for investigating stress damage mechanisms, has been used for detecting tolerance to chilling, freezing, drought, and air pollution stress. It may prove equally useful for salinity tolerance screening (Mekkaoui et al. 1989, Monnieveux et al. 1990) or for detecting salt effects before visible damage occurs (West 1986).

Allenrolfea occidentalis (Wats.) Kuntze (Chenopodiaceae), a C_3 plant common in the western U.S., is found in an environment where halomorphic soil induces extreme osmotic stress in concert with erratic and low precipitation during the growing season (Trent et al. 1997). During drought this species exhibits low photosynthesis, stomatal conductance, and transpiration in comparison to years with high moisture (Skougard and Brotherson 1979). *Allenrolfea occidentalis* is restricted to a few communities directly at the margin of playas where soils are often poorly drained and have high soil salinity (Hansen and Weber 1975).

Because little information is available on the growth and salt tolerance of *Allenrolfea occidentalis*, the objective of this study was to determine the physiological responses of *A. occidentalis* to salinity and seedling density. We hypothesized that increased salinity and seedling density would decrease the growth response of *A. occidentalis*.

MATERIALS AND METHODS

We collected *Allenrolfea occidentalis* seedlings from an inland salt playa located on the east of Goshen, in northwestern Utah (39:57:06N 111:54:03W, 4530 ft). Equal-sized seedlings (about 1 sq cm in size) were transplanted into 12.7-cm-diameter \times 12.7-cm-tall plastic pots containing nutrient-free sand. We used 3 planting densities (low, 25 plants per pot, which was equal to the rate of 2000 plants m^{-2} ; medium, 50 plants per pot, equal to the rate of 4000 plants m^{-2} ; and high, 75 plants per pot, equal to the rate of 6000 plants m^{-2}). Six salinity (0, 200, 400, 600, 800, and 1000 mM NaCl) treatments were used. Four replicate pots were used for each saline treatment group, and pots were placed in plastic trays containing half-strength Hoagland's nutrient solution. All pots were watered immediately

after planting. Seedlings were thinned by removing excess plants from the pots to produce 3 treatment densities equal to 2000, 4000, and 6000 plants m^{-2} . Plants were grown for 1 wk in a greenhouse by subirrigation by placing the pots in plastic trays containing half-strength Hoagland's solution; the 2nd wk different salinities were applied. Plants were subirrigated by placing the pots in plastic trays and adjusting the water level daily to correct for evaporation. Once weekly we completely replaced salt solutions to avoid buildup of salinity in pots. At the initiation of the experiment, we gradually increased salinity concentrations by 200 mM at 1-d intervals until the maximum salinity level of 1000 mM NaCl was obtained. Seedlings were grown in a greenhouse at a thermoperiod of 25°C:35°C (night:day) for a total of 90 d after final salinity concentrations were reached.

Dry mass of plant shoots and roots was measured 90 d after the highest salt concentration was reached. Dry mass of plants from an individual pot was determined after drying for 48 h in a forced-draft oven at 80°C. Ion concentration was determined by boiling 0.5 g of plant material in 25 mL of water for 2 h at 100°C using a dry-heat bath. This hot water extract was cooled and filtered using Whatman no. 2 filter paper. One mL of hot water extract was diluted with distilled water for ion analysis. Chloride, nitrate, and sulfate ion contents were measured with a DX-100 ion chromatograph. Cation contents, Na^+ , K^+ , Ca^{2+} , and Mg^{2+} , of plant organs were analyzed using a Perkin Elmer model 360 atomic absorption spectrophotometer.

Using an LI-6200 portable photosynthesis system (LI-COR, Inc., Lincoln, NE), we measured the net CO_2 assimilation rate of 4 plants for each treatment. Level of stress in plants growing at different salinities was determined to be the amount of fluorescence measured from photosystem II with a Morgan CF-1000 chlorophyll fluorescence measurement system (PK. Morgan Instruments, Andover, MA). Stress is measured as a ratio of F_v (variable fluorescence) to F_m (maximum fluorescence). Water potential was measured at midday with a pressure chamber (PMS Instrument Co., Corvallis, OR). Results of growth, ion contents, net CO_2 exchange rate, water potential, and stress were analyzed with a 3-way ANOVA to determine if significant differences were present among

means. A Bonferroni test determined whether significant ($P < 0.05$) differences occurred between individual treatments (SPSS 1996).

RESULTS

A 3-way ANOVA showed significant individual effects of plant density, salinity, plant part, and their interactions on dry mass of *A. occidentalis* plants. Interactions between density and salinity and among all factors were not significant. Dry mass of shoots at low density (2000 plants m^{-2}) was not affected by low salinities (200 and 400 mM NaCl; Fig. 1). There was a significant ($P < 0.001$) promotion in shoot growth at 600 mM NaCl (Fig. 1). Shoot growth at 1000 mM NaCl was not significantly different from the nonsaline control at medium density. At high seedling density (6000 plants m^{-2}), there was no significant difference in shoots among various salinity treatments (Fig. 1). As density increased, shoot growth progressively decreased at all salinity treatments. Root growth at low density and 200 mM salinity was similar to 0 salinity (Fig. 2). Salinity ≥ 600 mM generally decreased dry mass of roots. At low salinity, dry mass de-

creased with increased density, but there was no density effect at higher salinities (Fig. 2).

A 3-way ANOVA showed a significant individual effect of salinity ($P < 0.05$) and shoots-roots ($P < 0.001$), while density was not significant in affecting succulence. Interactions between density and plant part were significant. Shoot tissue water showed significant increase at 400 mM NaCl compared to 0 mM NaCl. At high densities (4000 and 6000 plants m^{-2}) and all other salinities, the effect was not significant (Fig. 3). At low planting density, root succulence was higher except for 1000 mM NaCl, where at high density there was a substantial increase in succulence. A 3-way ANOVA showed a significant ($P < 0.0001$) effect of various concentrations of NaCl on net photosynthesis, water potential, and F_v/F_m ratio. Net photosynthesis was higher at 200 mM NaCl and then significantly declined with increased salinity (Table 1). Water potential progressively decreased with increasing salinity, reaching -6.7 MPa at 1000 mM NaCl. The F_v/F_m ratio declined with increasing salinity.

A 3-way ANOVA showed significant individual effects of shoots-roots, salinity, density, and their interaction in affecting ion content

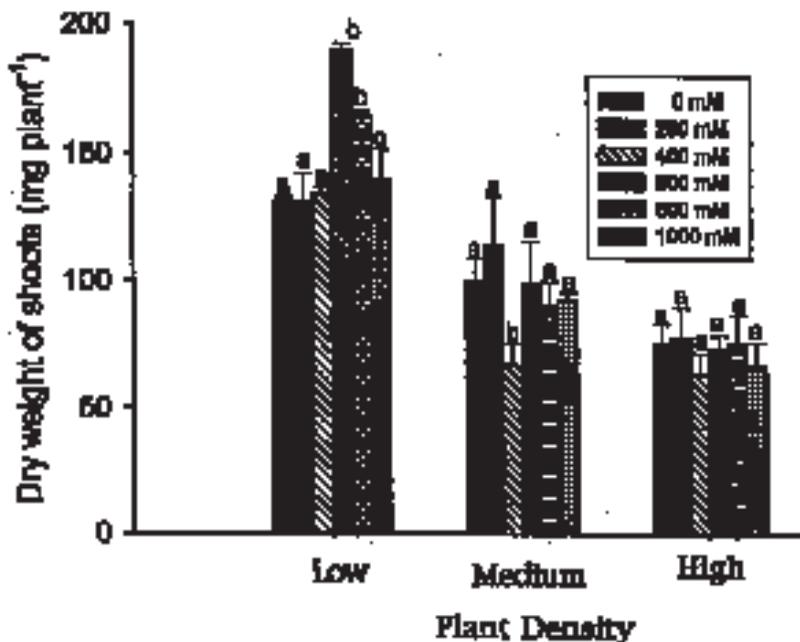


Fig. 1. Effect of NaCl (0, 200, 400, 600, 800, and 1000 mM) on dry mass of shoots of *Allenrolfea occidentalis* plants grown at low (2000 m^{-2}), medium (4000 m^{-2}), and high (6000 m^{-2}) plant density. Bar represents mean \pm s_x . Different letters above bars represent significant differences ($P < 0.05$) among treatments.

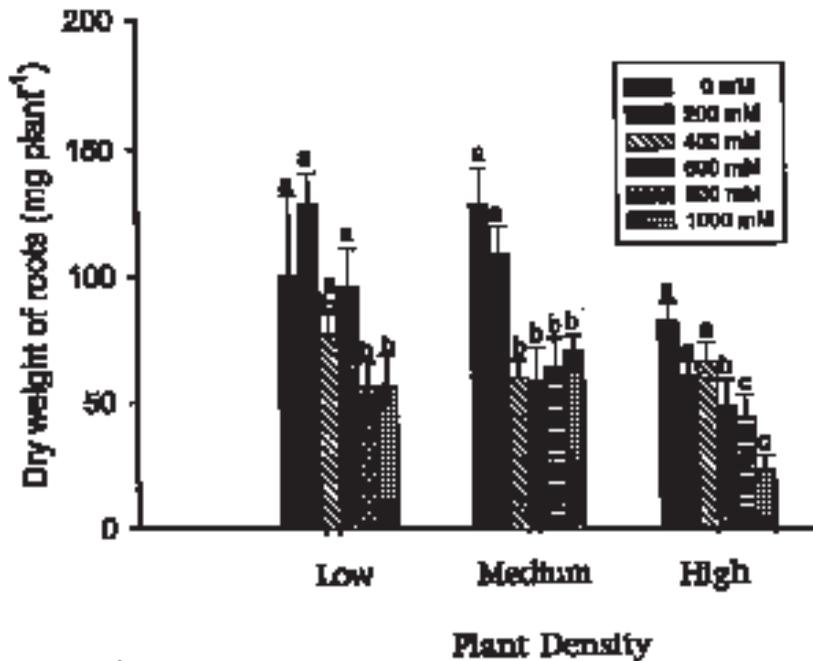


Fig. 2. Effect of NaCl (0, 200, 400, 600, 800, and 1000 mM) on dry mass of roots of *Allenrolfea occidentalis* plants grown at low (2000 m⁻²), medium (4000 m⁻²), and high (6000 m⁻²) plant density. Bar represents mean \pm s.e. Different letters above bars represent significant differences ($P < 0.05$) among treatments.

of *A. occidentalis*. Sodium content in shoots increased at lower salinity, but a further increase in salinity had no effect (Table 2). Change in density had little effect on shoot Na⁺ concentration. Chloride concentration progressively increased with increases in salinity, but change in density had no effect (Table 2). Tissue concentrations of Ca⁻², Mg⁻², K⁺, NO₃⁻, and SO₄⁻² were very low in comparison to Na⁺ and Cl⁻, and they decreased with increases in salinity (Table 2). Root ion concentrations followed a pattern similar to that of the shoot (Table 3).

DISCUSSION

Allenrolfea occidentalis showed optimal shoot growth at seawater salt concentration and higher (600–800 mM NaCl). Most halophytes show optimal growth in the presence of salt (Naidoo and Rughunanan 1990, Rozema 1991, Ayala and O'Leary 1995); however, most halophytic species are inhibited by high salt concentration, with none showing optimal growth at seawater concentration (Ungar 1991). Khan and Aziz (1998) reported that *Cressa*

cretica showed optimal growth at 425 mM NaCl, and there was no inhibition of growth at 850 mM NaCl. Great Basin Desert species collected from similar habitat, i.e., *Salicornia rubra*, *S. utahensis*, *Suaeda moquinii*, *Kochia scoparia*, and *Sarcobatus vermiculatus*, also showed optimal growth at or above seawater salinity (Khan, Gul, and Weber unpublished data). *Allenrolfea occidentalis* appears to be one of the most salt tolerant species reported.

Increased competition caused a progressive reduction in growth of *A. occidentalis*. High planting density decreased growth even at low salinities. At higher planting densities there was no significant difference in growth among various salinity treatments. Intraspecific competition may affect biomass production, reproduction, survival, and growth of halophytes in saline habitats (Badger and Ungar 1990, Ungar 1991, Federaro and Ungar 1997, Keiffer and Ungar 1997). Keiffer and Ungar (1997) reported that such species as *Salicornia europaea*, *Atriplex prostrata*, *Hordeum jubatum*, and *Spergularia marina* produce plants of similar biomass under all salinities when grown in higher density treatments. Keddy (1981)

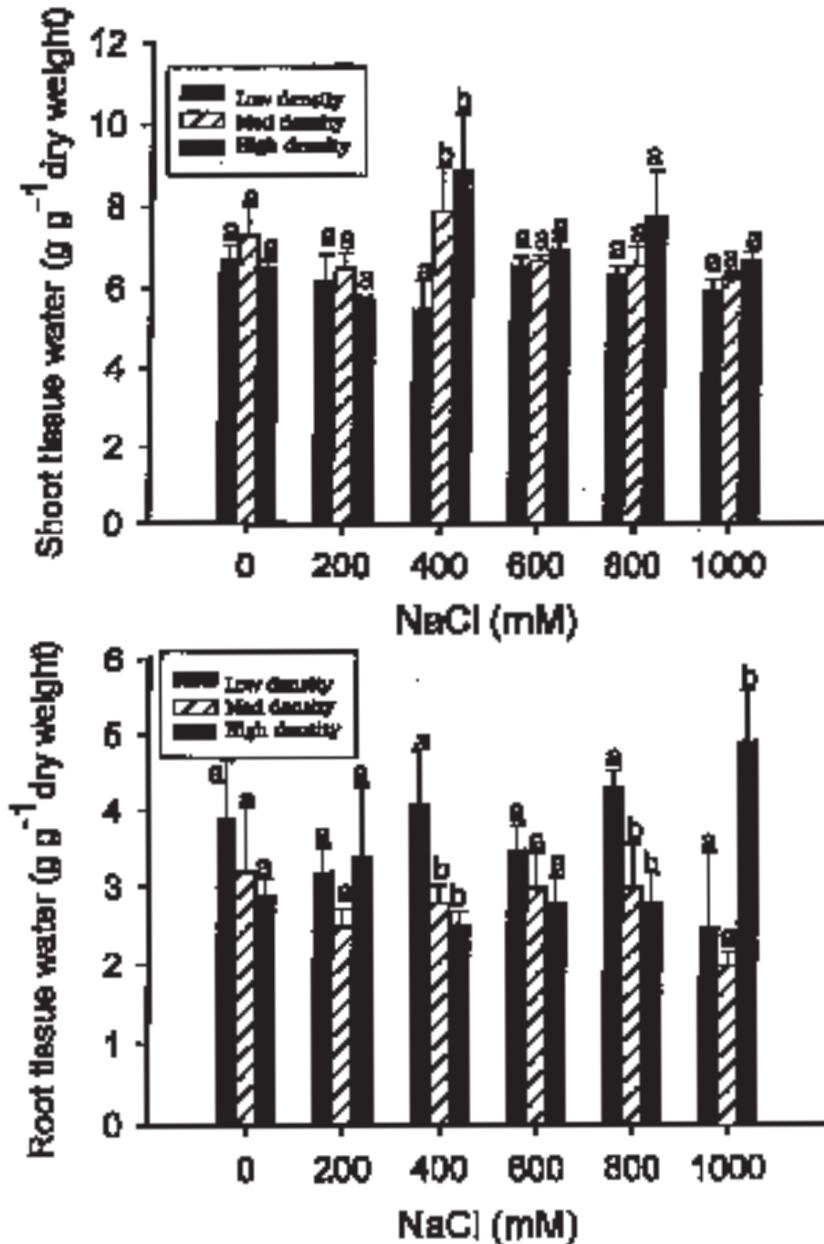


Fig. 3. Effect of NaCl (0, 200, 400, 600, 800, and 1000 mM) on shoot and root water content of *Allenrolfea occidentalis* plants grown at low (2000 m⁻²), medium (4000 m⁻²), and high (6000 m⁻²) plant density. Bar represents mean \pm s.e. Different letters above bars represent significant differences ($P < 0.05$) among treatments.

reported the relative importance of density-dependent and density-independent effects can change along environmental gradients.

To avoid toxic effects of salt, halophytes have developed a number of mechanisms, including succulence, salt exclusion, and secretion (Ungar 1991). Succulence is thought

to contribute to salt regulation by increasing the vacuolar volume available for ion accumulation (Greenway and Munns 1980, Albert 1982, Ungar 1991). Salinity increased the water content of *Suaeda torreyana* (Glenn and O'Leary 1984), *Salsola kali* (Reimann and Breckle 1995), and *Arthrocnemum fruticosum* (Eddin

TABLE I. Effect of salinity on net photosynthesis, midday water potential, and F_v/F_m ratio of *Allenrolfea occidentalis*.

NaCl (mM)	Net photosynthesis ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Water potential (-Mpa)	F_v/F_m ratio
0	9.8 ± 0.6	-3.1 ± 0.3	0.74 ± 0.02
200	12.4 ± 0.6	-3.4 ± 0.3	0.68 ± 0.02
400	7.3 ± 0.7	-4.1 ± 0.2	0.61 ± 0.01
600	6.1 ± 0.7	-4.4 ± 0.6	0.71 ± 0.04
800	7.7 ± 1.1	-4.9 ± 0.2	0.64 ± 0.01
1000	7.4 ± 0.4	-6.7 ± 0.4	0.53 ± 0.03

and Doddema 1986), with this increase in succulence presumably being a result of salt accumulation. However, our results showed a significant increase in salt accumulation, but a significant reduction in succulence, at higher salinity and plant density. Roots showed a clear increase in water content over the entire salinity range, except at 1000 mM NaCl in low-density treatments. Species with succulent leaves (*Salicornia europaea*, *Allenrolfea occidentalis*, and *Batis maritima*) show a remarkable degree of dehydration when treated with high (720 mM NaCl) salinity (Glenn and O'Leary 1984). A progressive accumulation of salt with increase in salinity was found.

In dicotylenous halophytes, water relations and the ability to adjust osmotically are reported to be important determinants of the growth response to salinity (Flowers et al. 1977, Munns et al. 1983, Ayala and O'Leary 1995). Our results indicate that water potentials of plants reflect osmotic potentials of external solutions, especially at higher salinities. *Allenrolfea occidentalis* adjusted osmotically, maintaining a more negative water potential. Antlfinger and Dunn (1983) found that species growing in higher soil salinities had a lower xylem pressure potential than plants growing in less saline areas.

Growth inhibition under saline conditions is usually associated with dehydration at high salinity, which is due to increased water stress and the resultant loss of cell turgor because of inadequate tissue osmotic adjustment (Hellebust 1976, Ungar 1991). One major difference between plants grown at different salinities was photosynthetic response. In supraoptimal salinity conditions, plant growth was accompanied by reduced photosynthetic rates. In sub-optimal salinity conditions, similar growth reduction was accompanied by photosynthetic rates equal to or greater than those of plants

growing at optimal salinity. Differences in photosynthetic rates were not consistent with differences in growth (Ayala and O'Leary 1995). Our results indicate a small promotion of photosynthesis at low salinity, while all other treatments showed similar effect.

Changes in F_v/F_m were more evident when *A. occidentalis* was treated with 1000 mM NaCl. Low F_v/F_m values were found in the control and low-salinity treated plants, although lowest values logically appeared in higher salt treatments. Sharma and Hall (1998), Larcher et al. (1990), and Jimenze et al. (1997) also reported similar reduction in F_v/F_m values. At high salinity (1000 mM NaCl) *A. occidentalis* plants showed a slight decrease in mean F_v/F_m values, but this variation could not be attributed to salinity stress alone (Brugnoli and Lauteri 1990, 1991, Brugnoli and Björkman 1992).

A tendency to accumulate NaCl has been reported for many other halophytes and is associated with salt tolerance (Storey and Wyn Jones 1977, Greenway and Munns 1980, Glenn and O'Leary 1984, Naidoo and Rughunanan 1990, Nerd and Pasternak 1992, Khan and Aziz 1998). Total concentration of inorganic ions in *A. occidentalis* plants increased with salinity; this increase is due primarily to an increase in the concentration of Na^+ and Cl^- . These 2 ions also contributed substantially to the dry mass content of plants. At all salinities *A. occidentalis* maintained Na^+ concentrations higher than external solutions. *Allenrolfea occidentalis* plants grew poorly in the absence of NaCl; optimum growth occurred at 180–540 mM NaCl and was inhibited by 40% at 720 mM NaCl compared with 320 mM NaCl, similar to that for *Atriplex canescens* (Glenn and O'Leary 1984). In shoots and roots of *A. occidentalis*, increasing salinity significantly reduced potassium content. Sodium

TABLE 2. Effect of salinity on the concentration of cations and anions in shoots of *Allenrolfea occidentalis* at low (L), medium (M), and high (H) densities. Values represent means \pm s.e. Means in same column followed by the same letter are not significantly different ($P < 0.05$) according to Bonferroni test.

NaCl (mM)	Na ⁺ (mM)		K ⁺ (mM)		Ca ²⁺ (mM)		Mg ²⁺ (mM)		Cl ⁻ (mM)		SO ₄ (mM)		NO ₃ (mM)						
	L	H	L	H	L	H	L	H	L	H	L	H	L	H					
0	1270 ^b ±86.2	1671 ±486	52 ^a ±6	38 ^a ±12	48 ^a ±4	78 ^b ±6	109 ^a ±24	44 ^a ±6	395 ^a ±10	267 ^a ±25	360 ^a ±7	1616 ^a ±213	2121 ^a ±105	1845 ^a ±340	280 ^a ±13	722 ^a ±170	331 ^a ±15	50 ^a ±5	46 ^a ±16
200	4434 ^b ±153	4859 ±88	42 ^a ±3	22 ^a ±4	40 ^a ±2	145 ^b ±68	61 ^b ±2	49 ^a ±8	394 ^a ±24	175 ^b ±32	340 ^a ±8	6290 ^b ±640	1088 ^b ±174	9742 ^b ±662	338 ^b ±80	426 ^b ±93	334 ^a ±44	178 ^b ±14	29 ^a ±18
400	5218 ^c ±274	5303 ±99	28 ^a ±12	27 ^a ±5	28 ^a ±1	85 ^a ±17	81 ^b ±19	117 ^b ±34	339 ^a ±15	154 ^b ±3	306 ^a ±10	6833 ^c ±874	1472 ±577	11130 ^c ±147	263 ^a ±28	275 ^c ±71	337 ^a ±77	87 ^a ±7	28 ^a ±9
600	5272 ^c ±29	5655 ±109	30 ^a ±4	26 ^a ±3	25 ^a ±2	56 ^a ±6	96 ^b ±6	46 ^a ±7	304 ^a ±9	160 ^b ±4	281 ^a ±5	7161 ^d ±137	1619 ^c ±343	11337 ^c ±834	133 ^c ±11	212 ^c ±16	262 ^b ±76	83 ^a ±26	25 ^a ±6
800	5284 ^c ±66	5464 ±165	31 ^a ±3	24 ^a ±5	23 ^a ±5	26 ^a ±1	39 ^b ±14	23 ^a ±7	276 ^b ±13	148 ^b ±21	269 ^a ±7	8881 ^c ±776	4029 ^d ±170	12061 ^d ±1811	136 ^c ±34	181 ^d ±18	171 ^c ±8	41 ^c ±16	27 ^a ±14
1000	5392 ^c ±224	5742 ±272	35 ^a ±4	23 ^a ±12	22 ^a ±4	25 ^a ±5	34 ^b ±16	13 ^a ±8	257 ^b ±11	138 ^b ±23	217 ^a ±8	8685 ^c ±343	6096 ^c ±497	12437 ^e ±2192	146 ^d ±29	137 ^d ±17	152 ^c ±29	25 ^c ±8	17 ^a ±6

TABLE 3. Effect of salinity on the concentration of cations and anions in roots of *Allenrolfea occidentalis* at low (L), medium (M), and high (H) densities. Values represent Means \pm s.e. Means in the same column followed by the same letter are not significantly different ($P < 0.05$) according to Bonferroni test.

NaCl (mM)	Na ⁺ (mM)		K ⁺ (mM)		Ca ²⁺ (mM)		Mg ²⁺ (mM)		Cl ⁻ (mM)		SO ₄ (mM)		NO ₃ (mM)					
	L	H	L	H	L	H	L	H	L	H	L	H	L	H				
0	1630 ^b ±402	2084 ^a ±166	22 ^a ±6	51 ^a ±4	26 ^a ±3	107 ^a ±13	222 ^a ±78	112 ^a ±15	179 ^a ±21	356 ^a ±24	226 ^a ±24	1732 ^a ±113	1899 ^a ±238	844 ^a ±26	277 ^a ±55	764 ^a ±22	39 ^a ±12	98 ^a ±20
	4900 ^b ±176	4996 ^b ±93	21 ^a ±2	36 ^a ±2	20 ^a ±4	99 ^a ±9	158 ^b ±6	104 ^a ±8	174 ^a ±19	344 ^a ±6	195 ^a ±8	1783 ^a ±100	6204 ^b ±183	648 ^b ±69	269 ^a ±13	739 ^a ±23	43 ^a ±18	57 ^a ±9
400	5318 ^c ±213	5557 ^c ±196	18 ^a ±4	33 ^a ±2	18 ^a ±1	63 ^{ab} ±4	87 ^c ±8	95 ^a ±12	150 ^a ±13	352 ^a ±15	186 ^a ±13	1837 ^a ±175	9237 ^a ±169	499 ^c ±9	281 ^a ±7	596 ^b ±17	34 ^a ±12	56 ^a ±10
	5460 ^c ±81	5580 ^c ±221	16 ^a ±1	31 ^a ±2	18 ^a ±2	46 ^b ±6	81 ^c ±2	69 ^b ±9	131 ^a ±14	343 ^a ±12	185 ^a ±8	1886 ^a ±124	12189 ^d ±782	431 ^c ±11	262 ^a ±12	470 ^c ±18	30 ^a ±6	30 ^{ab} ±2
800	5501 ^c ±352	5598 ^c ±140	16 ^a ±3	26 ^a ±1	17 ^a ±2	45 ^b ±5	73 ^c ±2	66 ^b ±12	116 ^b ±17	306 ^a ±13	174 ^a ±7	2990 ^b ±726	13864 ^c ±976	304 ^d ±13	251 ^a ±18	305 ^d ±10	28 ^a ±12	21 ^b ±1
	5676 ^c ±332	5738 ^c ±84	14 ^a ±2	24 ^a ±0.9	16 ^a ±2	39 ^b ±8	45 ^c ±5	43 ^b ±9	96 ^b ±3	283 ^a ±11	150 ^a ±11	6963 ^c ±486	13789 ^c ±744	205 ^d ±19	211 ^a ±9	142 ^d ±18	24 ^a ±8	19 ^b ±5

content rose steeply with increasing substrate salinity. This pattern of K^+ - Na^+ balance is typical for relatively salt tolerant species such as *Suaeda maritima*, *Atriplex hortensis*, and *A. prostrata* (Flowers 1975, Jeshke and Stelter 1983, Karimi and Ungar 1984). Chloride concentration also increased with salinity, and this pattern is consistent with other perennial halophytes such as *Cressa cretica*, *Suaeda fruticosa*, *Atriplex griffithii*, *Haloxylon recurvum*, and *Halopyrum mucronatum* (Khan and Aziz 1998).

Allenrolfea occidentalis was found to complete its life cycle in 1000 mM NaCl and showed significant growth promotion in moderate salinity (600 mM NaCl) in low-density plantings. Density did not significantly affect growth. The mechanism for salt tolerance in this species could involve striking a delicate balance between ion accumulation, osmotic adjustment, maintenance of water potential, and growth. At salinities above 800 mM NaCl, this balance is perhaps disturbed. *Allenrolfea occidentalis* is one of the most salt tolerant and salt accumulating halophytes and could thus be used successfully to reclaim highly salinized areas in arid and semiarid regions of the world.

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MANAGING LIVESTOCK GRAZING FOR MULE DEER (*ODOCOILEUS HEMIONUS*) ON WINTER RANGE IN THE GREAT BASIN

Dennis D. Austin¹

ABSTRACT.—History and technical literature describing potential effects of livestock grazing on mule deer (*Odocoileus hemionus*) populations and winter range habitat are reviewed. Recommendations for livestock grazing on winter ranges within the Great Basin are advanced.

Key words: mule deer, *Odocoileus hemionus*, livestock grazing, plant succession, Great Basin, winter range, habitat management, grazing management.

Accounts of trappers and pioneers in the early to mid-1800s provide a clear record of the presettlement relationship between habitat and mule deer (*Odocoileus hemionus* Rafinesque) populations in the Great Basin. Prior to settlement, beginning about 1850, perennial grasses, representing climax plant communities, dominated foothill ranges (Simpson 1876, Stewart 1941, Leopold 1950, 1959, Passey and Hugie 1962, Christensen and Johnson 1964, Hull and Hull 1974, Vale 1974, 1975, Urness 1976, and others). *Odocoileus hemionus*, requiring shrub forages on winter ranges (Stoddart and Rasmussen 1945, Dietz and Nagy 1976, Willms et al. 1976, Carpenter et al. 1979, Austin and Urness 1983a, and others), were found in low densities and scattered populations (Leopold 1933, 1959, Hancock 1981, Rawley 1985, and others). On most mule deer management units populations are limited by forage resources on winter ranges (Hancock 1976, Clements and Young 1997).

Livestock grazing, usually season-long and with little regard to levels of utilization, shifted plant succession toward seral shrub communities on *O. hemionus* winter ranges (Stewart 1941, Cottam and Evans 1945, Reynolds 1960, Julander 1962, Christensen and Johnson 1964, Plummer et al. 1968, Thomas 1970, Urness 1981, Harniss and Wright 1982, Urness 1990, and others). Changes in plant communities were followed by dramatic increases in mule deer populations (Leopold 1950, Julander and Low 1976, Hancock 1981, and others). Conversely, cessation of livestock

grazing, which often overutilized grasses and forbs and lightly utilized shrubs, ended the growth advantage of shrubs. This led to increased fuel loads and subsequent fire susceptibility of winter ranges. These 2 factors, lack of livestock grazing and fire, resulted in many *O. hemionus* winter ranges shifting from seral shrub communities back to grasslands followed by declines in mule deer populations (Costello and Turner 1941, Cottam and Evans 1945, Laycock 1967, Anderson and Holte 1981, Austin et al. 1986, Austin and Urness 1998, and others).

This paper presents a synopsis of research conducted on mule deer–livestock grazing relationships and advances recommended strategies for future livestock grazing on winter ranges where *O. hemionus* are an important product of the land.

SYNOPSIS OF MAJOR BIG GAME–LIVESTOCK RELATIONSHIPS AND VEGETATION STUDIES ON MULE DEER WINTER RANGES

Cottam and Evans (1945) compared 2 adjacent watersheds near Salt Lake City, Utah. Red Butte Canyon had been protected from livestock grazing from 1905 to 1935, while Emigration Canyon had been annually and heavily grazed by both sheep and cattle. By 1935 total vegetative canopy cover in Red Butte Canyon was approximately double that of Emigration Canyon, including *Quercus gambelii* Nutt. (Gambel oak). In a reexamination of the site after 22 yr of reduced grazing followed

¹Rangeland Resources Department, Utah State University, Logan, UT 84322-5230.

by 26 yr of grazing protection in Emigration Canyon, and continuous protection in Red Butte Canyon, Austin et al. (1986) showed no differences in total vegetative cover between canyons. Stands of *Q. gambelii* had increased in size and recovered from the heavy livestock grazing prior to 1935.

Smith (1949) compared adjacent winter ranges used by *O. hemionus* in northern Utah. In this important paper, 1 range was heavily grazed by livestock during spring and early summer while the 2nd had been protected from livestock grazing the previous 11 yr. On the range protected from livestock grazing, native and perennial forbs and grasses had increased 141%, but big sagebrush and other shrubs had decreased 85%. In a reexamination of the sites following 34 yr of protection from grazing on both ranges, Austin and Urness (1998) showed both ranges had shifted to a grass-forb community with no big sagebrush plants remaining.

Mueggler (1950) reported on 2 paddocks grazed yearly between 1923 and 1948 by sheep at the U.S. Sheep Experiment Station near Dubois, Idaho. Paddock 1 was grazed only in the fall at the moderately heavy rate of 29 sheep-days per acre, whereas paddock 2 was grazed both spring and fall at the total moderate rate of 43 sheep-days per acre. After 25 yr of grazing, total herbage production was within 5% between pastures. However, the spring-and-fall-grazed paddock showed an increase of 73% in shrub production from the 9 native shrub species available, and decreases of 80% and 31% in native perennial forbs and grasses, respectively. Annual nonnative *Bromus tectorum* L. (cheatgrass brome) was unavailable in 1923, but by 1948 small quantities of 2 and 6 pounds per acre were available in paddocks 1 and 2, respectively. Laycock (1967) reported on long-term sheep grazing studies at the U.S. Sheep Experiment Station. Results indicated heavy grazing by sheep in spring on range in good condition increased production of *Artemisia tripartita* Rydb. (three-tip sagebrush) 78% and decreased perennial herbaceous production 53%. Conversely, fall grazing by sheep decreased *A. tripartita* production 11% and increased production of perennial grasses and forbs 14%. *Bromus tectorum* increased about equally under fall grazing and within exclosures, but more rapidly under spring grazing.

Julander (1955, 1962) described the expansion in Utah of deer populations on ranges overgrazed by livestock. He explained that livestock grazing causes large increases in shrubs and trees, but serious depletion of nutritious herbaceous forages of grasses and forbs preferred by livestock operators. Nonetheless, these changes resulted in greatly expanded *O. hemionus* populations.

Smith and Doell (1968) defined the period of cattle grazing to maintain productive shrub communities. This study, conducted in Cache County, Utah, showed summer and fall grazing decreased browse production for use by mule deer in winter. The study concluded that on mixed browse-herbaceous ranges used by mule deer in winter, grazing by cattle should be completed prior to 1 July.

Shepherd (1971) studied the effects of clipping selected browse species in Colorado over 12 seasons. He concluded that of the species studied, *Artemisia tridentata* Nutt. (big sagebrush) was the most susceptible to overutilization. Consistent overutilization for several years led to decreased productivity, plant decadence, and death. However, *A. tridentata* clipped at about 50% utilization showed sustained production. Similarly, Cook and Stoddart (1963) over a 6-yr study determined that overwinter use of *A. tridentata* and other desert shrubs should not exceed 60% if production is to be maintained. For antelope bitterbrush (*Purshia tridentata* Pursh, DC.), Shepherd found 50% utilization would be sustainable, but 80% would damage or eventually kill plants. Garrison (1953) recommended 50–65% utilization for *P. tridentata*. For *Amelanchier alnifolia* Nutt. (saskatoon serviceberry), *Cercocarpus montanus* Raf. (true mountain mahogany), *Q. gambelii*, and other deciduous shrubs, Shepherd (1971), in his literature review, suggested 60–75% utilization was acceptable.

Jensen et al. (1972) and Jensen and Urness (1976) investigated seasonal grazing on big game winter ranges with domestic sheep to ascertain seasons and intensity of forage use that would maximize use of grasses and forbs and minimize use of associated shrubs. Results from this study at Hardware Ranch in northern Utah showed grazing by sheep on big game winter ranges could be accomplished without significant utilization of *P. tridentata* and other shrubs. However, grazing should be terminated between 15 June and 1 July, or at

the time *P. tridentata* sets seed. Sheep grazing after 15 July resulted in considerable loss of current year's production of *P. tridentata*.

Smith et al. (1979) and Fulgham et al. (1982) determined spring grazing by sheep affected subsequent fall and winter diets of *Odocoileus hemionus*. No nutritional differences in mule deer diets were found between grazed and ungrazed sheep pastures. Because regrowth following fall precipitation increased the proportion of herbaceous forage in the grazed pasture, deer selected more herbaceous and less shrub forage in the grazed pasture during early winter, thereby saving browse forage for periods when snowcover limited herbaceous forages. They concluded that sheep grazing in spring was compatible with *O. hemionus* utilization on winter ranges in northern Utah, and furthermore, animal production, mule deer plus domestic sheep, was greatly increased through multiple use.

Harniss and Wright (1982) monitored changes in vegetation in sagebrush-grass range grazed by sheep between 1965 and 1974. Moderate grazing had no effect on vegetative composition or production. However, heavy grazing in early summer decreased production of grasses and some forbs, but increased production of *A. tridentata*.

Reiner and Urness (1982) grazed big sagebrush-grass big game winter range in northern Utah with domestic horses. Pastures were grazed during June and July at grass-removal intensities of 41–79%. Results indicated all pastures grazed by horses resulted in increased twig production of *P. tridentata* over nongrazed pastures.

Austin et al. (1983) studied overwinter use by *O. hemionus* on a big sagebrush-seeded crested wheatgrass range in northern Utah. They reported fall regrowth and spring growth of grasses was nutritionally important to mule deer and recommended using a rest-rotation grazing system.

Riggs and Urness (1989) and Riggs et al. (1990) studied the effects of domestic goats grazing in the *Q. gambelii* community in northern Utah. Summertime goat grazing was used during high-intensity, short-duration periods designed to maximize utilization of *Q. gambelii*. In this study Gambel oak production was reduced and big sagebrush was increased. The authors concluded that generally grazing

with goats on *Q. gambelii* winter range enhances the quality of deer diets in winter, especially under snow-covered conditions.

Austin et al. (1994a) studied the effects of horse grazing in spring on a shrub revegetation project using transplanted seedling Wyoming big sagebrush (*Artemisia tridentata* Nutt. *wyomingensis* Beetle and Young). The foothill winter range contained a variety of native and introduced grasses and forbs and no shrubs prior to treatment. Results following 6 growing seasons with herbage utilization ranging from 34% to 71% showed forage production of big sagebrush in paddocks grazed by horses in spring and protected from winter browsing by mule deer had increased 83% in browse production per plant compared to protected paddocks. Use by both horses in spring and mule deer in winter resulted in 13% increase in big sagebrush production per plant over protected paddocks. Conversely, browsing by deer in winter without horse grazing in spring resulted in a 40% decrease in big sagebrush production per plant compared to protected paddocks. Results concerning seedling survival during the first 3 yr following planting, as affected by horse use in spring and mule deer use in winter, were inconclusive. However, the effects of horse or mule deer grazing on survival on shrubs aged 4 to 6 yr were nil.

Austin and Urness (1995) investigated the effects of livestock grazing in spring on individual shrubs and seedling recruitment. Over 6 growing seasons mean herbaceous utilization was 59%. Results indicated survival rates of mature mountain big sagebrush (*Artemisia tridentata* var. *vaseyana* Rybd., Beetle) and *Cercocarpus montanus* shrubs were increased 119% and 25%, respectively; seedling recruitment of *A. tridentata* var. *vaseyana* was increased 130%, and winter injury to *C. montanus* was decreased 43%. Jensen and Urness (1979) reported similar results.

Clements and Young (1997) reviewed the history of the Lassen interstate mule deer herd in the far western Great Basin. They identified extensive and excessive livestock grazing as a major factor in establishing mixed shrub stands on *O. hemionus* winter range, and stated removal of livestock grazing from winter ranges would greatly increase difficulties in maintaining mule deer habitat.

Influences of livestock grazing and *O. hemionus* browsing are well defined on rangelands containing only native vegetation. The presence of introduced weedy species (Whitson et al. 1991) complicates and perhaps alters those influences as suggested by Mueggler (1950), Laycock (1967), and others. Palatability, season of growth, reproductive mechanisms, grazing sustainability, and competitive advantages and disadvantages compared to native species are some factors involved in evaluating grazing management systems complicated by introduced weedy species. Nonetheless, for many palatable weedy species, such as ubiquitous *Bromus tectorum* (Austin et al. 1994b), which was present on many of the study sites cited, livestock grazing in spring will sustain shrub productivity and decrease fire potential. However, the composition of herbaceous species may be altered in favor of those introduced species. Unfortunately *B. tectorum* and many other aggressive weedy species often increase regardless of rangeland protection. Although treatments designed for specific species, such as herbicidal spraying, hand removal, biological controls, and rangeland disking and reseeding, are utilized, currently a comprehensive solution is not available to address introduced weedy species on rangelands. Site-specific management using available research on the invading species must be evaluated.

RECOMMENDATIONS

The preceding studies, reports, and literature have led to the following recommendations for livestock grazing to maintain or increase browse production on *Odocoileus hemionus* winter ranges in the Great Basin. Considering the typical *O. hemionus* winter range, it must be recognized these guidelines are somewhat idealistic and few ranges could adapt all recommendations. Classes of livestock availability, pasture fences, variability in mule deer numbers, and personnel available to monitor utilization are some of the limiting factors.

1. Graze livestock between 1 May and 30 June. Livestock grazing should be conducted during spring only. During years with early green-up, grazing may begin as early as 1 April, and grazing may be extended into early July during years of high moisture in May-June. Grazing must be completed when livestock

begin to switch diets from grasses and forbs to shrub species.

2. Alternate between classes of livestock. Sheep and goats consume higher proportions of forbs, while cattle and horses consume higher proportions of grasses. By shifting classes of livestock, if available, between years, or grazing simultaneously with 2 or more classes, a better balance of grasses, forbs, and shrubs can be maintained.

3. Use a rest-rotation system, yearly grazing about 2/3 of the rangeland available. Because regrowth in fall and new growth of grasses in spring are important components to deer diet and nutrition, each year part of the winter range should be rested from livestock grazing. However, on ranges largely dominated by annual grasses and weedy forbs, and/or ranges highly susceptible to fire, livestock should annually graze the entire area.

4. Graze livestock at an intensity to remove 50% of understory grasses and forbs. A grazing removal of about 50% will maintain a mixed community of grasses, forbs, and shrubs and greatly reduce fire risk. Grazing at $\geq 70\%$ removal will increase the proportion of shrubs, while grazing at $\leq 30\%$ will slowly shift winter range plant communities toward more grasses and forbs.

5. Balance deer browsing in winter and livestock grazing in spring. Excessive utilization of browse by deer in winter over several years will gradually reduce shrub vigor and result in decreasing shrub density, regardless of the intensity of livestock grazing. Effects of drought or wet cycles confound the issue. However, to maintain browse vigor, utilization by *O. hemionus* should be restricted to 50% use of *A. tridentata* and other nondeciduous and evergreen species, and 65% use of *P. tridentata* and other deciduous species.

6. Monitor utilization using permanent plots. Vegetal utilization and community composition should be evaluated using permanent plots on critical or key areas of each deer unit. Spring utilization of grass and forb forages by livestock and overwinter utilization of browse forages by mule deer should be determined yearly. A minimum of twenty 100-m² plots per deer unit using ocular estimates is recommended. See DeVos and Mosby (1971), Rutherford (1979), Austin and Urness (1983b), and Austin (1987) for suggested methods. Trends in community composition must be evaluated

by detailed sampling at 5-yr intervals. See Poulton and Tisdale (1961), Davis et al. (1990), and Elzinga and Evenden (1997) for methods.

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VULNERABILITY OF FREMONT COTTONWOOD (*POPULUS FREMONTII* WATS.) INDIVIDUALS TO XYLEM CAVITATION

A. Joshua Leffler¹, Laura E. England², and Jon Naito³

ABSTRACT.—Embolism, the blockage of water transport in the xylem by air, is an important consequence of low water availability for all plant species. Riparian plants, since they typically experience mesic conditions, are not water stress tolerant and hence are vulnerable to xylem cavitation, the formation of emboli. We have constructed a composite vulnerability curve for *Populus fremontii* (Fremont cottonwood); assessed native state embolism, critical xylem pressure potential (Ψ_{cav}), and safety margin; and determined predawn and midday leaf water potential (Ψ_{L}) within a central New Mexico cottonwood population. Our results indicate (1) that this population of *P. fremontii* is extremely vulnerable to cavitation, with complete xylem blockage occurring at -2.25 MPa, and (2) that native state embolism is between 19% and 42%. Ψ_{cav} was determined to be -1.36 MPa. Measurements of predawn Ψ_{L} were typically near -0.5 MPa while midday Ψ_{L} values averaged -1.7 MPa. Estimates of midday xylem pressure potential (Ψ_{px}) were -1.1 MPa. These values suggest that these individuals maintain small safety margins (0.26 MPa) between Ψ_{px} and Ψ_{cav} . This small safety margin may be detrimental under increased variation in water availability caused by anthropogenic alteration of river systems.

Key words: cavitation, drought stress, embolism, plant water potential, *Populus fremontii*.

Water availability plays an important role in the physiology of virtually all plant species. Low water availability is known to influence patterns of physiological activity, distribution of species, and competitive interactions. Recently, the importance of xylem cavitation, the loss of water transport capability in a plant, has received increasing attention as an important consequence of drought.

Xylem cavitation is a process by which xylem elements become blocked by air, typically under conditions of low water availability. Negative xylem pressure (Ψ_{px}) causes the upward movement of water from soil into the vascular tissue of plants (Nobel 1983, Tyree and Sperry 1988, Pockman et al. 1995). However, if Ψ_{px} becomes very negative, as when water availability is low, catastrophic loss of hydraulic conductance (flow of water through the xylem) may occur through the process of cavitation. If the critical xylem pressure (Ψ_{cav} , the Ψ_{px} that can be maintained without causing catastrophic cavitation [Tyree and Sperry 1988]) is reached, an explosive phase change (liquid water to water vapor), or cavitation, occurs (Tyree and Dixon 1986). Embolism ensues as dissolved gases from surrounding tissue come out of solution, filling the cavitated

vessels and blocking water flow (Tyree and Sperry 1988). Embolized vessels cannot necessarily be refilled and cause a reduction in the capacity to conduct water. Vulnerability curves can be constructed to describe the loss of hydraulic conductance as a function of Ψ_{px} .

Although cavitation is an important consequence of drought in all plants, riparian plants are thought to be less frequently harmed by cavitation because they have access to a stable water supply. Plants typically operate at Ψ_{px} near Ψ_{cav} (Tyree and Sperry 1988), but given a stable water supply, cavitation should be infrequent. Riparian plants are known to have small safety margins, the difference between Ψ_{cav} and Ψ_{px} , because of their presumed stable water supply (Blake et al. 1996). However, *Populus* spp., important riparian trees in the southwestern U.S., have suffered significant declines in the past century, and it is widely thought that drought stress caused by anthropogenic alteration of stream flow regimes has been the primary cause of this decline (Rood and Mahoney 1990, Howe and Knopf 1991, Tyree et al. 1994, Busch and Smith 1995). Increased frequency of cavitation as a result of reduced water availability may be an important factor limiting the establishment, growth,

¹Department of Biology, University of New Mexico, Albuquerque, NM 87131. Present address: Ecology Center, Utah State University, Logan, UT 84322-5230.

²Department of Biological Sciences, North Carolina State University, Raleigh, NC 27695. Present address: Institute of Ecology, University of Georgia, Athens, GA 30602-2202.

³Biology Department, Reed College, Portland, OR 97202. Present address: Zaiji 392, Kora-cho, Inukamigun Shiga 522-0244 Japan.

and reproduction of *Populus* spp. Studies examining poplar vulnerability to cavitation are important for understanding water relations of the species and for management of riparian systems.

Previous studies have shown that *Populus* species are extremely vulnerable to drought-induced cavitation compared to other non-riparian, woody species (Tyree and Ewers 1991, Tyree et al. 1994, Pockman et al. 1995). In this study we investigated vulnerability to cavitation in *Populus fremontii* Wats. (Fremont cottonwood), the dominant native canopy tree in lowland southwestern riparian ecosystems. The 1st goal of this study was to construct a vulnerability curve for *P. fremontii* from a central New Mexico population and determine if our curve was similar to the Pockman et al. (1995) study, the only previous study on cavitation in *P. fremontii*, and to other *Populus* studies. Although comparisons between studies on the same species of *Populus* have been made previously (Blake et al. 1996), there are no published comparisons of *P. fremontii* among populations. The 2nd goal of this study was to calculate native embolism, the percent loss of hydraulic conductance, that has occurred in our study population under natural conditions. Native embolism has not been reported for *P. fremontii* and may provide clues to the actual impact of cavitation on water relations in situ; a vulnerability curve describes only potential consequences. Additionally, we wished to make repeated measurements of native embolism to determine if it increases during the growing season. Our final goal was to calculate and report Ψ_{cav} and the safety margin, values which further clarify the vulnerability of this species.

MATERIALS AND METHODS

Study Site and Plant Material

Populus fremontii, a native riparian tree of the southwestern U.S., is the predominant tree of western prairies (Rood and Mahoney 1990). Distributed from the western Texas/Mexico border (Vines 1960) to the northernmost population at Moffet Creek in northern California (Griffin and Critchfield 1972), Fremont cottonwood typically thrives in sand-gravel soils within 4 m of the water table (Tyree et al. 1994). Thus, it is a phreatophytic species, relying on groundwater as a primary water source (Rood and Mahoney 1990).

Our study population is located approximately 4 km east of Bernardo, New Mexico (34°25'12"N, 106°48'7"W, 1440 m) at the southern end of a 210-km corridor of riparian forest along the Rio Grande, an effluent river. Cottonwoods at our study site were 23–30 yr of age (27 ± 1.6 yr, mean \pm s). At this site *P. fremontii* is the dominant native canopy tree, while *Elaeagnus angustifolia* (Russian olive), *Tamarix ramosissima* (salt cedar), and *Salix exigua* (coyote willow) occur in the subcanopy.

Five trees were randomly chosen and sampled 3 times during June and July 1997. We began by excising a 1-yr-old branch from the lower canopy of each tree and transporting it to the laboratory (<10 min transit time) in a plastic bag to minimize cavitation in transit. In the lab branches were soaked in water for a minimum of 15 min (to reduce the likelihood of inducing embolism during sample preparation), and side branches and ends were trimmed under water to obtain a stem segment of 30 cm (Sperry et al. 1988). This procedure does not dissolve emboli because the water is not under pressure; pressurized water is required to refill xylem. We chose 30-cm segments because they are longer than the longest xylem vessel, ensuring that there are intact, or uncut, vessels present (Tyree and Dixon 1986, Sperry et al. 1988). Although vessel length was not measured in this study, other measurements on *Populus* spp. suggest that the majority of vessels are generally ≤ 15 cm, although vessels to 30 cm have been observed (*P. deltoides*, Lo Gullo and Salleo 1992; *P. balsamifera*, Hacke and Sauter 1996).

Measurement of Cavitation

We utilized the air-injection method of inducing embolism (Sperry and Saliendra 1994) to determine vulnerability to cavitation of our study trees. The air-injection method utilizes positive pressure to force air across pit membranes and yields results similar to the more traditional dehydration method which allows air to be pulled across pit membranes as a stem dries (Sperry and Tyree 1990). These methods yield similar results because the pressure required to push and the tension required to pull air across pit membranes are similar in magnitude. The air-injection apparatus consists of a double-ended pressure chamber, which allows induction of emboli and measurement of conductance in the same

system (Cochard et al. 1992, Sperry and Salendra 1994), an improvement over the dehydration method that requires 2 different systems. The chamber had a test gauge port for measurement of pressure and a port connected to a regulated compressed nitrogen tank. The proximal end of the stem inside the chamber was connected to a source solution used for measuring hydraulic conductance (see below). A T-junction and additional tubing allowed air bubbles to escape from the stem during the measurement process (see Sperry and Salendra 1994 for a diagram of the apparatus).

Construction of vulnerability curves consisted of 3 stages: (1) refilling of field-cavitated vessels via perfusion, (2) induction of emboli, and (3) measurement of hydraulic conductance (K). Prior to inducing embolism, we determined maximum hydraulic conductance (K_{\max}) by refilling all cavitated vessels. This was accomplished by perfusion, the forcing of fluid through the stem to dissolve emboli (Tyree et al. 1994). We perfused the stem using a filtered (0.2 μm Whatman) distilled water solution adjusted to pH 2 with HCl. This solution prevents microbial growth that could block water flow in xylem tissue (Sperry et al. 1988). The fluid was forced through the stem at ≈ 150 kPa for 20 min by pressurizing the vessel containing the solution. After 20 min K was measured (K = flow rate through stem/applied pressure). We repeated perfusions and measurements until flow had stabilized. This flow rate was taken as K_{\max} .

To construct a vulnerability curve, we induced emboli at air-injection pressures of 0.1–2.5 MPa and measured K , the rate of water movement through the stem. The 1st air injection was at 0.1 MPa, the 2nd at 0.25 MPa, and each subsequent injection was increased by 0.25 MPa. Air injection was performed for 10 min at each pressure. Between air injections we measured K . We connected the proximal end of the branch to the solution described above and induced flow by raising and maintaining the solution source approximately 50 cm above the stem (inducing a pressure of ≈ 5 kPa). Flow was allowed to equilibrate for 3 min, and then K was measured by collecting effluent from the stem in test tubes containing cotton. Effluent was collected for 1 min at 2-min intervals and was then weighed. During the measurement of K , we maintained a pressure of ≈ 0.1 MPa in the chamber to prevent

dissolution of induced emboli. Alternations of air injection at increasing pressure and measurements of K were conducted until $K = 0$.

Vulnerability curves were constructed for each stem by plotting injection pressure against percent loss of conductance (PLC):

$$\text{PLC} = 100 * (K_{\max} - K) / (K_{\max}) \quad (\text{Eq. 1})$$

where K is the hydraulic conductance at a given injection pressure and K_{\max} is the maximum hydraulic conductance from the perfusion step (Tyree and Dixon 1986, Sperry et al. 1994).

Native Embolism and Water Status

Native embolism is the blockage of the xylem present in situ. We measured native embolism for each branch prior to induction of cavitation. After branches were soaked and trimmed, we connected them to the solution source and measured K . After allowing the flow to equilibrate for 3 min, we measured the flow as previously described. Native embolism was calculated as a PLC by comparison with the perfusion flow rate (K_{\max}).

We measured the water status of 5 study trees throughout June and July to determine if *P. fremontii* individuals experience Ψ_{px} that can cause significant cavitation. Using a Scholander pressure chamber (Scholander et al. 1965), we measured predawn and midday water potentials of 3 lower canopy terminal branch segments per tree on each of 7 d. Since pressure chamber measurements determine leaf water potential (Ψ_{L}), an adjustment was made to calculate Ψ_{px} . Ψ_{px} was quantified by calculating the mean between predawn and midday Ψ_{L} (Alder et al. 1996). This calculation of Ψ_{px} is appropriate because predawn Ψ_{px} is \approx predawn Ψ_{L} and midday Ψ_{px} must be above midday Ψ_{L} but below predawn Ψ_{px} because the plant is transpiring at midday.

Calculation of Ψ_{cav} and Safety Margin

The lowest water potential that does not cause catastrophic cavitation (Ψ_{cav}) was calculated using the iterative procedure described in Alder et al. (1996). Briefly, a computer program was written to calculate Ψ_{px} from transpiration (E), soil water potential (Ψ_{s}), and the vulnerability curve function ($K(\Psi_{\text{px}})$):

$$E = (\Psi_s - \Psi_{px})K(\Psi_{px}) \quad (\text{Eq. 2}).$$

The program then computed the decline in K caused by Ψ_{px} (from a function fit to the vulnerability curve) and continued this loop until a stable Ψ_{px} was found. This program was run at increasing values of transpiration until stable Ψ_{px} could no longer be achieved (after 1000 iterations). The last stable Ψ_{px} at the highest transpiration rate was assumed to be Ψ_{cav} . For this analysis, Ψ_s was assumed to be equal to predawn Ψ_{Lr} and arbitrary values of K and transpiration were used. These arbitrary values have no impact on final Ψ_{cav} (Alder et al. 1996). Our vulnerability curve was fit with a 3rd-order polynomial which had a coefficient of determination = 0.98.

The safety margin, which is a measure of proximity to water potentials that could cause catastrophic cavitation, was calculated as the difference between Ψ_{px} and Ψ_{cav} (Alder et al. 1996).

Statistical Analysis

We wished to determine if the 5 trees we measured differed in their vulnerability to cavitation and native embolism, and if vulnerability curves and native embolism changed over time. To do so we utilized a 2-way ANCOVA (SAS 1990). In this analysis individual was the main effect used to test for differences among individuals, repetition was the main effect testing for differences through time, and injection pressure was the covariate. We also tested for differently shaped vulnerability curves among individuals by testing for a PLC*pressure interaction effect. Prior to this analysis, PLC was log-transformed because of the exponential relationship between PLC and injection pressure. We used a 2-way ANOVA to test for differences among individuals and through time for native embolism using the main effects above. For each analysis type III sums-of-squares were used in all calculations.

RESULTS AND DISCUSSION

All individuals measured in our population had statistically identical vulnerability curves; the individual effect in our ANCOVA model was not significant (Table 1). Furthermore, values did not vary over time (among repetitions), and individuals had the same slopes and intercepts for their vulnerability curve

TABLE 1. ANCOVA testing for differences among individuals and repetitions in vulnerability curves.

Source	df	F	P
Individual	4	2.16	0.080
Repetition	2	2.08	0.130
Injection pressure	1	381.10	0.001

(individual*injection pressure was not significant; Table 1). Therefore, we describe the vulnerability of this population with 1 composite vulnerability curve (Fig. 1). Here, we discuss vulnerability curves using pressure values >0 because we constructed our curves using the air-injection technique (positive pressure). Other studies are also discussed in this manner for consistency of presentation. Cavitation generally remained below 10% at injection pressures up to 1.0 MPa. Between 1.0 and 1.75 MPa, the catastrophic nature of this process became evident as cavitation increased from 10% to 75%. Complete loss of hydraulic conductance occurred by 2.25 MPa. At 1.5 MPa, 50% loss of conductance occurred.

Our vulnerability curve is nearly identical to the only other published study on cavitation in *P. fremontii* (see Pockman et al. 1995). Using a variety of methods to induce cavitation,

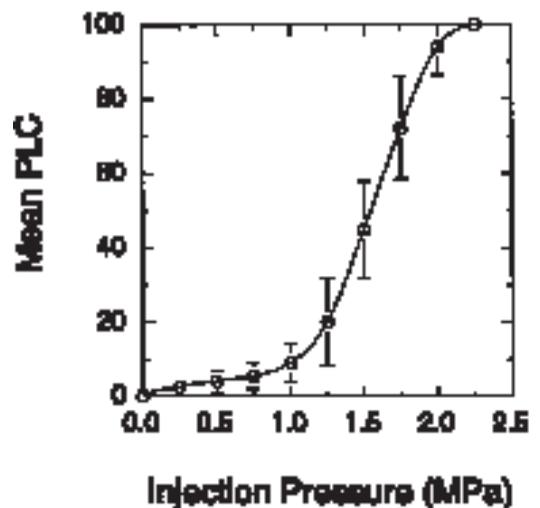


Fig. 1. Composite vulnerability curve using 3 measurements on each of 5 individuals constructed from percent loss of hydraulic conductance (PLC) as a function of injection pressure. Each datum is the mean \pm s among individuals. All values are positive because the air-injection technique, which used positive pressure, was utilized in vulnerability curve construction.

Pockman et al. (1995) constructed a curve that showed 10–20% loss of hydraulic conductance below 1.0 MPa, followed by a steep decline in conductance between 1.25 and 1.75 MPa. Fifty percent loss of conductance occurred at ≈ 1.5 MPa, and complete blockage was achieved by 2.0 MPa. Together, these 2 studies suggest that little variability in vulnerability exists among populations of this species, a result found for other *Populus* spp. (Blake et al. 1996). Variation in vulnerability among populations of *Quercus rubra* has, however, been observed (Tyree et al. 1992).

Other cavitation studies on the genus *Populus* have found similar vulnerability curves. Tyree et al. (1994) constructed vulnerability curves on *Populus* spp. from southern Alberta, Canada. Vulnerability curves of *P. balsamifera* and *P. angustifolia* were most similar to our samples, with little embolism below 1.0 MPa, followed by a rapid decline in hydraulic conductance and complete blockage by air above 2.25 MPa. Fifty percent loss of conductance was achieved at 1.7 MPa. However, *P. deltoides* was significantly more vulnerable, with 50% loss of hydraulic conductance occurring at 0.7 MPa.

Other *Populus* spp. have more resistant xylem. Sperry et al. (1994) constructed vulnerability curves for *P. tremuloides*, showing 50% loss of conductance from 1.5 to 3.5 MPa. *Populus tremuloides* occurs at higher elevations than *P. fremontii* (Elmore and Janish 1976). Its greater resistance to cavitation compared to our individuals likely reflects its exposure to freezing winter conditions. These results suggest that there can be variation in vulnerability to cavitation among species within a genus. This variation is likely related to environmental conditions experienced by individual species.

Native state embolism was not significantly different among individuals or repetitions within this population ($P = 0.590$ and $P = 0.780$, respectively). Native state embolism measurements on individuals ranged from 19% to 42%

with a mean of 30%. We did not observe statistically significant changes in native state embolism over the course of this study, although embolism was highest in early July, the period with lowest water potential (Table 2). Additionally, our observation that native state embolism decreased in late July from the early July maximum suggests that limited refilling of embolized vessels may be possible, a phenomenon that has been recently described in several species (Canny 1997, McCully et al. 1998).

The native state embolism we report is low and less variable compared with other studies: 30–90% in *P. deltoides*, 20–75% in *P. balsamifera*, 20–50% in *P. angustifolia* (Tyree et al. 1994) and $\geq 50\%$ in *P. tremuloides* and *P. balsamifera* (Sperry et al. 1994). These differences could arise from the timing of our study (June through July), conditions during 1997, or different adaptations to local conditions; additionally, they may suggest that our site experiences less water stress than those used in other studies.

Our leaf water potential (Ψ_L) measurements suggested that conditions stressful enough to result in significant in situ cavitation occurred on a regular basis. Predawn Ψ_L was essentially constant at -0.5 ± 0.02 MPa during the period of measurement. There was, however, greater variation in midday Ψ_L values, ranging from -1.27 MPa to -2.23 MPa (mean = -1.7 ± 0.06 MPa). Ψ_{px} , as estimated from the average of predawn and midday Ψ_L , was -1.1 MPa. Similar predawn and midday Ψ_L values have been observed in numerous studies on riparian tree physiology (Pallardy and Kozlowski 1981, Pezeshki and Hinckley 1982, Schulte et al. 1987, Tyree et al. 1994, Alder et al. 1996). It is likely that this pattern of plant water status is a general characteristic of riparian trees and may be caused by either little physiological control over water loss or a common midday Ψ_L set-point that induces stomatal closure.

Ψ_{cav} calculations suggest that there is a very small margin of safety between Ψ_{px} and

TABLE 2. Water potential and native embolism data during summer 1997. Values are means of individuals used in this study with standard error in parentheses.

	Predawn Ψ_L (MPa)	Midday Ψ_L (MPa)	Native embolism (%)
Early June	-0.46 (0.02)	-1.69 (0.05)	27.4 (8.53)
Early July	-0.56 (0.06)	-2.01 (0.09)	34.8 (4.63)
Late July	-0.45 (0.02)	-1.61 (0.12)	28.4 (8.58)

Ψ_{cav} in this species. Our iterative procedure produced a Ψ_{cav} of -1.36 MPa. The difference between Ψ_{px} and Ψ_{cav} was only 0.26 MPa, suggesting that *P. fremontii* individuals operate very close to the threshold Ψ_{px} that could cause catastrophic cavitation. Although on average, individuals maintain Ψ_{px} above Ψ_{cav} , the range in midday Ψ_{L} we observed suggests that Ψ_{cav} is often exceeded, potentially resulting in catastrophic cavitation. Leaf xylem is likely more resistant to cavitation than stem xylem, since leaves are typically subjected to lower Ψ values than stems. Ψ_{cav} values for other riparian poplars include -1.05 MPa for *P. deltoides* (Tyree et al. 1994) and -1.20 MPa for *P. fremontii* (Blake et al. 1996 citing unpublished data from Pockman and Sperry). Blake et al. (1996) suggested that species which are highly vulnerable to cavitation maintain small safety margins. Data from our study are consistent with this finding. Additionally, species with small safety margins are thought to have stomata that are highly sensitive to water status (Schulte et al. 1987), a result we have also observed.

Several authors have suggested that various impacts of water stress are responsible for the decline of cottonwood populations throughout western North America (Rood and Mahoney 1990, Howe and Knopf 1991, Busch and Smith 1995). The extreme vulnerability of individuals to cavitation and the small safety margins reported in this and other studies are strong evidence to support this theory. High vulnerability and small safety margins likely evolved under conditions of higher water availability, conditions similar to those in riparian areas prior to damming and channelization of rivers. The greater variation in water availability that these populations now experience may cause Ψ_{px} to exceed Ψ_{cav} on a regular basis, causing significant damage to trees.

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RUFFED GROUSE (*BONASA UMBELLUS*) FORAGING IN ASPEN STANDS DURING WINTER IN NORTHERN UTAH

David G. Hewitt^{1,2} and Terry A. Messmer¹

ABSTRACT.—Ruffed Grouse (*Bonasa umbellus*) population densities are lower in the Intermountain West than elsewhere in the species' range. Throughout much of its range, the Ruffed Grouse is closely associated with quaking aspen (*Populus tremuloides*), in part because aspen buds are an important winter food. Because population fluctuations of Ruffed Grouse have been associated with changes in aspen abundance or chemical composition, we studied winter foraging of the species in the Intermountain West where it has received little attention. Aspen buds were the most prominent forage in the bird's diet, although in contrast to other Ruffed Grouse food habits studies, reproductive buds were not eaten more than vegetative buds, and buds of other deciduous plants were also important (>20% of the diet). Excretion of high concentrations of ammonium nitrogen suggests that grouse in northern Utah are ingesting higher levels of secondary plant compounds than reported elsewhere. Our results show aspen is important in the winter ecology of Ruffed Grouse in northern Utah and suggest that continued loss of aspen may impact grouse populations.

Key words: Ruffed Grouse, *Bonasa umbellus*, quaking aspen, *Populus tremuloides*, food habits, foraging, Utah, ammonium, secondary plant compounds, protein.

The range of the Ruffed Grouse (*Bonasa umbellus*) covers the northern half of North America and extends south in the Appalachian, Rocky, and Pacific Coast Mountain ranges (Bump et al. 1947). While the species occurs in a wide variety of vegetation types across its range, highest densities are reported in areas dominated by quaking aspen (*Populus tremuloides*; hereafter referred to as aspen; Svoboda and Gullion 1972). In these areas Ruffed Grouse rely heavily on aspen buds as a winter forage. Consequently, aspen is considered a key food for Ruffed Grouse because it is abundant, can be harvested efficiently, and has adequate levels of nutrients (Svoboda and Gullion 1972). Changes in abundance, chemical composition, and grouse consumption of aspen buds have been correlated with population fluctuations of Ruffed Grouse (Jakubas and Gullion 1991).

Ruffed Grouse prefer staminate reproductive buds of quaking aspen over vegetative and pistillate buds and prefer certain aspen clones (Svoboda and Gullion 1972, Huempfer and Tester 1988). These foraging patterns can be explained in part by the large size, high levels of protein, and low levels of secondary plant compounds, especially coniferyl benzoate,

of reproductive buds in preferred clones (Doerr et al. 1974, Jakubas and Gullion 1991).

Relationships between Ruffed Grouse and aspen have been extensively studied in Minnesota (e.g., Svoboda and Gullion 1972, Huempfer and Tester 1988) and Alberta (e.g., Doerr et al. 1974). Although Ruffed Grouse are associated strongly with aspen in the Intermountain West (Stauffer and Peterson 1985), little research has been conducted on their foraging in aspen stands during winter in this region. Despite the abundance of aspen, Ruffed Grouse densities are lower in the Intermountain West than in northern and eastern portions of the species' range (Stauffer 1989). In addition, grazing by wild and domestic herbivores and fire suppression, which favors succession toward conifer forest types, threaten the abundance of aspen in the Intermountain West (DeByle and Winokur 1985). Thus, an understanding of the relationship between Ruffed Grouse and aspen in the Intermountain West may help explain why densities are lower and could assist efforts to enhance populations. The objectives of our study were to determine the proportion of aspen buds in the winter diet of Ruffed Grouse in the Intermountain West, to describe Ruffed Grouse

¹Jack H. Berryman Institute, Department of Fisheries and Wildlife, UMC 5210, Utah State University, Logan, UT 84322-5210.

²Present address: Caesar Kleberg Wildlife Research Institute, Campus Box 218, Texas A&M University-Kingsville, Kingsville, TX 78363.

foraging patterns in aspen stands, and to compare levels of secondary plant compound ingestion between grouse in the Rocky Mountains and elsewhere, as reported in the literature.

METHODS

We conducted our study on the Wasatch-Cache National Forest, east of Logan, Utah. Dominant overstory species in the study area are aspen, *Pseudotsuga menziesii* (Douglas-fir), *Acer grandidentatum* (bigtooth maple), and *Sorbus scopulina* (mountain-ash). Understory shrubs are *Prunus virginiana* (chokecherry), *Salix* spp. (willow), *Rosa* sp. (rose), *Ame-lanchier alnifolia* (serviceberry), and *Physocarpus* sp. (ninebark). Patches of *Artemisia* sp. (sagebrush) and diverse herbaceous species are scattered throughout the area. Elevation of the study site is 1760–2360 m. Snowpack during the study was 50–120 cm.

Because Ruffed Grouse in our study area are rarely found during winter where aspen are not present (Stauffer and Peterson 1985), we used aerial photography to identify 21 aspen stands that were >0.5 km² and <2 km from a maintained roadway. Of these, 6 were chosen based on winter accessibility and confirmed presence of Ruffed Grouse. To sample each stand for foraging grouse and to collect aspen buds, we set up 900- to 1200-m-long transects perpendicular to land contours and marked them with colored flagging. Aspen was the dominant overstory species on all transects, but plant species common throughout the study area (listed above) were found on most transects. We searched for foraging grouse between 14 December 1995 and 28 February 1996 by slowly walking transects beginning 30 min before sunrise (once for each transect) or at sunset (2–3 times for each transect). Observers wore white clothing to camouflage their activities and minimize disruption of foraging grouse. When grouse were observed foraging, we recorded duration of observed foraging and marked trees in which birds foraged.

Vegetative and reproductive aspen buds were collected during March 1997 from the upper 1/3 of the tree canopy by removing a branch using a tree pruner on an expandable pole or by shooting with a shotgun. Buds were collected from mature aspen trees nearest every 200-m flag along each transect. If reproductive buds were not found on trees sampled

systematically, buds were collected from the nearest aspen tree. Buds were held on dry ice in the field and frozen at -20°C until freeze-dried.

Ruffed Grouse intestinal feces were collected along transects from snow roosts or from foraging paths identified from grouse tracks in snow. We did not collect cecal droppings because their composition varies from that of intestinal droppings (Moss and Parkinson 1972) and they could not be collected with every fecal sample. Feces were analyzed to estimate food habits and nitrogen excretion patterns. Only feces <24 h old, based on flushing the bird or fresh sign in new snow or melting snow, were used for nitrogen analysis. All galliform feces collected were assumed to be from Ruffed Grouse. Although Blue Grouse (*Dendragapus obscurus*) inhabit the area, the species was not observed during the study and was unlikely to be found in the area because of preference for high-elevation conifer stands during winter (Stauffer and Peterson 1985).

Feces were freeze-dried and ground with a mortar and pestle. By mixing 1-g samples from each fecal collection, we made a composite of all feces collected from each aspen stand. Forage species composition was determined by microhistological analysis for each of 6 composite samples (Wildlife Habitat Lab, Washington State University, Pullman, WA). Because vegetative and reproductive buds of aspen can be distinguished through this analysis, a correction factor was established to account for differences in the amount of recognizable material between the 2 types of buds. The analysis indicated that both bud types had similar amounts of recognizable material per unit mass (1.1:1.0 for reproductive:vegetative), and thus proportions of these bud types in feces were assumed to represent relative proportions in the diet. Nitrogen content of feces and aspen buds (for samples with enough biomass for analysis) was determined in duplicate by the Kjeldahl technique and converted to crude protein by multiplying by 6.25 (Robbins 1993). Ammonium nitrogen in feces was assayed using only the distillation and titration steps of the Kjeldahl procedure.

RESULTS

Transects were walked once each at sunrise and 2–3 times each at sunset, resulting in 353

and 670 min of observation, respectively. We observed grouse foraging on 6 occasions on 4 different transects. Group sizes of 3, 2, and 1 were observed for a total of 9 birds. One of these birds foraged on both *Prunus virginiana* and aspen buds, another only on *P. virginiana*, and the remainder foraged entirely on aspen. We observed grouse foraging 7.52 ± 1.52 min ($\bar{x} \pm s_{\bar{x}}$; $n = 8$; one bird in a group of 3 was not fully visible while foraging). This is a minimum estimate of the duration of foraging bouts because 3 birds were foraging when first seen. The others were first seen flying into the trees in which they foraged. Foraging grouse were first observed 28 ± 4 min ($n = 6$) after official sunset. All foraging in aspen trees occurred in the upper 1/3 of the canopy, and birds moved higher into the canopy as they foraged, finishing in the uppermost branches. Birds foraged at a fast rate (25–45 bite motions/min) and rarely stopped foraging for >15 sec. Of 10 trees in which grouse were observed foraging, only 1 had reproductive buds; these were staminate buds. No grouse were observed foraging in the morning, although tracks indicated they foraged on shrubs at ground level in the morning.

Thirty-seven fecal samples were used for food habits analysis. Aspen buds were the predominant forage at 5 sites, averaging 41% of feces (Table 1). *Amelanchier alnifolia*, *Salix* spp., and *Acer grandidentatum* were consumed in lesser amounts on all sites, and *Shepherdia canadensis* (buffalo-berry) and *Prunus virginiana* occurred in feces at 1 site each. Aspen

vegetative buds made up a larger percentage of the diet than reproductive buds on 5 sites. Ammonium averaged $40.2 \pm 1.4\%$ ($n = 24$) of nitrogen excreted in feces (Table 1). Vegetative and reproductive (male and female) buds of aspen averaged $6.7 \pm 0.5\%$ ($n = 12$) and $11.2 \pm 0.4\%$ ($n = 16$) crude protein, respectively.

DISCUSSION

Foraging behavior of Ruffed Grouse in Utah was similar to that of grouse in Minnesota and Alberta (Svoboda and Gullion 1972, Doerr et al. 1974, Huempfer and Tester 1988). Ruffed Grouse began foraging after sunset and often continued past the time sunlight was visible on the horizon. Arboreal foraging was more common in the evening than morning and was intense during evening as birds appeared to maximize intake rate to fill their crops before roosting for the night. Foraging patterns observed during this study differed from those reported previously (Doerr et al. 1974, Svoboda and Gullion 1972). Ruffed Grouse in Utah did not concentrate their foraging on reproductive buds, despite the higher nitrogen content and larger size of reproductive buds.

Crude protein of reproductive buds from random trees in Utah was similar to that of trees in Alberta (9.2–10.0%; Doerr et al. 1974) and Minnesota (9.3–13.9%; Jakubas and Gullion 1991, Guglielmo and Karasov 1995). Jakubas and Gullion (1991) argue that aspen buds should have $\geq 11\%$ crude protein and

TABLE 1. Percent forage species composition of Ruffed Grouse feces collected December 1995–March 1996 on 6 study sites in northern Utah and the percentage of fecal nitrogen excreted as ammonium (NH₄) in feces collected within 24 h of excretion.

Study site	<i>Acer grandidentatum</i>	<i>Amelanchier alnifolia</i>	<i>Populus tremuloides</i>		<i>Prunus virginiana</i>	<i>Salix</i> spp.	<i>Shepherdia canadensis</i>	NH ₄ %
			Reproductive	Vegetative				
Mill Hollow	22	25	3	30	0	20	0	— ^a
Creek Crossing	10	22	11	21	23	13	0	33
West Hodges								
Creek	7	21	39	22	0	12	0	30
Red Banks	8	21	21	29	0	22	0	34
Franklin Basin	22	22	18	26	0	12	0	44
Beaver Mountain	14	17	7	19	0	8	35	44
AVERAGE	13.8	21.3	16.5	24.5	3.8	14.5	5.8	40.2 ^b
($s_{\bar{x}}$)	(2.8)	(1.1)	(5.3)	(1.8)	(3.8)	(2.2)	(5.8)	(1.4)

^aFeces <24 h old were not found on this study site.

^bAverage and standard error for 24 separate samples.

≤1.8% coniferyl benzoate to be preferred by foraging Ruffed Grouse. Using only the protein criterion, 40% of trees with staminate buds sampled would be suitable for Ruffed Grouse foraging.

Foraging sign in the snow and analysis of material in grouse crops ($n = 5$) indicated that aspen and *Prunus virginiana* were predominant forages of Ruffed Grouse during winter in the Wellsville Mountains, southwest of Logan, Utah (Phillips 1967). Foraging sign also indicated grouse ate buds of *Salix* spp., *Aemilanchier alnifolia*, and *Acer grandidentatum*, although these shrubs were not considered important (Phillips 1967). Grouse in our study consumed a similar array of species, although *P. virginiana* occurred in feces at only a single site, and *A. grandidentatum*, and *A. alnifolia* were consumed at most sites. Aspen may have been overrepresented relative to the diet of all Ruffed Grouse in the study area because feces were collected from areas in which aspen trees were part of the overstory. Because grouse were more likely to forage on understory plants during the day and in the canopy of aspen trees during evening, food habits analyses could be biased if daytime and nighttime feces were not collected in representative proportions. Of 29 fecal samples for which we recorded the type of collection (snow roost or grouse foraging path), 16 (55%) were from snow roosts. However, birds were flushed from 2 of these snow roosts in the afternoon, and thus some snow roosts contained feces from daytime foraging. Therefore, we do not feel our food habits data are strongly biased by unrepresentative proportions of feces produced from daytime feeding.

Excretion of ammonium nitrogen increases as a result of metabolic acidosis, which may arise from consumption of forages high in secondary plant compounds (Foley et al. 1995) or from starvation (DelGiudice et al. 1994). Because we saw no indication of malnourished grouse and starvation is rarely documented in grouse (Bergerud 1988), ammonium excretion may serve as an index to ingestion of secondary plant compounds (Foley et al. 1995). Such an index was preferred because analyses of common secondary plant compounds, such as phenolics or tannins, have not been useful in explaining Ruffed Grouse foraging behavior (Jakubas et al. 1989).

Ammonium was <7% of fecal nitrogen in grouse consuming pelleted diets with few secondary plant compounds (Jakubas et al. 1993, Hewitt and Kirkpatrick 1997) and was >10% in grouse consuming native forages or diets containing secondary plant compounds (Hewitt and Kirkpatrick 1997 and references therein). The highest reported ammonium excretion in grouse was 33–55% by Blue Grouse consuming conifer needles (Remington 1990). The high percentage of ammonium nitrogen excreted by Ruffed Grouse in Utah suggests they were ingesting high levels of secondary plant compounds. Although grouse on the West Hodges Creek study area had the lowest level of ammonium excretion and highest proportion of aspen reproductive buds in the diet (Table 1), there was no clear relationship between ammonium excretion and aspen level in the diet (regression analysis, $P > 0.25$). Ammonium concentrations reported in our study may be inflated because cecal feces, which often contain higher concentrations of nitrogen and lower concentrations of ammonium nitrogen (Moss and Parkinson 1972), were not collected. Correcting for cecal feces is unlikely to shift nitrogen excretion patterns dramatically because cecal feces are usually <15% of excreta dry matter (Moss and Parkinson 1972).

CONCLUSIONS

Aspen buds were the primary forage of Ruffed Grouse on our study sites. For this reason, and because Ruffed Grouse during winter in our area use aspen or aspen/conifer stands almost exclusively (Stauffer and Peterson 1985), we feel maintaining aspen in the ecosystem contributes to productive grouse populations, although inclusion of several browse species in Ruffed Grouse diets suggests that diverse communities of deciduous trees and shrubs are likely to provide the best habitat for foraging during winter. High levels of ammonium nitrogen excreted by Ruffed Grouse in the study area may indicate that grouse were consuming browse containing high levels of secondary plant compounds and that improvements in the winter diet may be possible. Whether different diets would influence grouse survival, production, or density is not known. However, further study of Ruffed Grouse foraging will advance our understanding of plant-herbivore interactions and provide new information

regarding management options that can be implemented in the Intermountain West to enhance Ruffed Grouse populations.

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IMPORTANCE OF MIGRATING SALMON SMOLT IN RING-BILLED
(*LARUS DELAWARENSIS*) AND CALIFORNIA GULL (*L. CALIFORNICUS*)
DIETS NEAR PRIEST RAPIDS DAM, WASHINGTON

Darryl L. York¹, John L. Cummings¹, John E. Steuber², Patricia A. Pochop¹,
and Christi A. Yoder¹

ABSTRACT.—Ring-billed (*Larus delawarensis*) and California Gulls (*L. californicus*) have been implicated in depredations on migrating salmon smolt in the Columbia River. As part of a gull management program conducted in 1995 and 1996, we collected *L. delawarensis* ($n = 120$) and *L. californicus* ($n = 45$) near Priest Rapids Dam, Washington, and analyzed stomach contents to determine food habits and thus the importance of fish in gull diets. Percent volume measurements and index of relative importance rankings suggested a greater reliance on fish by *L. californicus* than by *L. delawarensis*. Peak percent consumption of fish by both species occurred in May, coinciding with peak salmon out-migration through Priest Rapids Dam; and for both species number of fish consumed by gulls was higher below Priest Rapids Dam. Gulls collected prior to, and after, peak smolt migration indicated low importance rankings for fish in both *L. delawarensis* and *L. californicus* diets. However, the importance ranking of fish in gull diets changed over time and was higher for both species as the smolt migration peaked in May.

Key words: California Gull, Columbia River, dams, diet, *Larus delawarensis*, *Larus californicus*, Ring-billed Gull, salmon migration, salmon smolt.

The Columbia River was once known for having some of the world's largest runs of anadromous salmon. Fish runs that historically numbered 10–16 million have been severely reduced (Groen 1992). These decreases in salmon have been attributed to a number of factors including overfishing at sea and on the river, development, dams, fish disease, and predation by fish and birds; but the impact of each of these factors, especially losses to birds such as gulls, is not well documented (Ruggerone 1986).

Salmon smolt migration begins around early April from upper portions of the Columbia River, and numbers peak at Priest Rapids Dam from late April through May. The timing of this migration corresponds with the initiation of Ring-billed (*Larus delawarensis*) and California Gull (*L. californicus*) nesting on Columbia River islands. Cabin Island, located 1.5 km upstream of Priest Rapids Dam, had an estimated breeding population of 7000 *L. delawarensis* and 200 *L. californicus*. In addition, an aerial survey conducted June 1995 along the Columbia River from Chief Joseph Dam south to the Dalles Dam (9 dams and 310 km of river) found that gulls occupied 17

Columbia River islands. Gull populations on 5 of the 17 islands were estimated at 35,000 breeding adults (C. Yoder 1995 unpublished data).

Ruggerone (1986) reported juvenile salmonids being vulnerable to avian predation immediately below Columbia River dams because of the disorienting and stunning effect of passing through a turbine and currents carrying fish close to the surface. His data indicated *L. delawarensis* consumed approximately 120,000 migrating juvenile salmonids during a 25-d smolt-migration period at Wanapum Dam (approximately 24 km upstream of Priest Rapids Dam), representing 2% of the total hatchery-reared and wild salmon spring out-migration. It has been estimated that 17% of migrants are killed by dam turbines independent of gull predation (McKenzie et al. 1984, Ruggerone 1986).

We collected *L. delawarensis* and *L. californicus* during the peak of salmon smolt migration at Priest Rapids Dam, Desert Aire, Washington, and at the nesting colony on Cabin Island. Cabin Island is 30 ha with approximately 4 ha used by *L. delawarensis* and *L. californicus* as a loafing/nesting area. Collections

¹U.S. Department of Agriculture, Animal and Plant Health Inspection Service, National Wildlife Research Center, 4101 LaPorte Ave., Fort Collins, CO 80521.

²U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services, 2800 North Lincoln Blvd., Oklahoma City, OK 73105.

were made to quantify the relative importance of salmon smolt in the diet of these 2 gull species during salmon smolt migration.

METHODS

We collected gulls on 19 April, 5 May, and 13 June 1995 from the breeding colony on Cabin Island and on 7 and 21 May 1996 below Priest Rapids Dam. We categorized sample dates according to nesting stage: 19 April, prenesting; 5–25 May, nesting; and 13 June, postnesting. Gulls were frozen within 4 h of collection. In the laboratory each carcass was weighed to the nearest 0.1 kg and aged as adult or juvenile according to plumage characteristics. We removed the stomach-esophageal contents from each gull and placed them in isopropyl alcohol.

Stomach-esophageal contents were flushed onto a 40-gauge wire screen. Contents were washed with water to remove mucus and to separate food items, and then drained. Total

volume of each food category per sample was measured to the nearest 0.5 mL by water displacement in a 100-mL graduated cylinder. For each sample we recorded total number of individuals, volume of each category (i.e., fish, grain, insect, mammal, earthworm, herbaceous plant matter, and miscellaneous debris), collection site, and collection date (Jarvis and Southern 1976). We used the index of relative importance (IRI) to create tables indicating relative importance of various food items (Pinkas et al. 1971), which reduced biases introduced by numerous small or a few very large items occurring in only 1 or a few stomachs (Duffy and Jackson 1986).

RESULTS

Cabin Island Samples

Larus delawarensis ($n = 77$) and *L. californicus* ($n = 22$) stomach contents indicated diet varied as the breeding season progressed, with herbaceous plant matter consistently ranking

TABLE 1. Percent frequency^a (F) and volume in mL (V) of most common food items in Ring-billed (*Larus delawarensis*) and California Gull (*L. californicus*) stomachs collected on Cabin Island, Washington, 1995.

Sample dates No. individuals	19 April 1995 n ^{RB} = 16, n ^{CG} = 4		5 May 1995 n ^{RB} = 18, n ^{CG} = 5		25 May 1995 n ^{RB} = 22, n ^{CG} = 13		13 June 1995 ^b n ^{RB} = 21	
	F	V	F	V	F	V	F	V
Fish								
RB	0	0	22	4	5	t ^c	0	0
CG	25	t	2	13	31	54		
Grain								
RB	6	t	6	t	14	13	29	4
CG	25	0.5	0	0	0	0		
Insect								
RB	25	t	28	0.6	73	15	29	47
CG	0	0	0	0	8	t		
Mammal								
RB	6	0.5	6	49	9	45	5	0.5
CG	0	0	0	0	0	0		
Earthworm								
RB	0	0	11	6	0	0	5	0.5
CG	0	0	0	0	0	0		
Herbaceous plant matter								
RB	93	87	78	35	86	25	86	35
CG	50	82	80	41	77	44		
Miscellaneous debris ^d								
RB	81	12	72	5	23	2	57	13
CG	75	17	80	46	77	2		

^aNumber of gulls with food item divided by total sample size

^bNo California gulls collected on this date

^cTrace volumes and numbers less than 0.5 mL

^dUnidentifiable or nonfood items

RB Ring-billed Gull

CG California Gull

among the more important food items. Collections made on 19 April 1995 found no fish in *L. delawarensis* samples and only a trace volume in *L. californicus* (IRI = 4; Table 3). On 5 May, *L. delawarensis* samples contained small amounts of fish (4% volume, IRI = 5) as did *L. californicus* samples (13% volume, IRI = 3; Table 3). On 25 May, *L. delawarensis* samples contained only a trace volume of fish (IRI = 10), but we found a much larger amount in *L. californicus* samples (54% volume, IRI = 3; Tables 1, 3). On 13 June, *L. delawarensis* samples contained no fish (Table 1), and no *L. californicus* were present in the collection area during this time.

Priest Rapids Dam Samples

We found an increase in fish consumption from *L. delawarensis* ($n = 43$) and *L. californicus* ($n = 23$) collected below Priest Rapids Dam compared to those from Cabin Island. On 7 May 1996, *L. delawarensis* and *L. californicus* samples contained fish (26% volume,

IRI = 4 and 65% volume, IRI = 1, respectively; Tables 2, 4). On 21 May, *L. delawarensis* samples contained 41% volume of fish (IRI = 2), and *L. californicus* samples contained an even larger amount of fish (85% volume, IRI = 1; Tables 2, 4).

DISCUSSION

Percent-volume measurements and index of relative importance rankings suggest a greater reliance on the fish resource by *L. californicus* than by *L. delawarensis* for both sampling locations and all sampling dates. Peak percent consumption of fish by both species occurred in May, coinciding with peak salmon out-migration through Priest Rapids Dam. The number of fish consumed by gulls was higher below Priest Rapids Dam for both species. This result would be expected because gulls below the dam are almost exclusively feeding on fish, whereas gulls collected at Cabin Island could have recently returned

TABLE 2. Percent frequency^a (F) and volume in mL (V) of most common food items in Ring-billed (*Larus delawarensis*) and California Gull (*L. californicus*) stomachs collected below Priest Rapids Dam, Washington, 1996.

Sample dates	7 May 1996 (nesting)		21 May 1996 (nesting)	
	$n^{RB} = 21, n^{CG} = 17$		$n^{RB} = 22, n^{CG} = 6$	
No. individuals	F	V	F	V
Fish				
RB	43	26	50	41
CG	65	65	83	85
Grain				
RB	29	26	9	t ^b
CG	6	0	0	0
Insect				
RB	67	15	36	2
CG	41	2	33	t
Mammal				
RB	5	t	0	0
CG	6	0.5	0	0
Earthworm				
RB	0	0	0	0
CG	12	1	0	0
Herbaceous plant matter				
RB	81	31	59	55
CG	88	21	83	15
Miscellaneous debris ^c				
RB	33	3	23	2
CG	65	10	5	t

^aNumber of gulls with food item divided by total sample size

^bTrace volumes and numbers less than 0.5 mL

^cUnidentifiable or nonfood items

RB Ring-billed Gull

CG California Gull

TABLE 3. Index of relative importance (IRI_i) = $(N + V) \times F$ on Cabin Island, Washington, 1995, of individual prey items of Ring-billed (*Larus delawarensis*) and California Gulls (*L. californicus*). Shown are importance rankings of 7 food categories and (IRI values).

Sample date	Fish	Grain	Insect	Mammal	Earthworm	Plant ^a	Miscellaneous ^b
19 Apr ^{RB}		5	3	4		1	2
	(0)	(18)	(450)	(21)	(0)	(11346)	(4050)
19 Apr ^{CG}	4	3				1	2
	(360)	(363)	(0)	(0)	(0)	(5550)	(4500)
5 May ^{RB}	5	7	3	4	6	1	2
	(308)7	(18)	(381)	(312)	(121)	(6162)	(2736)
5 May ^{CG}	3					1	2
	(48)	(0)	(0)	(0)	(0)	(6800)	(7200)
25 May ^{RB}	6	5	2	3		1	4
	(10)	(280)	(3650)	(441)	(0)	(5676)	(299)
25 May ^{CG}	3		4			1	2
	(2170)	(0)4	(32)	(0)	(0)1	(6468)2	(3234)
13 June ^{RB}		4	3	5.5	5.5	1	2
	(522)3	(1769)	(13)	(13)	(6536)	(2280)	

^aHerbaceous plant matter

^bUnidentifiable or nonfood items

^{CG}Ring-billed Gulls

^{RB}California Gulls

N = percentage by number of prey of type I

V = percentage by volume of prey of type I

F = frequency of occurrence of prey of type I

TABLE 4. Index of relative importance (IRI_i) = $(N + V) \times F$ below Priest Rapids Dam, Washington, 1996, of individual prey items of Ring-billed (*Larus delawarensis*) and California Gulls (*L. californicus*). Shown are importance rankings of 7 food categories, and (IRI values).

Sample date	Fish	Grain	Insect	Mammal	Earthworm	Plant ^a	Miscellaneous ^b
7 May ^{RB}	4	3	2			1	5
	(849)	(1073)	(2747)	(0)	(0)	(5103)	(594)
7 May ^{CG}	1	6	4	7	5	2	3
	(5720)	(12)	(697)	(15)	(60)	(4576)	(2145)
21 May ^{RB}	2	5	3			1	4
	(3450)	(45)	(828)	(0)	(0)	(5192)	(345)
21 May ^{CG}	1		3			2	4
	(9794)	(0)	(429)	(0)	(0)	(3984)	(100)

^aHerbaceous plant matter

^bUnidentifiable or nonfood items

^{CG}Ring-billed Gulls

^{RB}California Gulls

N = percentage by number of prey of type I

V = percentage by volume of prey of type I

F = frequency of occurrence of prey of type I

from terrestrial foraging forays. Gulls collected prior to, and after, peak smolt migration indicated low overall importance of fish in *L. delawarensis* and *L. californicus* diets. However, the importance ranking of fish in gull diets changed over time and was higher for both species as the smolt migration peaked in May. The reason for greater use of fish by *L. californicus* versus *L. delawarensis* is presently unknown and should be the focus of future research. However, the 35:1 ratio of breeding *L. delawarensis* to *L. californicus* on Cabin Island suggests the former consumed the majority of salmon smolts even though their diets were more diverse than *L. californicus*

diets. A study comparing *L. californicus* and *L. delawarensis* food habits in Alberta, Canada, reported fish also occurring more frequently in *L. californicus* samples (Vermeer 1970). The *L. californicus* diet was characterized by a heavy reliance on plant matter and fish, but the *L. delawarensis* diet was more varied and contained large volumes of several food items. In addition to plant matter, grain, insects, and mammals consistently occurred more frequently and in greater volumes in *L. delawarensis* samples, indicating a preference for terrestrial foraging habitat. Reliance on plant foods by both species early in the season, followed by a switch to animal foods as the

breeding season progressed, was also documented in Alberta and the Great Lakes and was presumed to indicate opportunistic feeding habits (Vermeer 1970, Jarvis and Southern 1976).

Although only a small percentage (2%) of total migrating salmon smolt were eaten by gulls, and of this amount a certain number (17%) were recently killed by dam turbines, the cumulative impact of gull predation on salmon populations at each of the 9 Columbia River dams and 4 Snake River dams is substantial, especially in combination with other negative impacts on Columbia River salmon (e.g., passage through turbines, nitrogen supersaturation, migration delays, and disease [Ruggerone 1986]). Management actions at Cabin Island to disperse gull nesting greater distances from hatchery release points, as well as active gull hazing below Priest Rapids Dam, should continue so as to provide disoriented smolts an opportunity to recuperate and continue their migration. In addition, monitoring population changes in *L. delawarensis* and *L. californicus* at Cabin Island could provide further information on foraging competition between these two species.

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RECORDS OF MAMMALS FROM THE EAST TAVAPUTS PLATEAU, UTAH

Duke S. Rogers¹, Dana J. Shurtleff², and Clyde L. Pritchett²

Key words: East Tavaputs Plateau, Book Cliffs, small mammals, Utah range extensions.

The East Tavaputs Plateau, or Book Cliffs, comprises an area of approximately 300,000 ha in central eastern Utah. Bounded to the north and west by the White and Green rivers, respectively, to the south by the Roan and Book Cliffs proper, the Book Cliffs region is continuous with the Roan Plateau of western Colorado. Previous records of mammals from this region of Utah were reported by Kelson (1949, 1951), Durrant (1952), Ranck (1961), and Hasenyager (1980). Based on collecting during the summers of 1994–1996, we report 7 species new to the mammalian fauna of central eastern Utah. Usage of scientific and common names follows that of Hall (1981). Localities were plotted by latitude and longitude to the nearest 5" using U.S. Geological Survey 7.5-minute series (topographic) quadrangle maps. These maps also were used to estimate range extensions to within 5 km. Elevation was estimated to the nearest 10 m. General vegetation type(s) inhabited by each species are presented. All specimens reported are represented by museum vouchers and are deposited in the Mammal Collection, Monte L. Bean Museum, Brigham Young University (BYU). When available, reproductive data are reported.

Sorex cinereus.—The masked shrew was previously known from scattered localities in the Uintah, Wasatch, and High Plateau provinces in Utah (Durrant 1952, Hall 1981, Junge and Hoffman 1981). We collected 3 in pitfall traps from 2 localities in Rat Hole Canyon, Uintah Co., as follows: 39°34'30"N, 109°05'30"W, 2330 m (1 male and 1 female; BYU 16265 and 16263, respectively), and a male (BYU 16270) from 39°35'50"N, 109°05'45"W, 2130 m. These records document a range extension of

ca 120 km east and south of previous localities in Utah. The westernmost record for Colorado is from Collbran in Mesa Co. (Armstrong 1972). This locality is ca 90 km east of Rat Hole Canyon records documented here.

Sorex cinereus were taken in pitfall traps placed in riparian habitat. Vegetation at capture sites consisted primarily of various grasses and sedges (*Carex*), sagebrush (*Artemisia tridentata*), chokecherry (*Prunus virginiana*), rabbitbrush (*Chrysothamnus nauseosus*), and willows (*Salix*). BYU 16265 collected on 3 July had testes measuring 4 mm. BYU 16263 taken on 19 June had 6 embryos, 3 in each uterine horn, measuring 7 mm from crown to rump. Although *S. cinereus* has one of the broadest distributions of any shrew in North America (Junge and Hoffman 1981), it appears to be less abundant in the Book Cliffs than *S. monticolus*. In the same habitat types and equivalent trapping effort, we collected 18 *S. monticolus*.

Sorex palustris.—Previous records of the water shrew in Utah include the La Sal and Uinta Mountains and the Manti National Forest (Durrant 1952, Hall 1981). Seven were taken in Rat Hole Canyon, Uintah Co., as follows: 30°35'20"N, 109°05'30"W, 2160 m (2 males, BYU 13402 and BYU 16273, and 5 females, BYU 16272 and 16274–16277). These specimens were collected in Sherman live-traps baited with "scratch grain." An adult female (BYU 17387) was collected in a pitfall trap located in Willow Creek Canyon, 39°36'50"N, 109°34'10"W, 1775 m, Uintah Co. These sites are ca 100 km north of the most proximal locality in Utah (Manti La Sal National Forest; Hall 1981). However, the water shrew is known from ca 40 km to the east near Mack, Garfield Co., Colorado (Armstrong 1972).

¹Department of Zoology and Monte L. Bean Life Science Museum, Brigham Young University, Provo, UT 84602.

²Monte L. Bean Life Science Museum, Brigham Young University, Provo, UT 84602.

Specimens from Rat Hole Canyon were collected in riparian habitat like that described for *S. cinereus*. The habitat in Willow Creek Canyon was similar but included cottonwood trees (*Populus fremontii*) and was adjacent to an alfalfa field (*Medicago sativa*). BYU 16273 collected on 1 July had testes measuring 2 mm.

Lasiurus cinereus.—Published records of the hoary bat in Utah list 1 or more localities from Carbon, Davis, Garfield, Grand, Salt Lake, San Juan, Utah, Washington, and Weber counties (Hardy 1941, Shuster 1957, Hasenyager 1980, Mollhagen and Bogan 1997). Five male hoary bats were collected as follows: Kelly Canyon, 39°27'30"N, 109°06'45"W, 2000 m, Grand Co. (BYU 13418); Augusi Canyon, 39°37'35"N, 109°07'45"W, 2090 m, Uintah Co. (BYU 16307 and 16308); and Tent Canyon, 39°35'50"N, 109°05'45"W, 2130 m, Uintah Co. (BYU 16309 and 16310). For Utah, these records represent a range extension of ca 250 km to the north from near Blanding, San Juan Co., and ca 220 km to the west from Thistle Valley, Utah Co. (Hall 1981). This bat is known from various locations throughout Colorado, the closest record from ca 100 km to the southeast near Grand Junction, Mesa Co. (Armstrong 1972). All were taken in mist nets over water in areas predominated by *Artemisia tridentata*. BYU 16307 collected 14 July had testes measuring 5 mm, whereas BYU 16308 taken 19 June had testes measuring 3 mm.

Nyctinomops macrotus.—This bat occurs in western and central United States (Hall 1981), Mexico and Central America, the Greater Antilles, and the northern 2/3 of South America east of the Andes (summarized by Milner et al. 1990). In Utah, *N. macrotus* had been recorded from the southern 1/3 of the state in Millard, San Juan, and Washington counties (Hasenyager 1980).

On the evenings of 23–25 August 1994, one of us (DJS) observed large, fast-flying bats at ca 2000 h in Kelly Canyon, Grand Co. Two mist nets were placed over a small 6 × 4-m pond near the location where these bats were sighted. Several *Myotis evotis*, *M. ciliolabrum*, and *Pipistrellus hesperus* were captured the first 2 evenings. On the 3rd night, 2 adult female *N. macrotis* (BYU 13437 and 13438) were collected between 0100 h and dawn (Kelly Canyon, 39°27'30"N, 109°32'35"W, 1990 m,

Grand Co., Utah). This site is ca 180 km north of the locality near Blanding, San Juan Co., Utah. This species also occurs in western Colorado, where it is known from ca 100 km to the southeast near Grand Junction, Mesa Co. (Armstrong 1972). Vegetation surrounding the pond was dominated by *A. tridentata* intermixed with cheatgrass (*Bromus tectorum*), juniper (*Juniperus osteosperma*), and pinyon pine (*Pinus edulis*).

Glaucomys sabrinus.—Prior to this report, the northern flying squirrel was known in Utah from throughout the northern and central portions of the state (Hall 1981) in the Uintah, Wasatch, and High Plateau provinces as defined by Durrant (1952). A single sub-adult female (BYU 13334) was taken in South Canyon, 39°27'40"N, 109°15'30"W, 2350 m, Uintah Co., in a stand of quaking aspen (*Populus tremuloides*) and Douglas-fir (*Pseudotsuga menziesii*). The understory was composed of snowberry (*Symphoricarpos albus*), chokecherry (*Prunus virginiana*), and Oregon grape (*Berberis repens*). This locality is ca 190 km west of the nearest site previously recorded (near Ephraim, Sanpete Co.) in Utah (Hall 1981). Although *G. sabrinus* is not known from Colorado (Armstrong 1972, Fitzgerald et al. 1994), this new record is only ca 25 km from the Colorado border. Given the existence of similar habitat in the extreme western portion of that state, we consider it likely that flying squirrels also occur in westernmost Colorado.

Microtus montanus.—The montane vole was known to occur at moderate- to high-elevation localities throughout the northern, central, and western portions of Utah (Hall 1981). A total of 20 montane voles were collected from the following localities: Kelly Canyon, 39°27'25"N, 109°32'30"W, 2000 m, Grand Co. (3 females, BYU 13556–13558); Bitter Creek, 39°35'05"N, 109°09'50"W, 1960 m, Uintah Co. (2 females, BYU 13559 and 13560); Bitter Creek Canyon, 39°40'05"N, 109°14'W, 1860 m, Uintah Co. (1 male, BYU 16596); Bull Canyon, 39°34'20"N, 109°31'45"W, 2100 m, Uintah Co. (1 male, BYU 17485, and 1 female, BYU 17486); Chipeta Canyon, 39°31'30"N, 109°08'10"W, 2060 m, Uintah Co. (1 female, BYU 13560); Rat Hole Canyon, 39°35'20"N, 109°05'30"W, 2160 m, Uintah Co. (2 males, BYU 16603 and 16612); Rat Hole Canyon, 39°34'40"N, 109°03'50"W, 2290 m, Uintah Co. (1 male, BYU 16599);

Taylor Canyon, 39°30'05"N, 109°07'35"W, 2110 m, Uintah Co. (2 males and 1 female, BYU 13561–13563, respectively); Willow Creek Canyon, 39°36'50"N, 109°34'10"W, 1775 m, Uintah Co. (2 females, BYU 17495 and 17501); Willow Creek Canyon, 39°36'55"N, 109°32'30"W, 1980 m, Uintah Co. (1 female, BYU 17503); Willow Creek Canyon, 39°37'10"N, 109°32'35"W, 2000 m, Uintah Co. (1 female, BYU 17505); Willow Creek Canyon, 39°37'15"N, 109°33'40"W, 1770 m, Uintah Co. (1 male, BYU 17507). In Utah these new records represent a range extension of ca 90 km to the south from the marginal record listed as "Vernal" by Hall (1981: 797). *Microtus montanus* are known from east of Grand Junction, Mesa Co., Colorado, a locality ca 110 km southeast of the Book Cliffs localities (Armstrong 1972).

Microtus montanus were taken in a variety of vegetation types at elevations ranging from 1700 to 2290 m. They were more common in riparian associations as described for *S. cinereus* and *S. palustris* as well as in aspen and coniferous forest stands. In addition, they were occasionally trapped in habitat consisting of *A. tridentata*, greasewood (*Sarcobatus vermiculatus*), *C. nauseosus*, and *B. tectorum*. BYU 17501 and 17505 collected 8 and 6 June had uteri that were not swollen. BYU 17507 collected 24 May had testes measuring 4 mm.

Zapus princeps.—The former distribution of the northern jumping mouse in Utah was the Uinta, Oquirrh and Wasatch Mountains, as well as the Beaver Mountains in the northern and central portions of the state (Durrant 1952, Krutzsch 1954, Hall 1981). In addition, they have been recorded from the La Sal Mountains (Lee and Durrant 1960). Fifteen specimens, all from Uintah Co., were collected in Sherman live-traps from the following localities: Bitter Creek, 39°35'05"N, 109°09'50"W, 1960 m (2 males and 5 females, BYU 13649–13655); Rat Hole Canyon, 39°35'20"N, 109°05'30"W, 2160 m (5 females, BYU 13656–13658, BYU 17204 and 17205) and 39°36'05"N, 109°03'30"W, 2300 m (1 male, BYU 17706); Tent Canyon, 39°35'50"N, 109°05'45"W, 2130 m (1 female), 39°35'50"N, 109°03'30"W, 2330 m. These localities are ca 100 km north of the nearest collecting site located near Beaver Creek, La Sal Mountains, San Juan Co., Utah (Lee and Durrant 1960). However, the western jumping mouse also is known from ca 50

km to the east, south of Rangely in Garfield Co., Colorado (Armstrong 1972).

Zapus princeps were collected in riparian habitats. Vegetation was the same as that described for *S. cinereus*. BYU 17204 collected 2 July had 4 embryos, 2 in each uterine horn, whereas BYU 17207 collected 4 July had 6 embryos, 3 in each uterine horn, and measured 10 mm crown to rump length. BYU 17269 collected on 14 July was lactating.

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SEXUAL REPRODUCTION OF GAMBEL OAK (*QUERCUS GAMBELII*) NEAR ITS NORTHEASTERN LIMIT

Jamie L. Reynolds¹, Timothy N. Feinstein¹, and James J. Ebersole^{1,2}

Key words: *Quercus gambelii*, *Gambel oak*, *saplings*, *seedlings*, *sexual reproduction*, *Colorado*.

Gambel oak (*Quercus gambelii* Nutt.) is a deciduous, clonal, white oak that ranges in size from shrub to small tree (Harper et al. 1985). It occurs throughout much of Arizona, New Mexico, Utah, and Colorado, with small ranges in Nevada, Wyoming, Oklahoma, and northern Mexico (Little 1971). In the southern part of its range the oak has wide elevational limits, and these limits narrow in the north (Neilson and Wullstein 1983). It generally grows with ponderosa pine (*Pinus ponderosa*; Harper et al. 1985), pinyon pine (*Pinus edulis*; Neilson and Wullstein 1986), or just below the lower limit of pinyons and junipers (personal observation).

Neilson and Wullstein (1983) showed that Gambel oak in northern Utah likely migrated to its present range using sexual reproduction during the mid-Holocene hypsithermal and that the species now persists there through asexual reproduction. They found mortality of planted 1-yr-old *Q. gambelii* to be very high in northern Utah and low in Arizona and New Mexico. Neilson and Wullstein (1983) found no more than 20 natural seedlings in northern Utah in 4 yr of fieldwork, but reported a high density in Arizona and New Mexico (range 120–1320 ha⁻¹, generally 300–900 ha⁻¹ [Neilson and Wullstein 1986]). Neilson and Wullstein (1983) concluded that young, sexually reproduced individuals in northern Utah died due to late spring freezes and especially summer/fall drought caused by absence of Arizona summer monsoons in northern Utah. This explanation is consistent with relatively high survival of individuals planted at and north of *Q. gambelii* limits in Wyoming, where summer monsoons extend farther north than in Utah (Neilson and Wullstein 1983). In west central

Colorado, Brown (1958) found sexual reproduction “less evident” than vegetative reproduction.

There is no published information on occurrence of sexual reproduction in northeastern parts of *Q. gambelii*'s range. In this study we asked whether sexual reproduction occurs near the northeastern limit of the species, and we discuss ages and microhabitat preferences of individuals we did find.

We searched for seedlings (<1 yr old) and saplings (small stems >1 yr old) in areas with mature oaks in October 1997 at 3 sites from Colorado Springs to Canon City, Colorado. Site 1 is immediately west of Colorado Springs along Lower Gold Camp Road (38°48'N, 104°53'W, 2440 m elevation), about 70 km south of the northern limit of the species in this portion of its range. Colorado pinyon (*Pinus edulis*), one-seed juniper (*Juniperus monosperma*), and mountain-mahogany (*Cercocarpus montanus*) mix with Gambel oak on steep (40°–45°) colluvial slopes with many large boulders. Site 2 is in Aiken Canyon Preserve (38°37.5'N, 104°52.5'W, elevation 2070 m), about 30 km south of Colorado Springs. We searched gentle slopes several hundred meters east of the abrupt transition between the Great Plains and the Front Range where clearly defined groups of *Q. gambelii* stems are separated by meadows. Site 3 lies 4 km north of Canon City (38°24'N, 105°15'W, 1710 m). Moderate oak cover occurs among *J. monosperma* and *P. edulis* on 15°–20° slopes.

When searching for seedlings and saplings, we walked all habitats within 20–30 m of mature oaks and pushed vegetation aside when necessary to ensure no individuals were missed. Small stems beneath mature oaks were not examined due to the very large number of

¹Department of Biology, Colorado College, Colorado Springs, CO 80903-3294.

²Author to whom reprint requests should be addressed.

small, vegetatively produced stems there. Candidate stems were identified as being sexually reproduced by the spent, attached acorn or by long, tapering taproots and lack of horizontal rhizomes (Neilson and Wullstein 1986). For each seedling/sapling or cluster of these, we noted its relative shading during summer and early fall in 3 categories: little shade (<20% of the day), intermediate shade, and nearly continuous shade (>80%). We estimated ages of individuals by counting terminal bud scale scars. We generally could do this with high confidence to about 4 yr and with reasonable confidence on older stems.

All seedlings and saplings occurred in bare soil, and none were within herbaceous vegetation. Sexual reproduction occurred close to edges of mature clones, with 64% of seedlings and saplings within 3 m, 30% within 3.1–5.0 m, and the remainder within 7.7 m. Seedlings and saplings generally showed strong preference for sites receiving partial summer shade; at Aiken Canyon and Canon City 80% of clusters or single individuals occurred in this type of microsite. At the Colorado Springs site all individuals were in full sun and were 1–2 yr old in a recently eroded area.

For all individuals with acorns still attached (roughly 50% of those found), acorns were several cm below the surface. Seventy-three percent of seedlings and saplings occurred in clusters of >1 stem with stems <1 cm from each other (Table 1). These originated from groups of 2–20 acorns that were touching each other several cm below the soil surface.

Most individuals from sexual reproduction (71%) were 1–2 yr old, and only 1 sapling was >7 yr old (Table 1). Heights for seedlings ranged from 2 to 15 cm, and for 2-yr-old saplings from 2 to 20 cm. The tallest sapling found was a 60-cm-tall, 6-yr-old stem. Occasional short, old saplings were found, e.g., a 15-yr-old, 16-cm-tall stem.

Occurrence of seedlings and saplings in partially shaded sites agrees with results of Neilson and Wullstein (1986), who found most seedlings on the northeast side of sheltering objects. In most situations apparently only individuals experiencing moderate shade can withstand summer drought stress (Neilson and Wullstein 1983).

Competition with herbaceous vegetation could conceivably limit sexual reproduction to bare soil since young *Q. gambelii* presumably

experience the same competition with herbaceous vegetation as another oak in southwestern North America (Weltzin and McPherson 1997). However, even if this were an important limiting factor, it seems likely we would have found at least some seedlings or saplings within herbaceous vegetation. It is likely that animals dispersing acorns to bare soil contribute to the pattern we found.

Means of acorn dispersal for *Q. gambelii* are not clear from our data and likely include more than 1 vector. More research is necessary to definitively determine vectors, but possibilities will be considered here. Acorns that germinated on the soil surface may be simply gravity-dispersed. Several animal species could bury acorns in soil. Western Scrub Jays (*Aphelocoma californica*) were commonly observed caching Gambel oak acorns, and 96% of 211 caches were of single acorns on the west side of Colorado Springs in 1983–1986 (R. Bunn unpublished data). Western Scrub Jays usually pushed acorns into the soil until they were from just below the surface to 1.5 cm deep. They most often chose to place acorns into the soil in small bare areas within clumps of the short-grass blue grama/hairy grama (*Bouteloua gracilis*/*B. hirsuta*), but when caching near mid-grasses jays tended to place them in bare soil at the edges of clumps (R. Bunn unpublished data). It is these caches, when not recovered, which seem likely to produce some of the single seedlings and saplings we observed. Steller's Jays (*Cyanocitta stelleri*), which also disperse acorns (Vander Wall 1990), are markedly less common at our study sites than Western Scrub Jays.

Based on ranges and information on foods and storage habits (Fitzgerald et al. 1994), several small mammals could bury acorns in clusters. Rock squirrels (*Spermophilus variegatus*) commonly eat acorns when they are available (Ortega 1987) and carry large stores of acorns in cheek pouches (J. Ortega written communication). Other mammals that eat seeds and might bury clusters of acorns include golden-mantled ground squirrels (*Spermophilus lateralis*), Colorado chipmunks (*Tamias quadrivittatus*), least chipmunks (*T. minimus*), and deer mice (*Peromyscus maniculatus*).

Sexual reproduction does occur in the northeastern portion of the range of *Q. gambelii*, though apparently it is not common. We caution against inferring from our limited data on

TABLE 1. Gambel oak (*Quercus gambelii*) seedling and sapling numbers by site, by occurrence singly or in clusters, and by age.

Site	Search time (h)	Seedlings and Saplings							
		Total no.	Single	In clusters	No. / cluster (min, max)	No. clusters	Age in yr		
							1-2	3-7	>7
Colorado Springs	4	31	8	23	3, 20	2	10	0	0
Aiken Canyon	25	33	9	24	2, 4	6	12	3	0
Canon City	6	25	7	18	2, 11	3	3	6	1

age structures (Table 1) that essentially no sexually reproduced individuals successfully mature. Larger stems, which may have originated from acorns, were less likely to be excavated by us to determine seedling status. Variation through time in successful sexual reproduction is also unknown based on our observations in a single season. In spring 1998 a small number of Gambel oak seedlings were observed in an area ca 0.3 ha of western Colorado Springs while none were observed in unirrigated parts of the same area the previous 8 yr (personal observation). Since sexual reproduction of *Q. gambelii* in northern Utah is limited primarily by late summer and fall drought (Neilson and Wullstein 1983), the above-average precipitation for June through October 1997 at Colorado Springs (NOAA 1997) caused by an El Niño event (Webster and Palmer 1997) may have increased seedling survival compared to most years. Thus, while sexual reproduction commonly occurs in the southern part of the *Q. gambelii* range (Neilson and Wullstein 1986), sexual reproduction is rare, or possibly episodic, in the northwestern (Neilson and Wullstein 1983) and northeastern (this study) portions of the range. The species apparently maintains itself in the northern part of its range primarily vegetatively; and occasional sexual reproduction creates possibilities of new clones, genetic variation, and dispersal to new areas.

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DISTRIBUTIONAL NOTES ON THE MANGROVE WARBLER
(*DENDROICA PETECHIA CASTANEICEPS*) NEAR THE NORTHERN
EDGE OF ITS RANGE IN EASTERN BAJA CALIFORNIA SUR, MEXICO

Robert C. Whitmore¹, R. Craig Whitmore², and Michael M. Whitmore³

Key words: Mangrove Warbler, *Dendroica petechia castaneiceps*, Baja California Sur, mangrove, distribution.

In Baja California Sur (hereafter BCS) the Mangrove Warbler (*Dendroica petechia castaneiceps*; nomenclature follows Browning 1994) is distributed in suitable mangrove (family Rhizophoraceae and Avicenniaceae [Roberts 1989]) habitat from Cabo San Lucas (22°53'N [all coordinates are according to Topography International, Inc. 1986 and Baja Almanac Publishers, Inc., undated]) to Laguna Pond (26°45'N) on the west coast and Laguna San Lucas (26°13'N) on the east coast (Wilbur

1987, Browning 1994, Howell and Webb 1995). Since suitable mangrove stands are widely separated, especially on the east coast of BCS, initial documentation of individual locations was thought to be warranted. During spring and fall 1996, and spring 1997 and 1998, we conducted systematic surveys of potentially suitable habitat, including all accessible mangrove sites, between Laguna San Lucas and the southern end of Bahía Concepción (26°32'N; Fig. 1). Potential warbler sites were

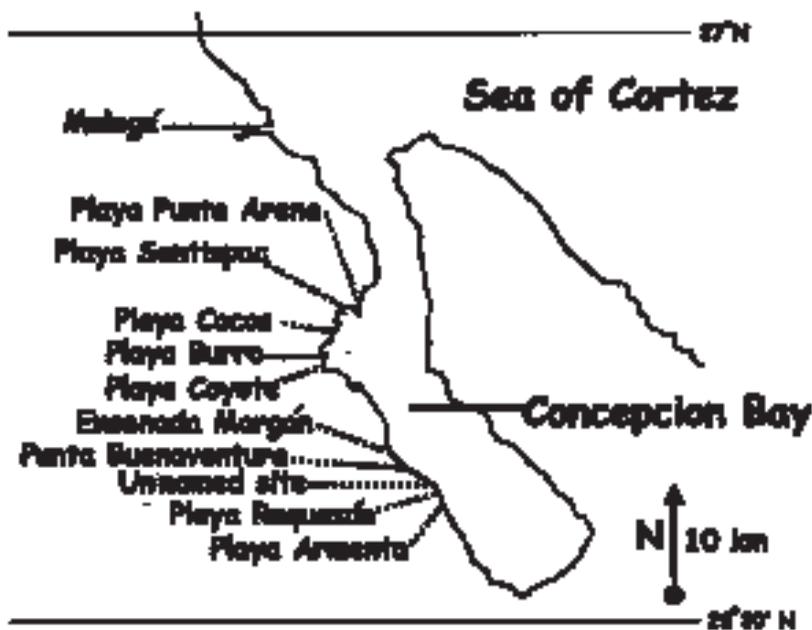


Fig. 1. Principal study area in the region of Concepción Bay, Baja California Sur, Mexico. Playa San Lucas is approximately 44 km north of Mulegé and does not appear on this map. Place names follow those from Baja Almanac Publishers, Inc. (undated).

¹Division of Forestry, PO Box 6125, West Virginia University, Morgantown, WV 26506-6125.

²Oasis Rio Baja, Mulegé, Baja California Sur, Mexico.

³1313 Dogwood Avenue, Morgantown, WV 26505.

TABLE 1. Distribution of Mangrove Warblers on the east coast of central Baja California Sur, Mexico. Parenthetical numbers refer to number of visits made over the study period.

Location name	Latitude ^a	Location ^b	Years checked	Status ^c
Playa San Lucas (3)	27°13'N	North 179	1998	2M, 1F, 1IM
Boca el Majón (1)	27°02'N	South 155	1998	Sparse mangroves
Mulegé (>15)	26°53'N	South 135	1996–98	4M, 3F
Playa Punta Arena (3)	26°47'N	South 118	1997–98	No mangroves
Playa Santispac (6)	26°46'N	North 114	1997–98	1M, >2F
Playa Cocos (4)	26°44'N	North 111	1997–98	3M, 2F
Playa Burro (2)	26°44'N	North 109	1997–98	No mangroves
Playa Coyote (2)	26°43'N	North 108	1997–98	No mangroves
Ensenada Morgán (4)	26°39'N	North 95	1997–98	5M, 1F, 1IM
Playa Buenaventura (2)	26°38'N	South 95	1998	No mangroves
Unnamed beach (4)	26°38'N	South 94	1998	2M, 1F [?]
Playa Requesón (5)	26°37'N	North 93	1997–98	2M, 1F
Playa Armenta (4)	26°36'N	North 90	1998	1M, 1F

^aLatitudes are approximate and based on Baja Almanac Publishers, Inc. (undated) and Topography International, Inc. (1986).

^bLocation of site in relation to nearest Mexico Highway 1 kilometer marker with the zero point at Loreto, Baja California Sur.

^cBased on maximum number of responding adult males (M), females (F), and immature males (IM) at any single trip to the site. Areas with dense underbrush, such as acacia thorn scrub, were also surveyed.

surveyed by quietly moving through the habitat while playing a generic recording of Yellow Warbler (*Dendroica petechia*) song (Thayer's Birding Software 1997). Positive response to the played tape was recorded if either check notes song or full visual cues were detected. All surveys were conducted between 0700 and 1000 h or 1600 and 1730 h.

We surveyed 13 sites, 8 of which contained territorial male warblers (Table 1). Males aggressively responded to the tape by approaching the speaker while giving both territorial song and check notes. Females responded, usually in the accompaniment of a male, by approaching the speaker while giving check notes. Both sexes gave wing-flutter displays. Four of 5 non-mangrove sites were checked because they contained dense patches of acacia (*Acacia* sp., family Mimosoideae) and/or mesquite (*Prosopis* sp., family Mimosoideae), which superficially approximated the structural density of mangroves, and because they were within the geographic limits of our study. The 5th site, Boca el Majón, had a few widely scattered mangroves, but apparently these were of insufficient density for warbler use.

The maximum number of male Mangrove Warblers detected at a single time was 5 at Ensenada Morgán and 4 at the estuary at Mulegé (although the latter received more sampling effort). Suitable warbler habitats are widely separated (e.g., 44 km from Playa San Lucas to Mulegé) because these birds have stenotopic requirements, are presumed to be nonmigratory, and at any 1 site territorial male populations are low. Therefore, concern for

their long-term viability seems warranted, and detailed studies of the reproductive biology of banded individuals are strongly encouraged. Moreover, mangrove habitats themselves are being fragmented at an alarming rate (Massey and Palacios 1994), subjecting these systems to concomitant dilemmas such as species elimination by stochastic processes, reduction of dispersal, genetic problems associated with small populations, and reduction of habitat core area (Meffe and Carroll 1994).

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BOOK REVIEW

A Color Guidebook to Common Rocky Mountain Lichens. Larry L. St. Clair. M.L. Bean Life Science Museum, Brigham Young University, Provo, Utah 84602. 1999. \$19.95 (\$2.50 shipping and handling for 1st book; \$1.00 for each additional book), softcover. ISBN 0-8425-2454-1.

A Color Guidebook to Common Rocky Mountain Lichens includes a wide variety of species, from small microlichens of granite boulders to large, showy genera that hang from trees. Most lichen books either do not include color photos or cover only the larger macrolichens, simply omitting the small crustose, but often showy, saxicolous species. With this guidebook, amateur enthusiasts can now picture key their collections or simply gain familiarity with lichens from a variety of substrates and Rocky Mountain habitats. This is the first of its kind for North America. However, similar to wild-flower books that encompass large geographic areas, this text does not contain all the species one might encounter in the field. Technical lichen floras will need to be consulted for more detailed identification. The photographs are those of Steven and the late Sylvia Sharnoff, who deserve much of the credit for making this book a winner. I would recommend that all biologists and outdoor enthusiasts who live in or visit the West obtain a copy. I believe it will introduce more students and amateurs to lichens than any other book published to date by a North American lichenologist. Considering the cost of reproducing color photos and the wide geographic coverage of this book, it is a very good value.

Given the general nature of the guidebook, it is perhaps inconsistent to not include any common names for these organisms. This would add appeal for the novice in particular.

Identification keys are straightforward and well written, but they lack important details and omit mention of similar species that could be encountered within the Rocky Mountains. Some of the common showy species are not included. For example, the bright sulfur green crustose lichen, *Acarospora chlorophana*, which covers canyon walls throughout the Rocky Mountains, is not included in the book. In addition, there is no index to search for species that might be listed under another name. Serious lichen students will need to obtain additional technical lichen floras to satisfy their desire to name all the lichens they encounter.

A Color Guidebook to Common Rocky Mountain Lichens is well organized and is similar in format to the recently published *Macrolichens of the Pacific Northwest* (McCune and Geiser 1997, Oregon State University Press). In comparison, St. Clair's guidebook contains equally good information on the usefulness of lichens as indicators of air quality, but much less on habitat, ecology, and taxonomy. Notes on similar species and morphological characteristics used to distinguish among them would have improved the usefulness of this book. In addition, southern Rocky Mountain species are better represented than are those from the northern Rocky Mountains. The geographic range of a species is discussed briefly under the category "substrate/habitat" though the descriptions are very general. Although in paperback format, this book is well bound, and its 6 × 9-inch size easily accommodates for use in the field.

Roger Rosentreter
Botanist
Bureau of Land Management
1387 S. Vinnell Way
Boise, Idaho 83709