Tiger beetles of the genus *Cicindela* are predatory insects that prefer open, sparsely vegetated habitats. Adults are active, visual hunters that use their large mandibles to capture and eat small arthropods. Larvae are sedentary predators that live in permanent burrows in the ground. They also use large mandibles to capture small arthropods that pass near the mouth of their burrows. There is considerable interest in tiger beetle conservation. Two species (*Cicindela d. dorsalis* Say, *C. puritana* G. Horn) are listed as threatened by the U.S. Fish and Wildlife Service (USFWS). Two species (*Cicindela d. dorsalis* Say, *C. puritana* G. Horn) are listed as threatened by the USFWS. Nearly all of the population is found in the primary habitat, a 300-m-wide × 2.7-km-long area in the southern part of the dune field. Small numbers of adults and larvae have been found at the far north end of the dune field.

Mark-recapture studies indicated that most adults moved only short distances (<300 m), but a few moved 1000 m. This beetle has a 2-year, modified spring–fall life cycle. Adults are most abundant from April through early June, but some adults from the following year’s adult cohort emerge and can be found from late August to early October. Adults are active on warm or sunny days, but they dig burrows which they use at night or during unfavorable weather. We observed little evidence of parasitism or predation of larvae or adults, but these limiting factors were not fully studied.

Surveys of dominant plant species, arthropod (potential tiger beetle prey) abundance, and OHV activity indicated that these vary throughout the dune field and may explain, in part, the distribution of *C. l. albissima*. The primary habitat is a transition area between the highly dynamic south end of the dune field and the more stabilized north end. *Psoralidium lanceolatum* Rybd., *Sophora stenophylla* Gray, and *Stipa hymenoides* R.&S. are the dominant plants in the interdunal swales of the primary habitat, but other species are dominant in other parts of the dune field. Numbers of arthropod individuals and taxa are greatest in the primary habitat. Off-highway vehicle activity was greatest at the south end of the dune field and lowest at the far north end. Run-over trials and observational data revealed that adult beetles are killed by OHVs, but more important impacts may be damage to vegetation, reduction of arthropod prey of *C. l. albissima*, and disturbance and increased desiccation of the larval microhabitat. We anticipate that the conservation agreement will provide long-term protection for this species at CPSD.

**Key words:** *Cicindela limbata albissima*, Coral Pink Sand Dunes, tiger beetle, conservation, off-highway vehicle impacts, population dynamics.

Tiger beetles of the genus *Cicindela* are predatory insects that prefer open, sparsely vegetated habitats. Adults are active, visual hunters that use their large mandibles to capture and eat small arthropods. Larvae are sedentary predators that live in permanent burrows in the ground. They also use large mandibles to capture small arthropods that pass near the mouth of their burrows. There is considerable interest in tiger beetle conservation. Two species (*Cicindela d. dorsalis* Say, *C. puritana* G. Horn) are listed as threatened by the U.S. Fish and Wildlife Service (USFWS). Several others are under consideration for listing. Among the 10+ *Cicindela* species occurring in sand dune habitats in the western United States are several endemic species or subspecies, including *Cicindela arenicola* Rumpf from the Bruneau and St. Anthony dunes of Idaho, *C. theatina* Rotger from the Great Sand Dunes of Colorado, *C. scutellaris yampa* Rumpf from southwestern Colorado, and *C. formosa rutilovirescens* Rumpf from the Mescalero dunes of southeastern New Mexico. The only published study of these species is that of Bauer (1991) on *C. arenicola*.

*Cicindela limbata albissima* was described by Rumpf (1961) from specimens collected at the Coral Pink Sand Dunes in southwestern Utah. He distinguished it from other subspecies of *C. limbata* by the greatly reduced elytral pigmentation (the elytra are white except for a narrow medial line) and its disjunct geographic range in southern Utah, a distance of over 600
km from other populations of the species. The other subspecies of *C. limbata* have separate, more northern geographic ranges, are east of the Continental Divide, and have more pigmentation on the lateral portions of their elytra. *Cicindela limbata limbata* occurs in the western Great Plains, *C. limbata nympha* occurs from North Dakota northwest into southern Canada, and *C. l. hyperborea* is found in northern Canada. Johnson (1989) recently described *C. l. labradorensis* from Goose Bay, Labrador, although Larson (1986) suggested this form was *C. l. hyperborea*. Rumpp (1961) believed that *C. l. albissima* was more closely related to *C. l. nympha* that, he said, followed a southward migration route during the Pleistocene when climatic conditions were more favorable. He suggested that the lack of elytral pigmentation may be a thermoregulatory adaptation to the warmer temperatures where *C. l. albissima* occurs. Acorn (1992) provided support of the relationship between coloration and thermoregulation in *C. limbata* and other dune *Cicindela*. He also reported on the ecology of *C. limbata nympha* and other sand dune *Cicindela* in the southern Canadian plains (Acorn 1991). A recently completed analysis of the mtDNA in *C. limbata* and its relatives found that *C. l. albissima* is genetically distinct from the other subspecies and that it should be given full species status (Morgan et al. 2000).

*Cicindela l. albissima* was first listed as a category II species in 1984 (Federal Register 49:21664). In 1994 the USFWS was petitioned by the Southern Utah Wilderness Alliance to list *C. l. albissima* as endangered and to designate critical habitat. The service’s response (Federal Register 59[178]:47293–47294) indicated that the petition presented substantial information in support of listing, but progress toward its listing was interrupted by the listing moratorium in 1996. Currently, *C. l. albissima* is a candidate species. In 1997 a conservation agreement was signed by the USFWS, Bureau of Land Management (BLM), Utah State Parks and Recreation, and Kane County. The provisions of this agreement include the establishment of a 350-acre conservation area in the southern part of the dune field that is the primary beetle habitat (Fig. 1B). The western portion of this area is signed off to prevent vehicle access, while the eastern portion serves as a travel corridor for vehicles to move between the northern and southern portions of the dunes. An additional 370-acre conservation area at the northern part of the sand dunes has also been proposed. In this paper we present the results of our 1992–1999 studies of this rare insect, including information on distribution and abundance, seasonality, habitat, and possible OHV impacts.

**METHODS**

**Geographic Distribution**

Because tiger beetles are a popular, well-collected group of insects, our initial work in determining the distribution of *C. l. albissima* involved a compilation of collection records from various sources. We examined tiger beetle specimens in 23 museum and university holdings or were likely to have many Utah records. Among the most important collections were those at Brigham Young University, California Academy of Sciences, Utah State University, U.S. National Museum, American Museum of Natural History, and Yale Peabody Museum. We also obtained label information from several individuals who had large cicindelid collections. We conducted field surveys of all major sand dunes and many other sandy areas in Utah and adjacent states where potential habitat for this species might occur (Fig. 2). All of these sites were visited 1 or 2 times in May 1993, 1994, and 1995. At each site we spent several hours to several days searching for tiger beetles in areas of suitable habitat. The searching method involved walking through the open areas of potential habitat and looking on the ground 5–10 m ahead for the adults to run or fly up as they were approached. This visual search method is commonly used to survey for tiger beetles (Knisley and Schultz 1997) and is effective when done during a species’ peak activity period (warm, sunny days from mid-April to early June for *C. l. albissima*). At most of these sand dune sites we also surveyed dune arthropods using pitfall traps. We set out 20–32 sixteen-oz cup traps (Carolina Biological Supply Co., Burlington, NC) with approximately 100 mL of ethylene glycol (no longer recommended for this use) for 5- to 7-day periods in May 1993, 1994, and 1995.

**Studies on Distribution, Abundance, and Biology**

Much of our initial work at Coral Pink Sand Dunes (hereafter CPSD) in May 1992 involved...
determining the distribution of adults and larvae within the dune field. We spent 4–6 hours per day for several days walking over all parts of the dune field and making preliminary counts of adults and larvae and recording their distribution relative to physical landmarks, Global Positioning System (GPS) readings, and wooden stakes which we placed in interdunal swales (see below). We separated the CPSD dune field into 7 areas, AAA at the north end to E at the south end (Fig. 1A). Our preliminary surveys indicated that adults and larvae were largely concentrated in an area ~300 m wide × 2.7 km long in the southern portion of the dune field (area C). Most of our studies were within this area, which we call the primary habitat (Fig. 1B).

Relative population size of adult *C. l. albissima* at the Coral Pink Sand Dunes was determined each year in May from 1992 to 1998 using index counts and mark-recapture. In this paper we include only the results of the index counts, which were conducted throughout the entire primary habitat during 2- to 3-day periods each year in mid-May from 0930 to 1230 hours on sunny, mild (>20°C) days. During this time of day, most beetles were active and primarily concentrated along the edges of the interdunal swales and on adjacent lower slopes. In making the counts, 2 individuals positioned themselves 20–25 m apart and walked back and forth across the width of the dune field, progressing from north to south and counting all observed beetles. We kept
separate counts for each swale-slope area. We also counted adults of another tiger beetle, Cicindela tranquebarica, which co-occurred with C. l. albissima in some swales.

The distribution and abundance of tiger beetle larvae can be determined by searching the ground and counting numbers of burrows during times when larvae are active (Knisley 1987, Knisley and Schultz 1997). The 3 larval instars can be distinguished by differences in burrow diameter, which is fixed within an instar. Accurate estimates of larval numbers are difficult to obtain for sand dune species like C. l. albissima because their larval burrows may be plugged and thus unrecognizable during the day when the sand surface becomes warm and dry, and at other times when conditions are unfavorable (Knisley 1987). We surveyed larval burrows from 0700 to 1100 hours when a high percentage of larvae are active. Preliminary surveys in 1992 indicated that larvae were most abundant in open or sparsely vegetated edges of interdunal swales and low slopes.

To establish fixed survey points, we placed wooden stakes within these swales of the primary habitat near the centers of patches where larvae were aggregated and counted all larval burrows within a 10-m-diameter circle drawn in the sand around each stake. GPS readings were taken at each stake location so lost or vandalized stakes could be replaced. New stakes were added as we discovered new concentrations of larvae. Additionally, in 1996, 1997, and 1998 we also estimated total numbers of larval burrows in each swale (including those outside the fixed plots) by walking back and forth through the swale areas and counting all observed burrows. This number was added to plot counts to obtain a total count of larval burrows in each swale. We also compiled April–October rainfall records for Kanab, the nearest weather station to CPSD, because we hypothesized that rainfall might be an important factor affecting the population dynamics of C. l. albissima.

Movement of adults was determined by marking and releasing 200–400 adults each year during a 2–3 day period in mid-May. Beetles were marked by removing a 1-mm section from the tip of one of their elytra. By cutting at different angles, we had unique marks for many of the swale areas. Beetles were recaptured 3–10 days after marking, and distances between mark and recapture locations were measured. Seasonal activity, life cycle, and other natural history information of C. l. albissima were determined from our adult and larval surveys and field observations during our May and September visits to the Coral Pink Sand Dunes between 1992 and 1998. Feeding habits of adult C. l. albissima were determined by capturing individuals that were feeding and then examining their prey.

Habitat Characteristics and OHV Impact Studies

We conducted surveys of dominant plant species and arthropod abundance in different areas of CPSD to determine if these might aid in explaining the distribution of C. l. albissima within the dune field and to characterize its habitat. Within each of the 7 areas of the dune field (Fig. 1A), we estimated the percentage cover of each plant species within 10-m-diameter circular plots located at 25-m intervals along a transect line running across the length
of each interdunal swale. A wire hoop subdivided into 4 quarters was placed on the ground at each sample point and the percentage cover of each species within each quarter estimated. The sum of the 4 quarters gave the total percent cover for a species. In the primary habitat we estimated the percent cover of plant species in most interdunal swales.

Surveys for swale arthropods (the prey resource base of adults and especially larvae of *C. l. albissima*) were conducted by placing 6 pitfall traps (see above) in 2 different swales in each of the 7 areas of the dune field for 6-day periods (9–15 July 1993, 5–11 September 1993, 21–27 May 1994, and 18–24 May 1996). Three traps were placed around the perimeter of the swale and 3 around the interior near the swale bottom. We transferred arthropods from each trap to separate plastic bags and later identified them to species (where possible). Mean numbers of individuals and taxa were determined from 12 traps (6 in each swale). Another pitfall trap survey from 16–22 May 1998 was designed to determine if there was a relationship between OHV activity and arthropod abundance. In this experiment we set 4 sets of 6 traps in each of 4 different areas of the dune field (AA, B, C, E). Two sets in each area were placed in 2 swales that were in areas of higher OHV activity (determined by higher numbers of OHVs and OHV roads), and 2 sets were placed nearby in 2 swales with lower OHV activity. A paired t test was used to compare means for low- versus high-use swales in each area.

Off-highway vehicle activity at CPSD was assessed on Memorial Day weekends in 1997 and 1998 and on Labor Day weekend in 1998. These holiday weekends are among the highest use times for OHV activity at CPSD. We counted the number of OHVs that crossed 8 transect lines (2 in area C and 1 in each of the other dune areas; Fig. 1A) across the width of the dune field during 4 one-hour periods, 2 on Saturday and 2 on Sunday, of each weekend. We also measured the width of all OHV paths or roads that crossed each of these 8 transect lines and summed them to obtain a total road width for each area. We determined the amount of motorized play, primarily the riding back and forth over the dunes, for the 8 areas of the dune field by obtaining the mean minutes per hour that all OHVs (vehicle minutes) were engaged in this activity.

Direct effects of OHVs on tiger beetles were determined from experimental run-over trials and by examination of individual beetles collected during mark-recapture studies. Run-over trials were performed at CPSD in May 1994 on 3 different substrates (dry sand, wet sand, mixed sand and stones). In preparation for the trials, we tied 1 end of a 50-cm length of thread around the thorax of a beetle and tied a piece of plastic surveyor flagging to the other end. The beetles were held in place on the sand surface by covering the middle portion of the string with a handful of sand. The groups of beetles were run over by 10 passes of a 1994 Honda 4-wheeled vehicle. They were examined after 1, 5, and 10 passes of the vehicle. Another indication of probable direct effects of OHVs was noted during our 1994 mark-recapture studies when we found adult beetles with injuries similar to those in the run-over trials. In 1994 and subsequent years, we examined all beetles captured during mark-recapture studies and recorded the numbers that were injured.

**Results**

**Distribution and Abundance**

Only 1 of 65 locality records researched for the distribution of *C. l. albissima* was from a site other than CPSD. That record was of a specimen collected by H.P. Boyd (personal communication 1994) from a sandy floodplain of the Virgin River south of Mt. Carmel Junction (~15 km north of CPSD). We did not find *C. l. albissima* at any of the 19 sites that we surveyed (Fig. 2), although other Cicindela sp. were found at some sites (Table 1). Five sites (2, 4A, 4B, 4C, 5) seemed likely prospects for *C. l. albissima* because of their close proximity to CPSD and the presence of *Asclepias welchii*, a rare milkweed that may have similar habitat requirements because it occurs only at these sites and at CPSD.

The index counts in the primary habitat, where nearly all adults were found, ranged from 331 in 1997 to 895 in 1993 (Table 2). Most of these adults (60–79%) were in swale rows and low slopes in the northern part of the primary habitat, swales 4 through GH. Highest mean adult numbers (based on annual index counts from 1993 to 1999) were in swales KJ (97), 2–3 (85), 1 (73), and H (60; Fig. 1B). Numbers of adults in adjacent areas to the north and south
of the high-density area varied among years, but highest total percentages were in 1998 (36%) and 1996 (40%; Table 2). Adults were always more abundant in the adjacent area to the south, which extended for about 1300 m south of GH and included many swales having at least some adults (Fig. 1B). The adjacent area of primary habitat to the north extended only about 500 m beyond swale 4 and included only a few swales with adults. The only adults we found beyond the primary habitat were small numbers (<20 per year) of scattered individuals in 1994, 1996, and 1998 south of the primary habitat (areas D and E) or in the far northern end of the dune field (areas AAA and AA).

Total rainfall from April through October (the activity period for adults and larvae of C. l. albissima) varied greatly from 1991 to 1998. Totals for the last 3 years were higher than all other years. We found a significant positive correlation (Spearman rank correlation, $r = 0.036$, $P = 0.035$) between the total April–October rainfall in one year and adult numbers the following year (Fig. 3). For example, very low rainfall totals in 1993, 1994, and 1996 were associated with very low adult numbers the following years.

Checks of recaptured beetles during 6 years (1993–1998) of mark-recapture studies indicated that C. l. albissima adults moved very little throughout the dune field at CPSD. Of 275 adults recaptured, 205 did not move beyond the swale row (<200 m) in which they were marked, 34 moved 200–300 m, 16 moved 300–500 m, 14 moved 500–700 m, and 6 moved 700–1000 m.

Our initial observations and subsequent surveys indicated that larvae were most common in sparsely vegetated outer edges (away from the high-density area) and were most abundant in the adjacent areas to the south. Adult distribution patterns were consistent with larval distribution patterns, as adults appeared to be attracted to areas with high larval densities.

### Table 1. Great Basin sand dunes sites surveyed for Cicindela limbata albissima.

<table>
<thead>
<tr>
<th>Site</th>
<th>Location</th>
<th>Elevation (m)</th>
<th>Species found</th>
</tr>
</thead>
<tbody>
<tr>
<td>1–UT, Coral Pink</td>
<td>15 km W Kanab</td>
<td>1830</td>
<td>C. l. albissima</td>
</tr>
<tr>
<td>2–UT, Sand Hills</td>
<td>14 km NNE Kanab</td>
<td>1830</td>
<td>C. tranquebarica</td>
</tr>
<tr>
<td>3–UT, Sand Mountain</td>
<td>10 km SE Washington</td>
<td>1250</td>
<td>none</td>
</tr>
<tr>
<td>4A–AZ, Sand Cove</td>
<td>45 km E Kanab</td>
<td>1615</td>
<td>none</td>
</tr>
<tr>
<td>4B–UT, Coyote Buttes</td>
<td>45 km E Kanab</td>
<td>1740</td>
<td>none</td>
</tr>
<tr>
<td>4C–UT, AZ, state line</td>
<td>45 km E Kanab</td>
<td>1585</td>
<td>none</td>
</tr>
<tr>
<td>5–AZ, Thousand Pockets</td>
<td>12 km W Page</td>
<td>1540</td>
<td>none</td>
</tr>
<tr>
<td>6–UT, Holden Dunes</td>
<td>10 km WNW Holden</td>
<td>1430</td>
<td>C. tranquebarica</td>
</tr>
<tr>
<td>7–UT, Oak City</td>
<td>5 km W Oak City</td>
<td>1435</td>
<td>C. lepida</td>
</tr>
<tr>
<td>8–UT, Little Sahara</td>
<td>12 km W Jerico Junction</td>
<td>1640</td>
<td>C. lepida</td>
</tr>
<tr>
<td>9–UT, San Raphael Desert</td>
<td>Rt. 24, 12 km S I-70</td>
<td>1341</td>
<td>none</td>
</tr>
<tr>
<td>10–UT, Hanksville</td>
<td>22 km N Hanksville</td>
<td>1585</td>
<td>none</td>
</tr>
<tr>
<td>11–UT, Snow Canyon SP</td>
<td>12 km N Santa Clara</td>
<td>1310</td>
<td>none</td>
</tr>
<tr>
<td>12–UT, Green River</td>
<td>Green River at Utah Co.</td>
<td>1700</td>
<td>C. formosa formosa</td>
</tr>
<tr>
<td></td>
<td>state line, Brown Park</td>
<td></td>
<td>C. tranquebarica</td>
</tr>
<tr>
<td>13–CO, Maybell Dunes</td>
<td>2 km E Maybell</td>
<td>1835</td>
<td>C. formosa formosa</td>
</tr>
<tr>
<td>14–CO, Great Sand Dunes</td>
<td>Great Sand Dunes National Monument</td>
<td>2130</td>
<td>C. theatina</td>
</tr>
<tr>
<td>15–WY, Boars Tusk Dunes</td>
<td>43 km N Rock Springs</td>
<td>1890</td>
<td>C. limbata limbata</td>
</tr>
<tr>
<td>16–ID, St. Anthony Dunes</td>
<td>11 km N St. Anthony</td>
<td>1524</td>
<td>C. arenicola</td>
</tr>
<tr>
<td>17–ID, Bruneau Dunes</td>
<td>Bruneau Dunes State Park</td>
<td>980</td>
<td>C. arenicola</td>
</tr>
</tbody>
</table>

### Table 2. Index counts of adult Cicindela l. albissima in the primary habitat at Coral Pink Sand Dunes, 1992–1998.

<table>
<thead>
<tr>
<th></th>
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<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Total for primary habitat</td>
<td>651</td>
<td>895</td>
<td>511</td>
<td>513</td>
<td>843</td>
<td>331</td>
<td>758</td>
</tr>
<tr>
<td>Swales north of swale 4</td>
<td>49</td>
<td>46</td>
<td>25</td>
<td>38</td>
<td>107</td>
<td>23</td>
<td>50</td>
</tr>
<tr>
<td>Swales south of GH</td>
<td>107</td>
<td>139</td>
<td>91</td>
<td>116</td>
<td>234</td>
<td>48</td>
<td>220</td>
</tr>
<tr>
<td>% of total north of 4 and south of GH</td>
<td>24</td>
<td>21</td>
<td>23</td>
<td>30</td>
<td>40</td>
<td>20</td>
<td>36</td>
</tr>
</tbody>
</table>
from the slipface) of the interdunal swales and in nonvegetated adjacent low dune slopes. Some larvae were also found in the more densely vegetated interior of some swales, and small numbers were occasionally seen on mid- and upper slopes, especially after rains. We also noticed that on days after a substantial rainfall many larvae appeared at the base of some slipfaces. (Tiger beetle larvae frequently clear out their burrows after rains.) Total numbers of larval burrows counted (permanent plots and other areas within the swales) in the primary habitat during May and September varied more than threefold over the years. May counts ranged from 3567 in 1996 to 908 in 1998, while September counts ranged from 2830 in 1996 to 1880 in 1993 (Fig. 3). As with adults, highest numbers of larvae were in the area from swale 4 south to swale row GH (Table 3). Most swale rows in this area had means near or >250 larvae in both May and September survey dates. Other swales with similar high mean larval numbers were QR, UVW, and OP. However, larval numbers in QR and UVW declined to <100 in 1996, 1997, and 1998, while numbers in OP increased about twofold during this same period. Mean number of burrows for the 5 swales north of swale 4 (5 to 9) was <100 in both May and September counts. Small numbers of larvae were also found ~4 km from the primary habitat in 12 swales in the far northern end of the dune field (areas AAA, AA). Prior to 1996 we found only a few scattered burrows in 1 or 2 swales in this area, but in 1996 we counted a total of 74 larvae in 5 swales, in 1997 we found 67 in 5 swales, and in 1998 we found 352 in 8 swales.

Seasonal Activity, Life Cycle and Behavior

We first saw adults of C. l. albissima on the dunes in late March or early April after they emerged from overwintering (Fig. 4). Emergence continues through May, with peak numbers occurring from early to mid-May. Numbers begin to decline in late May, and by late June most adults have died off. Few adults are found from July to mid-August. A small proportion of the previous year’s larvae completes its development, pupates, and emerges in late August. These adults are active until late September or early October, then dig overwintering burrows. Our estimates of adult numbers during this period were ~300 in 1991, ~100 in 1993 and 1994, and 160 in 1998. These fall adults will reemerge in spring along with the larger proportion of the cohort, which develops more slowly and does not emerge in the late summer.

Mating and ovipositing were observed soon after spring adults emerged and continued throughout the adult activity period. First-instar larvae were first seen in late May, and by July most of the new larval cohort had progressed to the second instar (Fig. 4). Many second instars completed their development by October before overwintering as third instars, but slower developing individuals overwintered as second instars. Third instars had
the longest developmental period, and most of the larval cohort continued in this stage through most of the 2nd year before pupating and emerging as adults during the 2nd fall or the following spring. The rate of larval development is greatly influenced by climate, the amount of food obtained, and perhaps other factors that may cause the larvae in a cohort to develop asynchronously. In Manitoba the life cycle of *C. l. nympha* was 3 years (Criddle 1910), probably because lower temperatures in the spring and fall reduce seasonal activity of larvae.

Observations on warm, sunny days in May indicated that adults begin to emerge from their overnight burrows and appear in swales and low slopes at about 0830–0930 hours (Fig. 5). Numbers increase rapidly, with peak abundance from about 1000 to 1230 hours, and then decline from about 1300 to 1600 hours as many adults dig burrows in the dune slopes to avoid high surface temperatures. Some of these adults reemerge from their burrows about 1600 hours and remain active until 1700–1900 hours, when they again dig burrows on dune slopes or interdunal swales to spend the night. On cloudy or windy days when surface temperatures remain <35°C, adults may be active most of the day. For several years in May we made observations on adults digging burrows. Adult beetles used their mandibles and legs to dig the burrow and push out the sand with an alternating back-and-forth, sweeping movement of the meso- and metathoracic legs. These burrows were 4–9 cm deep, slightly angled, and 7–16 cm long. Fifty-two of 111 observations were of females, 37 were of males, and 22 were of mated pairs. Adult males of *C. l. albissima*, like those of many other species, exhibit contact guarding (Knisley and Schultz 1997) and use the mandibles to grasp the female as she digs the burrow. Sixty-six percent of these burrows were within interdunal swales and low slopes, 24% in the mid-slope area, and 10% at or near the dune crest. The 85 prey items observed being eaten by adults included 27 ants, 21 already dead insects (mostly orthopterans and large ants), 11 flies, 9 homopterans, 7 beetles, and 10 unidentified insects.

Another tiger beetle, *Cicindela tranquebarica*, also common at CPSD, co-occurred (both adults and larvae) with *C. l. albissima* in some interdunal swales of the primary habitat where there was a layer of clay in the sand and/or presence of very moist soil (Romey and Knisley in preparation). Adults and larvae of *C. tranquebarica* were also common in similar types of swales outside the primary habitat (especially E, AA, A) where *C. l. albissima* was absent.

We observed little evidence of natural enemies attacking *C. l. albissima*. On 2 June 1994 we found an individual of the small, antlike parasitoid wasp, *Methocha* sp., entering a second-instar larval burrow. After the wasp exited the burrow, we dug out the larva and found it paralyzed and with an egg on it. In May 1995 we found 2 third-instar *C. l. albissima* larvae with larvae of the bee fly (possibly *Anthrax* sp.). Several days before, we observed an adult fly in the same area. None of the other 600+ larvae that we dug out between 1991 and 1998 were parasitized. Both parasitoids are specific to tiger beetle larvae, but their effects on tiger beetle populations are difficult to determine unless individual burrows are marked and
monitored. We frequently observed asilid flies on the dunes but did not see any instances of this known predator of adult tiger beetles attacking C. l. albissima.

Habitat Characteristics

Dominant plant species within the swales of the primary habitat (area C) were different from those in other dune areas (AAA, AA, A, B, D, E). *Psoralidium lanceolatum* Rydb. had the highest mean coverage percent in all but 1 of the swale rows of the primary habitat, while *Sophora stenophylla* Gray, *Stipa hymenoides* R. & S., and *Reverchonia arenaria* Gray were also abundant and widespread within this area (Table 4). These species were absent or much less common within swales of other dune areas. *Wyethia scabra* Hook. was absent or rare in primary habitat swales, but it was a dominant plant species in areas AAA, AA, A, B, and E, along with *Chrysothamnus* sp., *Eriogonum* spp., and several other species (*Gilia congesta* Hook, *Redfieldia flexosa*) included in the “other” category of Table 4. The northern half of the dune field (areas AAA to B) had a greater diversity of plant species and was dominated by *Wyethia scabra*, which also was the dominant plant species at the south end of the dune field (area E). *Juncus arcticus* Willd., abundant in many of the wetter swales in the northern and southern parts of the dune field, was nearly absent from swales of the primary habitat. *Dicoria brandegei* was observed to be extremely abundant and widespread in primary habitat swales during September, but it was absent or present only as seedlings in May when vegetation surveys were conducted. Total percent vegetation cover was higher in all swales of the primary habitat (means of 23–57%) than in swales in other areas (means of 12–17%; Table 4).

Mean numbers of arthropod taxa and individuals per area (12 traps in 2 swales) from the 1993–1996 pitfall surveys were significantly different (Kruskal-Wallis ANOVA, *P* < 0.05) among the 7 areas surveyed. Highest means were in areas C and AAA (Table 5). Mean numbers of both taxa and individuals collected in the 1998 surveys were significantly higher in the low OHV-use swales than in the high-use swales (paired *t* test, *P* < 0.05). Importantly, the highest numbers of taxa and individuals were in the low-use swales of area C, and the greatest difference in numbers of individuals (1027 and 422) and taxa (51 and 39) between low- and high-use swales was also in area C. This great difference in area C probably reflects the greater difference in amount of OHV use in high- and low-use swales of this area.

**OHV Activity and Impacts**

Mean numbers of OHVs, mean play time, and total width of OHV roads were greatest in

<table>
<thead>
<tr>
<th>Plant species</th>
<th>Other sp.</th>
<th>Total % cover</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>C (PRIMARY HABITAT OF C. L. ALBISSIMA)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5–9</td>
<td>10</td>
<td>60</td>
</tr>
<tr>
<td>4</td>
<td>13</td>
<td>75</td>
</tr>
<tr>
<td>1</td>
<td>68</td>
<td>21</td>
</tr>
<tr>
<td>2.3</td>
<td>22</td>
<td>71</td>
</tr>
<tr>
<td>IJK</td>
<td>26</td>
<td>65</td>
</tr>
<tr>
<td>GH</td>
<td>23</td>
<td>64</td>
</tr>
<tr>
<td>L–P</td>
<td>32</td>
<td>21</td>
</tr>
<tr>
<td>QR</td>
<td>10</td>
<td>58</td>
</tr>
<tr>
<td>ST</td>
<td>18</td>
<td>70</td>
</tr>
<tr>
<td>U–Y</td>
<td>16</td>
<td>62</td>
</tr>
<tr>
<td><strong>OTHER AREAS</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>AAA</td>
<td>2</td>
<td>6</td>
</tr>
<tr>
<td>AA</td>
<td></td>
<td></td>
</tr>
<tr>
<td>A</td>
<td>12</td>
<td>4</td>
</tr>
<tr>
<td>B</td>
<td>12</td>
<td>4</td>
</tr>
<tr>
<td>E</td>
<td>8</td>
<td>12</td>
</tr>
</tbody>
</table>
area E and lowest at the far northern end (area AAA; Table 6). Motorized vehicle play time was over 4 times higher in area E than in any other dune area. OHV activity parameters in the other dune areas were quite variable but indicated intermediate level of OHV activity between the 2 ends of the dune field. Areas E and A are major points of vehicle access to the dunes.

Numbers of injured adults of *C. l. albissima* found during our mark-recapture studies varied greatly among years. Numbers injured and total number captured and examined during Memorial Day periods were as follows: 1993, 14 of 179 injured in 1–2 days after Memorial Day; 1994, 0 of 363 injured before Memorial Day weekend, 6 of 125 after; 1996, 2 of 231 before and 41 of 287 after; 1997, 2 of 256 before and 6 of 64 after; and 1998, 1 of 168 before and 8 of 278 after. Results of run-over trials indicated that the type and/or condition of substrate and number of passes were important in the fate of beetles run over by an OHV. No beetles on dry sand were injured or killed when run over once, but a majority of those on either wet sand or gravel were injured or killed by a single vehicle pass (Table 7). Most or all beetles were killed or injured by 5 and 10 passes on all substrates.

**DISCUSSION**

**Distribution, Abundance, and Biology**

Our search of collection records and our field surveys indicate that *C. l. albissima* occurs only at CPSD. Its limited distribution in Utah and surrounding areas may be due to the absence of other high-elevation sand dunes. The Great Sand Dunes of Colorado is the only similar high-elevation site, and the closely related species *C. theatina* occurs there. *Cicindela l. albissima*, like its more northern relatives, is apparently restricted to habitats with cooler temperatures. Rumpp (1961) suggested that the distinct lack of elytra pigmentation in *C. l. albissima* may be a thermoregulatory adaptation to its presence in a more southern location than the other subspecies of this species. The single individual that was found north of CPSD may have been a dispersing individual since only one was encountered. Several searches of this area by us revealed no beetles or suitable habitat.

We believe that the index counts give an accurate representation of the year-to-year variation in numbers of adult *C. l. albissima*, but the counts clearly underestimate the actual population size at CPSD. Lincoln index values from mark-recapture studies that we conducted coincidentally with the 1993–1998 index counts (Knisley and Hill unpublished studies), other studies we have done with *Cicindela* (Knisley and Schultz 1997), and a study comparing different survey methods in 1999 (Gowan and Knisley in preparation) all suggest the actual population size may be 2–3 times higher than the index counts. The underestimate is probably the result of some beetles flying off before they are counted or occurring in patches of overlooked habitat or in burrows.

The significant year-to-year variation in *C. l. albissima* numbers is typical of many desert arthropods that are greatly affected by climatic conditions.
factors, especially rainfall (Seely 1991). The positive correlation we found between April–October rainfall amounts one year and adult numbers the following year suggests rainfall may be one of the key factors affecting population dynamics of *C. l. albissima*. Studies with other desert tiger beetle species in Arizona demonstrated that higher rainfall increases survivorship of larvae by reducing mortality from desiccation and starvation, especially of first instars (Knisley 1987, Knisley and Juliano 1988). Prey was more abundant during wet years, and this not only reduced the effects of starvation but also decreased development time and increased fecundity. We expected that these effects and the importance of soil moisture for oviposition and egg hatch should similarly result in higher larval numbers in September counts in years with high rainfall, but our data do not show this. Obviously, other factors are important in population dynamics of this species, and clear patterns of cause and effect are difficult to determine without more detailed studies. Our study does provide some evidence that larval survivorship is very low for this insect. Total adult numbers are consistently much lower than larval numbers, and larval numbers in September counts are lower than those in May. We also found survivorship was <20% for several patches of larvae that were marked as first instars in May 1996 and monitored through part of the third instar (Knisley unpublished study).

Much of what we learned about the biology of *C. l. albissima* was similar to that of other tiger beetles that have been studied. Its biology is especially similar to that of *C. l. nympha* in Canada (Acorn 1991) and *C. arenicola* from the St. Anthony Sand Dunes in Idaho (Anderson 1988, 1989, Bauer 1991). The amount of movement of marked individuals of *C. l. albissima* was, like *C. arenicola*, quite limited compared to many tiger beetle species. Anderson (1989) found that most marked adults of *C. arenicola* remained in the same general area where they were marked and only a few dispersed (in a “step-stone” manner) >500 m. The *C. l. albissima* found near Mt. Carmel Junction suggests that, at times, adults may disperse much greater distances than what we observed. The adults and larvae found at the far northern end of the dune field probably represent a colonizing event by adults that dispersed from the primary habitat. Dispersal may be greater during times of high density, as is common in many other animals. For example, we found that

### Table 6. OHV activity throughout different areas of CPSD. OHV numbers are means of two 1-hour counts each on Saturday and Sunday of Memorial Day weekends in 1997 and 1998 and Labor Day 1998. Vehicle play time is the mean number of OHVs multiplied by minutes per hour averaged for the 3 weekends (Cn is the northern part of C, Cs the southern part).

<table>
<thead>
<tr>
<th>Area of dune field</th>
<th>AAA</th>
<th>AA</th>
<th>A</th>
<th>B</th>
<th>Cn</th>
<th>Cs</th>
<th>D</th>
<th>E</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean number of OHVs per hour</td>
<td>3</td>
<td>19</td>
<td>69</td>
<td>60</td>
<td>67</td>
<td>70</td>
<td>51</td>
<td>94</td>
</tr>
<tr>
<td>Mean vehicle play (vehicle minutes per hour)</td>
<td>22</td>
<td>62</td>
<td>138</td>
<td>161</td>
<td>50</td>
<td>92</td>
<td>138</td>
<td>771</td>
</tr>
<tr>
<td>Total width of OHV roads (m)</td>
<td>75</td>
<td>125</td>
<td>188</td>
<td>181</td>
<td>122</td>
<td>108</td>
<td>226</td>
<td>230</td>
</tr>
</tbody>
</table>

### Table 7. Effects of OHV run-over trials on adults of *Cicindela l. albissima* on 31 May 1994.

<table>
<thead>
<tr>
<th>Substrate type</th>
<th>No. in trial</th>
<th>No. of passes</th>
<th>Effect on beetles</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dry</td>
<td>5</td>
<td>1</td>
<td>No effect</td>
</tr>
<tr>
<td>Wet</td>
<td>15</td>
<td>1</td>
<td>Injury</td>
</tr>
<tr>
<td>Wet</td>
<td>15</td>
<td>5</td>
<td>Injury</td>
</tr>
<tr>
<td>Wet</td>
<td>15</td>
<td>10</td>
<td>Injury</td>
</tr>
<tr>
<td>Gravel</td>
<td>5</td>
<td>1</td>
<td>Injury</td>
</tr>
<tr>
<td>Gravel</td>
<td>5</td>
<td>5</td>
<td>Injury</td>
</tr>
<tr>
<td>Gravel</td>
<td>5</td>
<td>10</td>
<td>Injury</td>
</tr>
<tr>
<td>Wet</td>
<td>15</td>
<td>1</td>
<td>Injury</td>
</tr>
<tr>
<td>Wet</td>
<td>15</td>
<td>5</td>
<td>Injury</td>
</tr>
<tr>
<td>Wet</td>
<td>15</td>
<td>10</td>
<td>Injury</td>
</tr>
<tr>
<td>Gravel</td>
<td>5</td>
<td>1</td>
<td>Injury</td>
</tr>
<tr>
<td>Gravel</td>
<td>5</td>
<td>5</td>
<td>Injury</td>
</tr>
<tr>
<td>Gravel</td>
<td>5</td>
<td>10</td>
<td>Injury</td>
</tr>
</tbody>
</table>

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highest proportions of adults in areas adjacent to the swale 4 to GH concentration area were in 1996 and 1998, 2 of the years of greatest adult abundance.

The seasonal pattern we observed for *C. l. albissima* represents a variation of the typical spring–fall life cycle common in many Cicindela sp. In this pattern most larvae complete their development in the summer, pupate, and emerge as sexually immature adults in late August and September. They dig burrows in October to overwinter and then reemerge in the spring. The very low counts of adult *C. l. albissima* in September suggest that most of the maturing larval cohort do not emerge in the fall, although they may molt into the adult stage and remain in their pupal burrows (Schultz 1998). Acorn (1991) found that numbers of adults of *C. l. nympha* in the Canadian dunes peak in June and September. This is the typical spring–fall pattern and similar to what Bauer (1991) found for *Cicindela arenicola*. The pattern of adult burrowing during midday to escape heat or unfavorable weather conditions and at night is similar to that of *C. arenicola* (Anderson 1988) and other Cicindela (Willis 1967, Knisley and Schultz 1997). Our finding of more females and mated pairs digging burrows may indicate that females could be using burrows to oviposit and thus position eggs deeper into the soil where more moisture is present. Such behavior has been observed in other species in the laboratory and in the field (Anderson 1989, Knisley and Schultz 1997). Our observations of predation and potential predators on adults indicate that predation may not be a major limiting factor for adults. Interestingly, Acorn (1991) found evidence that adults of *Cicindela formosa* are an important predator of adult *C. l. nympha*. More studies are needed to determine the importance of parasitism and predation for *C. l. albissima*.

What Factors Explain the Distribution of *C. l. albissima* at CPSD?

Results of this study provide some insight but do not fully explain the localized distribution of *C. l. albissima* within the CPSD dune field. The concentration of adults and larvae within the primary habitat and the presence of very few adults with moderate numbers of larvae in swales at the far north end of the dune field are puzzling. There is significant variation in the geology, vegetation, prey arthropods, and OHV activity throughout the CPSD dune field, and all of these could significantly affect the distribution and abundance of *C. l. albissima*. Importantly, the primary habitat is very closely associated with distribution of the transverse type of sand dunes at CPSD, while other dune types are present north and south of the transverse dunes where *C. l. albissima* occurs (Ford and Gillman 2000). There is also a distinct transition in the dynamics, physical characteristics, and elevation of the dune field progressing from southwest to northeast. The south end of the dune field (area E) is lowest in elevation (<1800 m) and nearest the sand source that feeds the dunes. It is the most dynamic area with the least vegetated interdunal swales (with little *P. lanceolatum* and *S. stenophylla*) and the best developed and most active dunes. *Wyethia scabra* is the dominant cover plant in this sparsely vegetated part of the dune field. This is also the part of the dune field with the highest level (by far) of OHV activity (a primary vehicle play area) and relatively low numbers of arthropods. The high OHV use probably contributes to the low vegetation cover, an effect that is well documented (Vollmer et al. 1976, Hosier and Eaton 1980, Luckenbaugh and Bury 1983). We have observed that many interdunal swales in this area had OHV tracks indicative of heavy use and were nearly devoid of vegetation. We cannot determine which of these differences in this part of the dune field explains the absence of *C. l. albissima*. Adults and larvae of *C. tranquebarica* were mostly found in swales with damp soils and lower OHV activity.

The northern half of the dune field (areas A to AAA) is the highest in elevation (>1900 m) and the least dynamic area, with large numbers of ponderosa pine stabilizing the dunes. Most of the swales, however, are sparsely vegetated, similar to that at the south end, and dominated by *Wyethia scabra* and a greater variety of plant species. Arthropod abundance is low and OHV activity moderate to heavy in areas B and A, but in the far north end (AAA) this pattern is reversed. Low OHV activity and high numbers of arthropods in AAA may partly explain the presence of *C. l. albissima* there and its absence in areas A and B. The increase in numbers of larvae in the past 3 years may be due partially to the exceptionally high rainfall and its effect on larval recruitment.
and survival (see above). However, the very low adult numbers here suggest that this north end of the dune field may be unfavorable for complete development and successful emergence of adults.

The primary habitat of *C. l. albissima* (area C) has some distinctive features that may contribute to the beetle’s predominance there. This area is a transitional zone between the highly dynamic south end and the stabilized dunes north of area B. Dune slopes and ridges are open and very active, but interdunal swales have higher percent vegetation cover relative to other areas. The dominance of *Psoralidium*, *Sophora*, and *Stipa* in these swales may provide a different and more favorable habitat for larvae by supporting a greater abundance of arthropods as a food source for larvae and adults. The level of OHV activity in this area is moderate, but numbers of OHV roads are fewer, play time less, and apparent OHV damage to swales more limited than in adjacent areas to the north and south. We have also observed during the years of our study that swales in the northwestern part of the primary habitat supporting most of the adults and larvae have received less OHV use than swales along the eastern side of the primary habitat.

Our studies show that some adults are killed each year from run-overs by OHVs, but it is not certain if this significantly impacts the population. A greater effect may occur when adults are run over and crushed in their shallow adult burrows on the dune slopes. We have not observed this effect. Low levels of OHV activity may not impact larvae because their burrows are deep enough (>20 cm) for them to avoid being crushed. In experimental run-over trials, Anderson (1989) found no effects to larvae of *C. arenicola* after 10 OHV passes. Heavy OHV activity, such as seen at some areas of CPSD, may impact the population through other direct or indirect effects on adults and larvae. Adult feeding, oviposition, and mating may be disrupted by OHVs, and this effect could reduce recruitment, as was reported for *C. dorsalis* on Virginia’s coastal beaches (Knisley and Hill 1992). The reduction of swale vegetation may coincidentally reduce prey arthropod abundance and negatively affect larval survival. Off-highway vehicles may cause a mixing of the upper sand layers, which can increase desiccation (Webb et al. 1978) or alter the soil moisture gradient of the larval micro-habitat (Schultz 1988). Soil moisture measurements taken in 1996 in different portions of the CPSD dune field indicated that areas in and near heavy-use OHV roads had significantly lower soil moisture readings than undisturbed areas nearby (Gwilliam, Hill, and Knisley unpublished study). Although it cannot be concluded from our study, it is possible that high levels of OHV activity in area E and parts of areas B and A, just north of the primary habitat, prevent the successful colonization of *C. l. albissima*.

Despite the potential negative impacts from OHV activity, there is no evidence of a progressive decline of the population of *C. l. albissima* at CPSD. There are no records of this species’ abundance prior to the beginning of OHV activity >20 years ago, and so it is unknown whether the population was historically larger. Year-to-year fluctuations in adult population size have been significant, but declines have been followed by a rebound in abundance. It is believed that implementation of the conservation plan in 1998, which prevents or reduces vehicle activity in most of the primary habitat, will provide long-term protection for this species at CPSD. Continued monitoring and study of the *C. l. albissima* population will help to determine this.

**Acknowledgments**

Logistic support and assistance in these studies were provided by Rob Quist, Dan Richards, and the staff at Coral Pink Sand Dunes State Park. Tim Smith was especially helpful in our early work at CPSD. Field assistance was provided by Kevin Fielding, Charles Davis, Ryan Knisley, Charles Gowan, Bruce Gwilliam, and Larry England (USFWS). Charles Gowan identified the plants. Charles Gowan produced several of the figures. We greatly appreciate the assistance, cooperation, and financial support made available by Ron Bolander of the Utah BLM through a Challenge Cost Share Agreement and Larry England of the U.S. Fish and Wildlife Service through a Cooperative Agreement.

**Literature Cited**


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The red squirrel (Tamiasciurus hudsonicus) is a small, semi-arboreal mammal of the Hudsonian and Canadian life zones of North America (Hall 1981). It inhabits coniferous and deciduous forests throughout the Rocky Mountains, most of Canada, the Great Lakes states, and New England (Hall 1981). The abundant literature on the ecology, behavior, and taxonomy of this species has been summarized by Steele (1998). Tamiasciurus hudsonicus has been divided into 25 subspecies, with the greatest diversity occurring in the Rocky Mountains south of Canada (Hall 1981, Lindsay 1987).

Western populations of pine squirrels of both T. hudsonicus and the closely related T. douglasii exhibit exclusive territoriality (Smith 1968). According to Smith (1968), the basis of territorial behavior is the need for individual squirrels to harvest, store, and defend a seasonal supply of food so that it will be available all year long. Vocal display is an important part of this territory defense behavior. Four of 5 different calls used by T. hudsonicus (growl, buzz, rattle, and screech) are related to territorial behavior (Embry 1970, Lair 1990, Price et al. 1990). The 5th call (bark) has been interpreted as expressing fear, anger, frustration, or a conflict of motivation (Klugh 1927, Embry 1970, Nodler 1973, Lair 1990), or as an alarm call (Smith 1978, Price et al. 1990, Greene and Meagher 1998). The bark is one of the most frequently heard vocalizations of the red squirrel (Embry 1970). Barking bouts can last for just a few seconds or can continue for nearly an hour (Embry 1970). The bark is also reported by both Smith (1978) and Embry (1970) as being the most variable of the 5 calls, and its function is somewhat contested. Smith (1978) interpreted the call strictly as an alarm call and invoked kin selection to explain its origin. Greene and Meagher (1998) also consider at least some bark calls to be alarm calls, which differ according to the type of predator. Searing (1977) interpreted the bark call as a low-intensity, aggressive call. Other authors (Embry 1970, Nodler 1973, Lair 1990) questioned its function as an alarm, preferring the broader interpretation mentioned above, and Lair’s (1990) work seems to be consistent with this concept. In his analysis of the behavioral context of red squirrel calls, Lair (1990) concluded that the bark was a poor indicator of the caller’s behavior. Embry (1970) quantified the variability in this call and identified at least 7 different types of bark calls.

There is a high degree of variability in the bark call of Tamiasciurus, which may indicate that the call conveys different meanings in different contexts (Lair 1990). Embry (1970) found this variation to exist within individuals, among individuals, between sexes, among age...
classes, and among subspecies in western Montana and an adjacent locality in northwestern Wyoming. Our study extended the analysis of geographic variation begun by Embry. The purposes of this study were to examine variation of the bark call over a broader geographic range, to better understand the geographic variability of this call, and to test the hypothesis that significant variation exists between the calls of different subspecies. This study aims to provide a basis for further research on the function of the call.

MATERIALS AND METHODS

Recording Method

While walking along a road or trail, we made tape recordings of Tamiasciurus bark calls at 15 localities from the western United States (Fig. 1). One call was recorded from each of 122 individuals representing 7 subspecies. As much of each call bout was recorded as possible (range = 30 seconds to 10 minutes). To prevent recording the same squirrel twice, we did not make 2 recordings in the same area unless we could determine that the calls were produced by different squirrels. Recordings were made at any time of day during daylight hours (not on stormy days) from any squirrel that began calling, and all recordings were made during August and September, after young of that year reached adult size. After completing the recordings at a locality, the individual making the field recordings estimated the size of the area that would include the position of all recorded squirrels at that locality: 3, 10, or 20 km

Fieldwork was done in 1992 by Barry Moore (Moore 1993) and in 1995 and 1996 by Osamu Yamamoto (Yamamoto 1998). There were differences in the recording and sound-analysis equipment available to us at these 2 time periods, but the differences did not affect our ability to accurately identify peeps and barks. Recordings were made with a Uher 4000 Report L tape recorder at a tape speed of 19 cm \cdot s^{-1}, or with a WM-D6C Sony professional walkman cassette-tape recorder. Filters were not used. The microphone was either a Sennheiser MKH 404 or ME-62, mounted on a 61-cm parabolic dish. Recordings were stored on laboratory standard polyester magnetic tape by Realistic, or on TDK MA110 metal bias IECIV/IV cassette-tapes.

Analysis of Recordings

Recordings from 1992 were analyzed on a Gateway 2000 personal computer with Kay Elemetrics Corporation Computerized Speech Lab (CSL) model 4300 hardware and version 4 software, with sound digitized at 40,000 Hz. Audiospectrograms were generated on the CSL system with the following parameters: frame length of 256 points, 0.80 pre-emphasis, Blackman window weighting, 18.00–48.00 darkness scale, 0 dB gain, 20 kHz display range, 2 \times 2 pixels grid size, and linear display (Kay Elemetrics Inc. 1991, Moore 1993).

Recordings from 1995 and 1996 were analyzed using a Macintosh computer with Canary 1.2.1 software. With this system, calls were digitized at 44,100 Hz and 16-bit sampling size, and audiospectrograms were generated with the following parameters: analysis resolution
of 69,940 Hz filter bandwidth and frame length of 256, time grid resolution of 2.902 ms with 50% overlap, frequency grid resolution of 86.13 Hz with 512 point FET size, and 20 kHz display range (Bioacoustics Research Program 1995, Yamamoto 1998). Calls were played into the audiospectrogram equipment on the same tape recorder with which they were recorded.

We analyzed a 20- or 30-second sample from each recording (localities 2, 5, 6, 7, 10, 11: 20 seconds; localities 1, 3, 4, 8, 9, 12–15: 30 seconds), with a total of 6373 notes (syllables). With the system used in 1992, it was not practical to analyze samples longer than 20 seconds because of the time required for producing sonograms with this equipment. In the 2nd part of the study, each 30-second sample consisted of three 10-second segments, one each from the beginning, middle, and end of the recording.

Embry (1970) described 2 components that form all variations of the bark call. She called these the alpha and the beta components, but we call them, respectively, the peep and the bark syllables (Fig. 2). The peep has a chevron-shaped structure, often with 3 harmonics. The bark is a column of noisy sound that commonly reaches 12+ kHz and frequently contains numerous harmonics.

In this paper we use the following definitions of terms: call bout—all of the vocalizations in one continuous interaction by a single squirrel; bark call—one of 5 types of calls used by red squirrels, composed of bark and peep syllables; syllable—a single sound, either a bark note or a peep note (Fig. 2); bark type—one of the combinations of peeps and/or barks used by red squirrels (Fig. 2); vocabulary—the number of bark types used by a given individual or population of squirrels.

The variables we analyzed were number of bark types, variation in frequency of use of bark types among populations, and variation in bark rate (syllables per second). The hypothesis that populations had equal vocabulary sizes (in number of bark types) was tested with 1-way ANOVA with the Tukey-B post test. Consistency of differences between populations in number of bark types, usage of bark types, and bark rate were evaluated with a discriminant analysis using Wilk's routine. This test analyzed data only for the 11 most frequently used bark types because the 8 remaining bark types were performed too infrequently for a valid discriminant analysis. After the discriminant analysis calculated its own canonical variables from the data, individuals were entered as unknowns, and the test was used to identify the population to which each belonged, as a test of consistency of the interpopulation differences in call parameters.

We performed a test to determine how many 10-second segments were needed to adequately represent the number of bark types used in a call. For each of 9 locations distributed throughout the research area, the longest recording (range = 1–10 minutes) was analyzed in 10-second segments. The cumulative number of bark types given by the end of each 10-second segment of the recording was plotted against number of 10-second segments analyzed to that point. The number of 10-second segments after which number of bark types ceased to increase indicated the total length of sample needed, on average, for a complete count of bark types. We then tested variation in vocabulary size in different segments of a call by comparing number of bark types in three 10-second segments in each of 73 recorded calls. The hypothesis that vocabulary size was not significantly different among 10-second segments of the call was tested with a chi-square test, with the actual number of call types in each segment of an individual call bout tested against the expected ratio of 1:1:1.

Variation in bark rate (syllables per second) between populations was tested with 1-way ANOVA with the Tukey-B post test. Consistency in bark rate between segments of a call was tested by comparing bark rate in three 10-second segments in each of 73 recorded calls. The hypothesis that bark rate was consistent...
throughout each call was tested with a chi-
square test, as described above.
All tests were considered statistically signif-
ificant at $P < 0.05$. Chi-square tests were done
with software written by David Cowles. All
other statistical computations were carried out
on Statistical Package for the Social Sciences
6.0 (SPSS; Norusis 1993).

RESULTS

Variation in Bark Types

This study describes 19 bark types made up
of different combinations of peeps and barks
(Figs. 2, 3). The most common bark calls are a
single bark (B bark type; 30.0%), a single peep
(P bark type; 14.6%), and the PB bark type (a
peep followed by a bark; 41.5%). In contrast, a
number of the longer bark types each constitut-
ed a fraction of 1% of the sample. Longer
combinations of barks and peeps are most
commonly used by the northern subspecies in
this study, $T. h. streatori$ and $T. h. richardsoni$,
and much less by the southern subspecies
(Fig. 3). Also, in the 2 northern subspecies the
single bark is the most common bark type,
replaced in most southern subspecies by the
PB bark type. In $T. h. grahamensis$ the single
peep is the most common type.

The column labeled COMB in Figure 3
includes rarely heard combinations of alter-
ning barks and peeps longer than those in
the other columns. The longest complex con-
sisted of 8 peeps alternating with 7 barks. This
call begins to sound like the territorial trill or
rattle call which consists of closely spaced barks,
but the rattle call was never found to have
associated peeps. These COMB call types
occurred 23 times (0.4%) in this study. Some
individuals from the $T. h. ventorum$ population
at locality 10 and a $T. h. dixiensis$ population in
central Utah (not included in this paper
because of small sample size) followed bark
calls with a heavy wheezing sound.

Vocabulary size, expressed as number of
bark types used, was significantly different
among populations (Fig. 4; $F = 4.65$; df = 14;
$P < 0.0001$). The southern subspecies used
fewer bark types and had lower variability in
number of bark types used. Although these
subspecies used the 3 most common bark types,
they used the more complex bark types much
less often, or not at all.

In most cases there were no significant dif-
fferences in vocabulary size among populations
within a subspecies. Of 15 pairs of populations
that differed significantly (Tukey-B test; Fig. 5),
only a single pair was within the same sub-
species. This pair consisted of 2 populations (8
and 10) on opposite sides of the species range
of $T. h. ventorum$, which differed significantly
in vocabulary size.
The test of the adequacy of our sampling method supported the use of 20- to 30-second samples from each recorded call. A 20- or 30-second sample included on average all bark types for the 4 southernmost subspecies (localities 11–15) but not for most populations in the 3 northern subspecies (localities 1–10; Fig. 6). Consequently, increasing the length of our samples would likely have yielded increased vocabulary size only for the northern subspecies, which in our study already had the largest vocabulary sizes. From this we infer that if we had used longer samples from each call, our results would likely have increased the difference between the vocabulary of the northern and southern populations, reinforcing rather than reducing our documented difference between northern and southern populations. This probable increase in vocabulary size would have involved the rarely used bark notes and is unlikely to have changed the conclusions reached in this paper. Also, the vocabulary size was in most cases not significantly different between different 10-second segments of a recorded call. Of 73 individuals (all with samples of 30 seconds) tested for variation in vocabulary size between the three 10-second segments of the sample, 65 (89%) showed no significant difference between segments ($\chi^2 = 0.0–2.0$ [$\bar{x} = 0.6$]; $P \geq 0.05$). The other 8 individuals showed significant differences between sample segments ($\chi^2 = 2.4–6.3$ [$\bar{x} = 4.2$]; $P < 0.05$).

The frequency with which different bark types were used varied between individuals in a subspecies. Figure 7 shows individual variation within one population each of T. h. richardsoni and T. h. ventorum, which represent the extremes in individual variation found in this study. Individuals from the T. h. richardsoni population show much more variation than those from the T. h. ventorum population. Despite this individual variation, there are highly significant differences in the frequency distribution of bark type usage between populations and subspecies (discriminant analysis; Table 1). When each individual was treated as an unknown in a discriminant analysis, 95% of the calls were placed in the correct population on the basis of bark type usage. Variability did not seem to correlate with the size of sampling area from which calls were recorded (and thus the potential relatedness of the squirrels; Fig. 4). Several populations with the smallest range of variation represented recordings from the largest sampling areas.

### Variation in Bark Rate

Bark rate was significantly different among populations (Figs. 4, 5; $F = 5.84$; df = 14; $P < 0.0001$), but there was no consistent geographic trend. Most populations within the same subspecies were not significantly different from each other in bark rate. The only 2 exceptions were 2 populations (6 and 7) on the west side of the range of T. h. richardsoni. Each differed
Bark rate tended to be consistent throughout the length of a recorded call. Bark rate did not differ between the three 10-second segments of individual calls in 69 of 73 individuals tested ($\chi^2 = 0.0–1.98$; $P \geq 0.05$). The remaining 4 showed significant differences between segments ($\chi^2 = 2.33–3.64$; $P < 0.05$).

**DISCUSSION**

Our data indicate considerable geographic variation in characteristics of the bark call in red squirrels. Variation exists at several levels: within individuals, among individuals of a population, and among subspecies (this study), and between sexes and among age classes (Embry 1970). The differences between some populations are consistent enough and large enough that bark-type frequencies could be considered in studies on the systematics of this group. The southern subspecies of red squirrel have a conspicuous lack of the more complex forms of the bark call, relative to the 2 northern subspecies (T. h. streatori and T. h. richardsoni).

Perhaps these more southerly populations, with their more homogeneous and unique calling patterns and reduced number of bark types, are farther from the center of origin of the species, and part of the call variability has been lost. If the bark call is involved in species recognition, the interpopulation differences in this common call could contribute to reproductive isolation if secondary contact between subspecies occurs. The behavior of these organisms has not been worked out in sufficient detail to test these ideas.

Red squirrels distinguish the rattle calls of neighbors and strangers and respond differently to each (Price et al. 1990). The extent of variation that exists within the bark call of T. hudsonicus suggests that bark calls may also contain the potential for individual recognition and perhaps also for information about the sex, age, and behavioral states of the individual. Whether it does convey this information is not known. Full understanding of these questions will require study of the amount and context of intra-individual variability in bark calls (which our study did not include) compared with inter-individual variation.

Greene and Meagher (1998) found that red squirrels used different bark types in response to aerial and ground predators. The squirrels used “seet” calls (the same as peeps in this paper) or seet-barks (PB bark type) in response to raptors, and barks (B bark type) in response to humans or dogs. They indicated that only one seet call was given in response to a bird but did not say if the seet-bark or bark vocalizations were used only as a single syllable in each predator encounter. The peeps and barks that we studied were not given as single syllables but were all part of extensive calling bouts. The difference between these single-syllable alarm calls and the longer bark call bouts that we studied deserves more study.

Our research does not address whether red squirrel bark calls are alarm calls. When we recorded calls, the squirrels did not necessarily appear to be calling in response to our presence, since the calls often began in the distance and it was necessary to quickly move close enough to record the call. We could not determine if they were responding to other sources of alarm.

Greene and Meagher’s (1998) study of barks and peeps as alarm calls occurred in Montana, where we found peep notes to be rare components of bark bouts. How might alarm calls differ in a population like T. h. grahamensis, in which the peep is the most common bark type? Will that subspecies still use a single peep as an alarm call? More study of the relationship between documented alarm calls, as studied
by Greene and Meagher (1998), and geographic variation in bark calls would be beneficial.

It may be that these peep or bark notes are used differently in different contexts, with single syllables given as the animal responds to a predator, or the same syllables given in long sequences in other contexts. If this is so, it seems to parallel the use of chips by chipmunks. Chipmunks give long series of chip calls, lasting for up to 20 minutes or more, and these chips are fairly consistent in structure. When chipmunks are startled by a ground predator, they often give a brief, rapid chippering call as they escape (Brand 1976). Chip syllables are used in both, but the context and length of the calling bout and specific parameters of the chips are consistently very different for the 2 types of calls. Chippering lasts a few seconds or less, with great variation in syllable structure, but chipping bouts last many minutes and have little variation in syllable structure.

Lair (1990), summarizing the varied contexts in which barks are used, reported that she could distinguish at least 4 distinct variants of the bark, some of which seemed to be given in a restricted set of contexts. Available data are not adequate to determine how those 4 variants relate to the bark types reported in this paper. More comparative study of red squirrel calls and associated behavior is needed before we will understand the contexts and functions of the different forms of bark calls.

Another variable that has not yet been studied is variation in the acoustic environment of these squirrels and possible environmental influences on their calls. It has been shown that physical differences between habitats can influence the properties of sound that are effectively transmitted in those habitats (Blumstein and Daniel 1997). Some features of bird vocalizations, for example, are apparently adaptations to the acoustic structure of their

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**Table 1. Results of discriminant analysis of differences between populations in bark type usage.**

<table>
<thead>
<tr>
<th>Function</th>
<th>Eigenvalue</th>
<th>Canonical correlation</th>
<th>Wilk’s lambda</th>
<th>Chi-square</th>
<th>df</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>3.1546</td>
<td>.8714</td>
<td>.0495</td>
<td>321.6</td>
<td>156</td>
<td>0.00001</td>
</tr>
<tr>
<td>2</td>
<td>1.4239</td>
<td>.7665</td>
<td>.1200</td>
<td>226.8</td>
<td>132</td>
<td>0.00001</td>
</tr>
</tbody>
</table>

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**Fig. 7.** Percentage distribution of call types used by all recorded individuals in 1 population each of *T. h. richardsoni* and *T. h. ventorum*. Each vertical bar gives the data for 1 individual.
habitats (Morton 1975, Nottebohm 1975). Whether similar factors influence red squirrel calls is not yet known.

Understanding the function of this call will contribute significantly to understanding the behavior of this ubiquitous mammal. Further detailed research on the characteristics and context of bark calls of marked individual squirrels is needed to increase our understanding of bark calls. Our data document significant geographic variation in the bark calls of red squirrels and suggest profitable lines of research regarding the adaptive significance of this variation.

ACKNOWLEDGMENTS

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LITERATURE CITED


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Nearly 50 years ago Jewett (1954) named a nemourid species from the Columbia River Gorge. He chose the name *Nemoura wahkeena* because he had collected his type series at Wahkeena Falls in 1947. Although he stated that it was distinctive, he tentatively assigned it to the subgenus *Zapada*. In his monograph of the Pacific Northwest stoneflies (Jewett 1959), he added that it was rare and had been recorded only from Wahkeena Falls, but probably had a wider distribution. Illies (1966) in his world catalog listed it in the genus *Zapada*, which he had elevated along with the other subgenera of Nemouridae. Since no additional specimens were available and the generic placement was questionable, Baumann (1975) listed it under *species incertae sedis*. During the intervening 25-year period, it has been included under the genus *Zapada* in the following publications: Stark et al. (1986), Stewart and Stark (1988), and Stark et al. (1998). However, because the true generic identity was questionable, new material was obtained for a detailed study. This remarkable little stonefly seems to be endemic to the Wahkeena Falls springs, and it represents an undescribed genus in the subfamily Nemourinae.

Our search for specimens and additional information on what is often called the Wahkeena stonefly (Federal Register 1991) has been aided by our colleagues. Stan Jewett, before his untimely death in 1991, led the authors and Riley Nelson to his study site at Wahkeena Falls, where we collected a single nymph of this species. We discovered that the species does not live in the falls or even in the large spring source. Instead, it occupies some large seepage areas along the trail to the upper spring.

Since that day in 1982, we have visited the area several times and have always been able to find specimens at the seeps during the spring months. In addition, repeated attempts have been made to find this stonefly in other localities in the gorge and especially along the trail to, and at, nearby Multnomah Falls. However, it still has not been found anywhere but at the Wahkeena Falls site.

*Nanonemoura*, new genus

**Type species.**—*Nanonemoura wahkeena*, by monotypy.

**Adults.**—General facies like a small grasshopper nymph (Fig. 1). Body dark brown dorsally, lighter ventrally. Legs yellow, darker at joints, proportionally long, especially hind legs, which are more than twice the length of abdomen. Wings very small, micropterous, and seldom extending beyond thorax, veination reduced to major veins, with few crossveins. Head with large, prominent eyes, antennae long with ca 35 segments. Thorax stout with oversized legs, wings found on dorsolateral margins. Abdomen as long as head and thorax combined, cerci one segmented.

**Male genitalia.**—Epiproct with large dorsal sclerite extending over entire dorsal
surface (Fig. 7), lightly sclerotized apically and laterally at median expanded areas, covered with numerous rows of small, wartlike processes (Fig. 6); ventral sclerite heavily sclerotized, subequal in area to dorsal sclerite, and bearing ca 30 stout, ventrally directed spines that are randomly spaced over most of ventral surface (Fig. 8). Paraprocts with heavily sclerotized inner lobe that terminates in a sharply bifurcate apex; outer lobe partially membranous, with sclerotized outer margin, bearing ca 25 short stout spines (Fig. 4). Hypoproct broadest at base, anterior 1/3 tapering to truncate apex, bearing a thin, sharp, pointed projection medially; vesicle present, thin and elongate (Fig. 3). Cerci sclerotized dorsolaterally, drawn out into a narrow apex that ends in a hooked tip (Fig. 2).

**Female genitalia.**—Seventh sternum enlarged into a pregenital plate, broadly rounded and extending over most of eighth. Eighth sternum more darkly sclerotized, forming small subgenital plate, with narrow, dark sclerotized band over vaginal opening. Cerci membranous but large and long, almost like tiny ears (Fig. 5).

**Nymph.**—Color uniformly brown, with darker pattern on head and thorax; head covered with numerous tiny hairs, eyes prominent, cerci well developed; thorax bearing many long, darkly sclerotized spines, pronotum completely encircled, meso- and metanotum bearing a pair of long, hairlike spines lateral to midline; legs short and stout, femur bearing 8–10 long spines scattered randomly on lateral margins, tibia with 2 rows of short,
stout spines, one on each lateral margin, a sparse fringe of long, thin hairs present on ventral margin (Fig. 10); abdomen without setae or spines, except for 2 rows of long, thin spines, one on each side of midline, running entire length of abdomen; cerci with ca 20 segments, intercalary spines present, anterior 2/3 of cercal segments encircled with whorls of long spines (Fig. 9). Two cervical gills present on each side of midline, thin and divided, 3 lobes each, lobes arising from midlength to apex, not from a common stalk (Fig. 11).

**Diagnosis.**—Adults are easily distinguished from all other Nemouriinae by their very long legs, especially those on metathorax, long maxillary palpi, and micropterous wings (Fig. 1). The male epiproct consists of dorsal and ventral sclerites that are large and flat and approximate each other in size, dorsal sclerite with lightly sclerotized, slightly swollen areas medio-
laterally, covered by rows of small, wartlike processes, ventral sclerite bearing ca 30 stout, ventrally directed spines scattered over entire ventral surface (Figs. 6–8). Male paraprocts with 2 well-developed lobes, inner lobe darkly sclerotized, narrow, and with bifurcate apex (Fig. 4). Female with well-developed pregenital plate that covers most of next segment, small sclerotized bar over vaginal opening (Fig. 5). Nymph with 2 pairs of cervical gills, each with 3 branches arising linearly and not from a common stalk (Fig. 11), leg setation mostly random on femora (Fig. 10).

_Nanonemoura_ can easily be separated from _Zapada_ by using the following characters: the male epiproct lacks lateral knobs at the basal corners and consists of only dorsal and ventral sclerites that are distinctly flattened dorsoventrally; male paraprocts are composed of 2 definite lobes, the inner being heavily sclerotized and terminating in a large bifurcate process; male cerci are sclerotized and modified into long structures with a pointed apex; the female has a small, lightly sclerotized pregenital plate and long, thin cerci; the nymph has 2 pairs of gills with 3 branches each; spines on the femur are sparse and randomly spaced rather than in definite rowlike whorls.

_Nanonemoura_ clearly belongs to the subfamily Nemourinae and would fit with the Nearctic genera _Lednia_ and _Visoka_ in the cladogram in Baumann (1975). Male terminalia of _Nanonemoura_ are really quite similar to those of _Lednia_ and _Visoka_. The epiprocts of all 3 genera are composed of large, nearly subequal dorsal and ventral sclerites. _Nanonemoura_ and _Visoka_ both have rows of wartlike structures on their dorsal sclerite, while _Lednia_ is covered by small spines. Their paraprocts consist of large, membranous outer lobes and thin, heavily sclerotized inner lobes. The inner lobes of _Lednia_ and _Visoka_ end in single pointed processes, while those of _Nanonemoura_ have a bifurcate apex. _Lednia_ lacks a vesicle on the hypoproct, but it is present in the other 2 genera. _Nanonemoura_ and _Visoka_ exhibit sclerotized, highly modified cerci, but those of _Lednia_ are simple and unmodified.

**DISTRIBUTION.**—Known only from tiny spring seeps along Wahkeena Creek in the Wahkeena Falls area of the Columbia River Gorge in northwestern Oregon.

**SPECIMENS EXAMINED.**—Oregon, Multnomah County, Wahkeena Creek near Wahkeena Falls, Columbia River Gorge: 5 April 1945, S.G. Jewett, Jr., holotype ♀/♂585, allotype ♀/♂586, and 1 ♀/♂585, 1 ♀/♂586 paratype (CAS, BYU); 16 April 1955, S.G. Jewett, Jr., 2 ♀/♂585, 3 ♀/♂ (USNM); 26 April 1955, Jewett & Wilson, 3 ♀, 1 ♀ (ROM); 4 May 1982, Baumann & Jewett, 9 ♀, 4 ♀ (BYU); 29 February 1984, Baumann, Jewett, Nelson, & Fiala, nymph (BYU); 22 March 1984, G.R. Fiala, 1 ♀ (BYU); 17 April 1984, G.R. Fiala, 5 ♀, 10 ♀ (BYU); 6 April 1985, G.R. Fiala, 8 ♀, 5 ♀ (BYU); 9 April 1988, G.R. Fiala, 5 ♀, 8 ♀ (BYU); 8 May 1988, G.R. Fiala, 4 ♀, 4 ♀ (BYU); 23 March 1992, G.R. Fiala, 8 ♀, 2 ♀ (BYU); 23 March 2001, G.R. Fiala, 3 ♀, 7 ♀ (BYU); 28 March 2001, G.R. Fiala, 9 ♀, 11 ♀ (BYU). Most of the specimens are deposited at Brigham Young University (BYU).

**ETYMOLOGY.**—The prefix nano is from the Greek and is defined as small. Combining nano with nemoura, which signifies sylvan,
Fig. 9. Nanonemoura wahkeena nymph, habitus.
results in a feminine name that means small, woodland stonefly.

ACKNOWLEDGMENTS

We are especially indebted to the late Stan Jewett, who shared his enthusiasm with us and showed us where to collect his prized little stonefly. Thanks to Vincent Lee of the California Academy of Sciences (CAS), who helped us examine the holotype and allotype. We also appreciate Oliver Flint of the United States National Museum (USNM) for the loan of specimens collected in 1955. Glenn Wiggins made his vial of specimens available when he was at the Royal Ontario Museum (ROM). Riley Nelson accompanied us twice when we collected specimens and was along the day we found the nymph. Ken Stewart and Bill Stark are to be thanked for encouraging us to describe this genus so that it could be included in their revision of the North American stonefly nymph book. Finally, the excellent illustrations were made by Jean Stanger Leavitt.

LITERATURE CITED


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SITE AND STAND CHARACTERISTICS RELATED TO WHITE PINE BLISTER RUST IN HIGH-ELEVATION FORESTS OF SOUTHERN IDAHO AND WESTERN WYOMING

Jonathan P. Smith and James T. Hoffman

ABSTRACT.—Successful infection of white pine species by white pine blister rust (WPBR) is contingent upon environmental conditions that are favorable to the spread and development of Cronartium ribicola. Site and stand factors related to this process have been studied elsewhere within the distribution of the disease, but few studies have concentrated on the high-elevation white pine forests of southern Idaho and western Wyoming. We found that mean summer precipitation, average tree diameter, and elevation were the most important variables in 3 logistic regression models of WPBR presence and intensity. The models were tested on a randomly chosen portion of our data set. The model with 9 variables correctly predicted categories of low-, moderate-, and high-disease incidence in 19% of cases. The 2 models with fewer variables had lower predictive efficiencies but were more parsimonious and generally easy to measure. The ability to use easily measured or remotely sensed site and stand characteristics to predict WPBR spread or intensification could be an important asset to land managers who need to decide where to focus disease mitigation efforts and predict disease effects on water quality, wildlife habitat, recreation potential, and other land-management activities.

Key words: white pine, whitebark pine, limber pine, white pine blister rust, Cronartium ribicola, tree diseases, Rocky Mountain forests, subalpine forests.

White pine blister rust disease (WPBR), caused by the introduced fungus Cronartium ribicola, is the most widespread and serious disease of Pinus albicaulis (whitebark pine; Arno and Hoff 1989) and P. flexilis (limber pine) in the Rocky Mountains (Smith and Hoffman 2000). The disease is also a potential threat to most, if not all, other white pine species (genus Pinus, subgenus Strobus, section Strobus, sub-sections Cembrae and Strobi, and section Parrya, subsection Balfourianae; Hoff et al. 1980). The rust causes branch and stem cankers that, in most cases, girdle and kill the host tree.

Cronartium ribicola has a complex life cycle that is characterized by 5 spore-producing stages that alternate infection between white pine species and plants of the genus Ribes (currants and gooseberries). Aeciospores are small, light spores that are produced on pine cankers and can travel long distances to infect the leaves of Ribes. Urediospores emerge on Ribes leaves and spread to other leaves on the same plant, or other nearby Ribes plants. Teliospores, produced on Ribes, germinate and form the basidium, which releases basidiospores to infect white pine needles. Fungal hyphae spread into woody tissue causing cankers, where the 5th type of spore-bearing structure, the pycnia, is produced. Upon completion of the pycnia stage, which probably involves mating, aecia are produced, completing the life cycle.

Like other pine rusts, transmission of spores and host infection depends on a favorable temperature and moisture environment, an abundance of spores (inoculum), and availability of susceptible hosts (Mielke 1943, Charlton 1963). These conditions may be affected by physical factors such as slope, aspect, elevation, and precipitation, as well as biological factors such as structure of the forest canopy and proximity of Ribes spp.

Site and stand factors associated with rust incidence have been identified by studying the distribution of WPBR and endemic pine rusts. Van Arsdel (1972) found that the size of forest canopy openings and certain topographic features were related to WPBR incidence in Pinus strobus (eastern white pine). In British Columbia, Hunt (1983) reported more WPBR
cankers in *P. monticola* (over 2.5 m high in the tree) as slope increased. Jacobi et al. (1993) found *Cronartium comandrae* (comandra blister rust) incidence in *Pinus contorta* subsp. *latifolia* (lodgepole pine) positively correlated with tree diameter, and negatively correlated with stand density and distance to the rust’s telial host. Beard et al. (1983) found a greater incidence of *C. coeleosporioides* (stalactiform blister rust) in central Idaho *Pinus contorta* forests at middle to upper elevations, and in *Abies lasiocarpa/Xerophyllum tenax* and *Abies lasiocarpa/Vaccinium scoparium* habitat types. *Endocronartium (=Peridermium) harknessii* (western gall rust) stem infections were negatively correlated with stand age in British Columbia *Pinus contorta* forests (van der Kamp 1988). Van Arsdale (1965) constructed a formula based on slope and canopy openings and predicted WPBR presence in southwestern Wisconsin with 89% accuracy. Charlton (1963) used aspect, elevation, slope, topographic position, and vegetation structure, along with climatic factors, to assess WPBR infection hazard in the eastern U.S. A comprehensive site-specific WPBR hazard model based on site, stand, alternate host, and physiological factors was developed by McDonald et al. (1981) for *P. monticola* in northern Idaho.

Very little of this type of work has been conducted in the southern portion of *C. ribicola*’s range in the Rocky Mountains because, historically, disease surveys revealed only trace levels of infection (Brown 1967, Brown and Graham 1969). However, WPBR has recently intensified and spread to new locations in the southern portions of the Northern Rocky Mountain and Middle Rocky Mountain provinces (Kendall et al. 1996, Smith and Hoffman 2000). As an initial step in modeling WPBR spread and intensification in this region, we used USDA Forest Service disease survey data (Smith and Hoffman 1999) to look for relationships between WPBR incidence and several site and stand characteristics.

**Study Area**

*Pinus albicaulis* and *P. flexilis* populations in the U.S. extend southward along the Rocky Mountains from the Canadian border to southeastern Idaho and southwestern Wyoming. *Pinus flexilis* extends even further south, throughout the mountains of Utah. There are also several disjunct *P. flexilis* and *P. albicaulis* populations in isolated mountain ranges of eastern Oregon and northern Nevada, and both species occur in the Sierra Nevada (Critchfield and Little 1966). Our study area encompasses those Rocky Mountain white pine populations that lie within southern Idaho and western Wyoming (Fig. 1). Within this region *P. albicaulis* and *P. flexilis* populations extend upward from the lower subalpine zone to the upper (cold) tree line. *Pinus flexilis* also has the unique ability to grow at lower (dry) tree line (Arno and Hammerly 1984).

**Field Methods**

In 1995 we installed 10 rectangular plots according to the methods specified by the Whitebark Pine Monitoring Network (Kendall 1995). In 1996 we used randomly located strip transects rather than rectangular plots to delineate trees. We switched to transects because white pine species in our study area 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 not possible. For the 68 sites sampled during 1996, we established a 4.6-m (15-ft)-wide strip transect, along the contour of the slope, from a random starting point. We traversed this transect until 50 white pines had been inspected or until we encountered a change in the character of the site or stand that did not match our sampling criteria, such as a different canopy structure, a sufficiently different aspect (>10° difference), slope (>5% difference), habitat type or phase, or a topographic change. Rather than cross this environmental gradient, we changed the direction of the transect by 180°, displaced it uphill or downhill 4.6 m (15 ft), and continued to sample until 50 trees had been inspected.

For each tree we recorded the presence of WPBR cankers and DBH (diameter at breast height, 1.37 m above the ground), in 5.1-cm (2-in) size classes. At the midpoint of each transect, we measured or calculated habitat type (Steele et al. 1981, 1983), presence/absence of *Ribes* sp., basal area, trees per hectare, canopy closure, elevation, aspect, slope angle, and topographic position (Table 1).

An additional variable, estimated mean summer precipitation, was generated from climate maps (Martner 1986, Molnau and Newton
1994). To estimate mean summer precipitation, we multiplied regionalized estimates of the summer (June, July, and August) proportion of total precipitation by the mean annual precipitation values taken from these maps. We interpolated precipitation values between isohyetal contours for each of our sample sites.

**Statistical Methods**

Because sampling location criteria and data collection procedures were identical for plots and transects, the data were combined for our analysis. We grouped the categorical independent variables, habitat type, canopy cover, and topography to reduce the number of categories for model calculation. For example, we identified 20 habitat type classes in the field but combined these into 4 categories based on a multidimensional scaling procedure that groups habitat series based on moisture requirements of understory plants (McDonald unpublished data). We used dummy coding for the categorical variables. Presence or absence of *Ribes* spp. was entered as a binary variable (i.e., a value of 0 for absent, 1 for present).
Elevation, slope, latitude (UTM northing), average tree size, and mean summer precipitation were entered as continuous variables (i.e., their actual measured values). The aspect measurement, which is azimuthal (circular data), was linearized by taking the cosine of the aspect in radians.

Logistic Regression Analysis

Percent of trees infected in a sample stand was the dependent variable, which was treated statistically as the number of successful events (infected trees) per number of trials (trees sampled) at each sample site. We performed a stepwise logistic regression procedure with the model development data set using the PROC LOGISTIC STEPWISE option in SAS (SAS Institute Inc. 1996). This procedure identifies predictive variables when the number of potential explanatory variables is large relative to the number of samples (Hosmer and Lemeshow 1989). We constructed 3 models of WPBR incidence with combinations of the variables selected by the stepwise procedure.

To determine if models were statistically significant, we compared 4 criteria to assess how well the models fit and to compare how well each model predicted WPBR incidence. First, we calculated \( r^2_L \), which is a measure of the reduction in the log-likelihood as a result of including the independent variables (Menard 1995). We tested the null hypothesis that the predictor variables contribute no more than chance to the explanation of the dependent variable with the \( G_m \) statistic (the model chi-square statistic). The Bayesian information criterion (BIC) was calculated as a selection device because it emphasizes parsimony by penalizing models with a large number of parameters (Ramsey and Schafer 1997). To measure the predictive efficiency of each model, we arbitrarily assigned broad classes of WPBR incidence, low (<25% incidence), medium (26–50%), and high (>50%), to the observed and predicted values and then calculated how frequently each model correctly predicted the observed category, was 1 category off, or was off by 2 categories.

Model Testing

We used a split-sample validation technique to develop and test the logistic regression models. Each record was assigned a random number, sorted by this number, and then split into a model-development data set (2/3 of the data), which was used to develop the models. The remaining 1/3 of the data \((n = 23)\) was treated as an independent data set to test the models’ statistical significance, fit, and predictive efficiency, and to assess the importance of the independent variables. We estimated the predicted proportion of trees infected in each sample with the predicted probability of infection (presence or absence of WPBR) for each tree in that sample.

### Table 1. Variables used in the stepwise logistic regression procedure and parameter estimates for the 3 models using the recombined (full) data set.

<table>
<thead>
<tr>
<th>Variable (description)</th>
<th>Model 1</th>
<th>Model 2</th>
<th>Model 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Elevation (meters, from topo map)</td>
<td>-0.613 (313)</td>
<td>-0.606 (321)</td>
<td>-0.546 (308)</td>
</tr>
<tr>
<td>Average DBH (diameter at breast height in 2-cm classes)</td>
<td>0.458 (212)</td>
<td>0.454 (210)</td>
<td>0.517 (301)</td>
</tr>
<tr>
<td>Mean summer precipitation (interpolated from maps)</td>
<td>0.278 (109)</td>
<td>0.304 (145)</td>
<td>0.250 (111)</td>
</tr>
<tr>
<td>Ribes (present/absent in stand)</td>
<td>0.237 (62)</td>
<td>0.239 (69)</td>
<td></td>
</tr>
<tr>
<td>Stand density (trees ( \cdot ) ha(^{-1}), all species)</td>
<td>-0.258 (61)</td>
<td>-0.222 (55)</td>
<td></td>
</tr>
<tr>
<td>Topographic position 3 (upper slopes)</td>
<td>0.215 (56)</td>
<td>0.212 (55)</td>
<td></td>
</tr>
<tr>
<td>Habitat type 1 (wet subalpine fir group)</td>
<td>0.123 (28)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Slope (percent)</td>
<td>-0.109 (12)</td>
<td>-0.118 (15)</td>
<td></td>
</tr>
<tr>
<td>Habitat type 4 (whitebark pine series)</td>
<td>0.007 (7)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Basal area (m(^2) ( \cdot ) ha(^{-1}), all species, white pines only)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aspect (cosine of aspect in degrees)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Latitude (UTM–northing)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Canopy (open, broken, closed)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Topography (valley/lower, mid, upper, ridge)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Habitat type (wet subalpine fir, cool/moist subalpine fir, cold/dry subalpine fir, whitebark series, Douglas-fir)</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Elevation, slope, latitude (UTM northing), average tree size, and mean summer precipitation were entered as continuous variables (i.e., their actual measured values). The aspect measurement, which is azimuthal (circular data), was linearized by taking the cosine of the aspect in radians.
The probability of WPBR infection in a tree \( P(Y) \) was obtained by inserting the test data independent variables into the equation for each model. The equations calculated \( \logit(Y) \) (the natural logarithm of the odds of WPBR infection) rather than \( P(Y) \) directly. The form of the equation was

\[
\logit(Y) = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_k x_k,
\]

where \( \logit(Y) = \ln \{P(Y)/[1 – P(Y)]\} \), \( \beta_0 \) is the Y-intercept, \( x_1 \) through \( x_k \) are the independent variables identified by the stepwise procedure as important predictors of WPBR incidence, and \( \beta_1 \) through \( \beta_k \) are the coefficients for these independent variables. It was necessary to linearize the predicted value to compare it to the linear observed proportion of trees infected. To accomplish this, \( \logit(Y) \) was converted to odds \( (Y) \) by exponentiation, and then to \( P(Y) \) by the formula \( P(Y) = \text{odds}(Y)/[1 + \text{odds}(Y)] \), where \( P(Y) \) is the predicted probability of infection in an individual tree and \( \text{odds}(Y) \) is the ratio of the probability that \( Y = 1 \) to the probability that \( Y \neq 1 \).

We used least-squares regression to compare the predicted proportion of trees infected with our observed proportion of infected trees and to calculate the significance of the regression and the coefficient of determination. Finally, we assigned the low, medium, and high classes to the predicted and observed values and performed a simple error assessment to see how well the model predicted incidence.

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### Analysis of the Independent Variables in the Model

To assess the importance of the independent variables, we evaluated the odds ratio, which approximates how much more likely the event (WPBR presence in a tree) becomes with increases or decreases in the value of each independent variable (SAS 1996). We also used the standardized logistic regression coefficients to evaluate the strength of the relationship between each independent variable and the dependent variable (Menard 1995).

### RESULTS

#### Model Development and Validation

The stepwise logistic regression identified 13 variables that were potentially related to WPBR infection. We used these to develop 3 candidate models. For the 1st model we removed 4 variables that were highly correlated \( r > 0.6 \) or that were not significant \( P > 0.05 \). We created the 2nd model by removing the variables with Wald-\( \chi^2 \) values <20. The 3rd model contained only the 3 variables that stood apart from the others because of their very high Wald-\( \chi^2 \) values (>100). Fit statistics, significance, and predictive efficiency for the 3 models are shown in Table 2A.

When applied to the validation set, all 3 regression models were statistically significant \( P \leq 0.001 \). The coefficient of determination \( (r^2) \) for the models ranged from 0.38 to 0.45.
The level of classification accuracy was highest for model 1, which correctly classified 79.2% of the cases. Model 3 correctly classified 62.5% of the test cases and had a higher $r^2$ than model 2 (Table 2B).

**Importance of Independent Variables in the Model**

The most important variables in all 3 models were elevation, mean summer precipitation, and average DBH. Although other variables were also statistically significant, when combined, these variables accounted for a much smaller proportion of the variation in WPBR incidence than the first 3 variables. Table 1 lists the parameter estimates for the variables in each model.

**DISCUSSION**

**Interpretation of Independent Variable Selection**

**ELEVATION.**—In Yellowstone National Park, Berg et al. (1975) reported that WPBR incidence in *Pinus albicaulis* and *Pinus flexilis* decreased with elevation. These researchers found that 92% of all infections occurred below 2591 m (8500 ft) elevation. Our results suggest a similar negative relationship between elevation and WPBR incidence. We found that 97% of the sample stands below 2591 m had WPBR, while only 53% of the stands above 2591 m were infected. However, the average proportion of trees infected in these stands did not decrease with elevation. In fact, the proportion of high-infection sites above 2591 m, 33%, was slightly greater than the proportion of high-infection sites below this elevation, 31%, suggesting that once WPBR is able to infect a high-elevation site, it is able to continue to intensify. However, this phenomenon was apparent only in the Greater Yellowstone Ecosystem portion of our study area. Some factors involved in the decrease in WPBR incidence with increasing elevation may include earlier *Ribes* leaf senescence, cooler temperatures at key times of development or spore dispersal, less susceptible *Ribes* species, or a less favorable spatial pattern of hosts at higher elevations.

**PRECIPITATION.**—Mean summer precipitation was an important predictor variable in our model. Other researchers have observed a relationship between WPBR incidence and regional moisture characteristics. For example, Van Arsdel et al. (1956) attributed low WPBR incidence in southwestern Wisconsin to the dry climate of the region.

Optimal temperature and moisture conditions for survival of *Cronartium ribicola* have been well documented (Mielke 1943, Van Arsdel et al. 1956). Infection of pines requires extended periods of time (Charlton 1963) during late summer and early autumn with nighttime temperatures below 19.4°C (67°F) and free moisture on the needle surfaces (Kimney and Wagener 1961). Van Arsdel et al. (1956) concluded that at least 2 consecutive days of these favorable conditions are required for infection of pines.

Extended temperature data from high-elevation weather stations within our study area were not available, and interpolating temperatures between low-elevation weather stations is inappropriate because of local temperature inversions that are common in mountain environments (Baker 1944). Thus, we did not include a temperature variable in our analysis. We were also unable to locate climate data for mountainous areas that included summer moisture estimates other than mean precipitation amounts. It is generally thought that moist summers are conducive to WPBR development and spread; however, mean summer precipitation alone is probably not the best indicator of favorable climate conditions. For example, Mielke (1943) noted that a heavy “flare up” of WPBR incidence occurred in Idaho during a summer of relatively low mean precipitation in 1937. In fact, dew may be an equally important source of moisture (Mielke 1943). Cloudy summer periods and high relative humidity periods may be better indicators of WPBR incidence than precipitation.

**AVERAGE TREE DIAMETER.**—The importance of average tree diameter at breast height (DBH) in the logistic regression model may be due to 2 factors. First, smaller-diameter trees tend to have less foliage than larger-diameter trees and are therefore smaller targets for spores. Second, most cankers we inspected were in the upper portion of tree crowns in the interior of stands or throughout the crown of trees on an open edge of the stand. We speculate that wind patterns during times of basidiospore dispersal from *Ribes* to pines concentrate infections along the windward and upper sides of a stand. Wind-dampening effects of
the forest canopy and screening of spores by larger trees may reduce the transfer of spores to smaller, more sheltered trees.

While diameter could reflect the length of exposure, the length of exposure is probably not important because even the smallest trees in our samples likely pre-date WPBR presence in the region.

Average DBH appears to be more important to the intensity of infection on sites that are infected than to WPBR incidence. Of 16 stands with an average DBH of <10 cm, all but 2 were infected, with an average infection level of 19.5% (2–85%) for the infected stands. Of 14 stands with ≥20 cm average DBH, 4 were uninfected, and the average infection rate for the infected stands was 46.3% (2–87%).

Other variables.—Other variables were statistically significant in the stepwise logistic regression analysis. However, these variables had much lower Wald-$\chi^2$ values and contributed proportionally much less to explaining observed variability in incidence than elevation, mean summer precipitation, and average tree diameter. Due to the low Wald-$\chi^2$ values and potential correlations between these variables, their statistical and biological significance is suspect. Also, since we did not test each of the independent variables, it is possible that we included irrelevant variables in the model.

Implications for Future Research

The potential relationships between site and stand characteristics that we identified in this analysis represent a “snapshot” in time for the current stage of the developing WPBR epidemic in our study area. These relationships help identify areas where WPBR will likely spread and/or intensify first. Aging cankers could help researchers (1) determine how WPBR has moved and intensified in the region and (2) differentiate between sites susceptible to long-range transmission and those where WPBR intensifies quickly. Such a study could also help researchers predict future spread and intensification of WPBR in the region. However, the characteristics of spread and intensification may change in the future due to genetic adaptations by Cronartium ribicola, an exponential increase in inoculum availability, changes in host distributions, or shifts in regional climate patterns.

Management Implications

The ability to identify areas of potential rapid intensification or areas with a low probability of infection or intensification over time would help land managers direct mitigation efforts. For example, a spatial model that identifies these areas of intensification could aid the ongoing search for phenotypically resistant trees, which are highly visible in severely infected stands. In some areas vegetative competition from Abies lasiocarpa (subalpine fir) is as much of a concern as WPBR (Keane et al. 1994). A spatio-temporal WPBR spread and intensification model would help managers decide where treatments to reduce this competition would be effective. Where WPBR intensification probability is low, silviculture and/or prescribed fire could be used to reduce competition and provide regeneration opportunities for white pines. Conversely, conducting these activities in areas with a high probability of WPBR intensification could potentially increase inoculum levels through the regeneration of susceptible white pines or an inadvertent increase in Ribes abundance. A predictive model could also help resource planners assess the future effects of white pine mortality on wildlife, water quality and quantity, avalanche activity, and recreation.

Acknowledgments

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Literature Cited


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National forests and parks have a mandate to manage against exotic plants both in their charters (U.S. Congress 1872) and recent executive directives (Clinton 1994, 1999). Management of exotics requires their identification. Plants exotic to specific regions (e.g., Whitson 1992) and management units (e.g., Whipple 2001) have often been listed to facilitate recognition and identification. A listing by ecological zones within a region would refine this capacity.

In addition, a listing by environmental types within a region would provide a key to environments (or sites) the plant might invade or might already have invaded. Identification of occupiable environmental types will enable managers to concentrate control efforts in a fraction of the management area. Two environmental qualities are important. First, one considers environmental types (defined in Methods), determined by physical characteristics such as climate and substrate (Holdridge 1947, Daubenmire 1968, 1970, Whittaker 1975) and indicated locally by potential natural vegetation (Pfister et al. 1977, Mueggler and Stewart 1980, Steele et al. 1983). And, within each of these, one compares sites on the competitive spectrum from freshly disturbed (noncompetitive) to late seral (very competitive; Grime 1979, Despain 1990).

The objectives of this paper are thus to list the common exotics of the northern Rocky Mountains, to provide separate lists of the exotics present in major upland environmental types of the region, and to compare exotic presence in an early (less competitive) and late (more competitive) seral stage in each environmental type. A companion paper extends our results to separately map the potential distribution of major exotics on disturbed and undisturbed sites in Yellowstone National Park (Despain et al. 2001).

METHODS

Our term environmental type is synonymous with Daubenmire’s (1968a, 1968b, 1970) habitat type (HT). (1) An environmental type (ET = HT) includes all environments (equivalent, but not identical) capable of supporting a climax...
association (series of plant communities of the same kind). (2) The concept is useful because it groups discrete sites (or environments as opposed to plant communities) likely to respond similarly to similar management (Daubenmire 1968b, 1976, Pfister et al. 1977, Mueggler and Stewart 1980). (3) The term environmental type is preferred because it clarifies the concept that the types represent physical environment (e.g., moisture and temperature) rather than habitat for a particular organism, since the latter “habitat type” may either extend across several environmental types (e.g., wide-ranging plants in Table 3) or may not exist in the organism’s optimal environmental type (e.g., if vegetation of the seral stage present provides too much competition [Walter 1960] or fails to provide necessary nutrients, cover, or structure). Daubenmire (personal communication) recognized the environmental type/habitat type confusion—especially among zoologists—and wished he had called his types “environmental types.”

To determine which exotics might invade a specific environmental type (e.g., a montane environment occupied by Pseudotsuga menziesii/Symphoricarpos albus at climax), we needed to observe exotic colonization of well-inoculated sites in that type. Thus, we sampled several (7–11) sites jointly in that type and near a major highway that has long delivered seed to it (Table 1).

To determine which “seral” vegetation types in that environmental type could be invaded, we needed to compare invasion of highly disturbed (low competition), less disturbed (early seral), and high competition (late seral) sites (Grime 1979) occupying that physical environment. Thus, we sampled relatively gentle road cuts, logged right-of-way (not reported here), and nearby undisturbed vegetation at each of the 7–11 sites studied. The fact that our work was primarily in national parks facilitated location of undisturbed sites adjacent to highly disturbed sites. The relatively low establishment of a species on a late seral site, perhaps 20–30 m away, is attributed to competition but could also be due to failure to disperse. We attribute most of the deficiency to competition, however, both because differences in distances from the highway are short and because dispersal is a characteristic selected for in opportunistic species.

To complete the list of exotics likely to invade our region, we needed to sample other major environmental types representative of the environmental gradient from steppe upward through forest to the alpine. Thus, we sampled 15 environmental types along highways crossing the mountains in Glacier and Grand Teton national parks (1984–1985) and in intervening lowland areas (in 1986). We identified major environmental types by using late seral vegetation as indicators (Holdridge 1947, Daubenmire 1968a, 1968b, 1970, Whittaker 1975).

While our exotic lists for major environmental types approach completeness, our regional list is incomplete because we omitted less widespread types such as those along streams or on unusual substrates. The environmental types (HT’s) sampled are listed, in altitudinal order, in Table 1, with abbreviations, general locations, and sample size (~10). Underlying changes in climate and soils along the gradient are compared in Table 2, as well as by Daubenmire (1968a, 1970), Pfister et al. (1977), Mueggler and Stewart (1980), and Steele et al. (1983).

Thus, our sample design included 15 environmental types (HT’s), 2 treatments reported here (and 3 others [Weaver et al. 1993]), and approximately 10 replications (sites). Vegetational characteristics of each of the approximately 800 sites studied were recorded with measures of presence, frequency, and cover of both native and exotic species present. (1) Presence was recorded by listing all exotic and native plant species present in a 1 × 25-m plot representative of the zone and parallel to the highway traveled. We separately noted any other species present in adjacent similar vegetation. Natives in the plots, not discussed here, are listed in Weaver et al. (1993). (2) Cover of a species was measured by recording the percentage of 75 points covered by that species. The 75 points were measured by lowering 3 pins into the vegetation in each meter point along the plot’s center line. Cover was integrated over a type by averaging cover measurements across sites, but only at sites where the species occurred. We omitted unoccupied plots in these calculations to measure the success of species at sites where they did occur. If desired, cover values for the environmental zone as a whole can be calculated by multiplying cover values presented by the associated constancy value; this will correct the cover
value downward for sites at which the species did not occur (Table 3). (3) Constancy was calculated as the percentage of sites in the environmental type at which the species occurred. We hypothesized that a strong presence of an exotic in roadside samples would result in a strong presence in adjacent undisturbed vegetation because a strong presence at the roadside indicates both good adaptation to the environment and production of many propagules for colonization of nearby sites. We tested this hypothesis, using both constancy and cover data, by comparing the presence of each exotic in disturbed vegetation on sites adjacent to occupied vs. unoccupied native vegetation. We tested this hypothesis, using both constancy and cover data, by comparing the presence of each exotic in disturbed vegetation on sites adjacent to occupied vs. unoccupied native vegetation. The Mann-Whitney test, a non-parametric t test, was used (Gibbons 1985). An alternative test, regression/correlation, was forgone because quantitative data from the undisturbed sites are currently unavailable.

In a companion paper (Despain et al. 2001), we map the potential range of an exotic in a region by using a map of the environmental types (HTs) of the region (e.g., Despain 1990b) as a base and shading ETs invasible by the species studied. We expect the range mapped on disturbed sites to enclose the range on undisturbed sites because competition is less rigorous on disturbed sites.

## RESULTS

Our observations of exotic plant presence on roadsides (outslopes) and adjacent undisturbed vegetation of 15 environmental types are summarized in Table 3. (1)Vertically, table segments list groups of exotic species found, according to their ranges on the altitudinal gradient studied: those with narrow, moderate, or broad amplitude and those with an interrupted range. (2) The elevational gradient ranges from dry steppe, through warm dry forests, warm moist forests, cool forests, to mountain meadows and alpine tundra. Fifteen segments (environmental types or habitat types) on this gradient are listed horizontally. These are named and characterized in Table 1. (3) Entries in Table 3 specify the presence of exotics, both on disturbed sites in corridors along which propagules are expected to move and on adjacent undisturbed sites. Presence on roadsides is indicated by constancy (the percent of occupied

<table>
<thead>
<tr>
<th>Environmental type (HT)</th>
<th>Abbreviation</th>
<th>Location</th>
<th>Sample</th>
</tr>
</thead>
<tbody>
<tr>
<td>GRASSLANDS/ SHRUBLANDS</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stipa comata/ Bouteloua gracilis</td>
<td>STCO/ BOGR</td>
<td>Broadwater MT</td>
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<tr>
<td>Agropyron spicatum/ Bouteloua gracilis</td>
<td>AGSP/ BOGR</td>
<td>Broadwater MT</td>
<td>8</td>
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<tr>
<td>Artemisia arbuscula/ Festuca idahoensis</td>
<td>ARAR/ FEID</td>
<td>Teton WY</td>
<td>10</td>
</tr>
<tr>
<td>Artemisia tridentata/ Festuca idahoensis</td>
<td>ARTF/ FEID</td>
<td>Meagher, Gallatin MT</td>
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<tr>
<td>Festuca scabrella/ Festuca idahoensis</td>
<td>FESC/ FEID</td>
<td>Glacier MT</td>
<td>10</td>
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<tr>
<td>DRY FORESTS</td>
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<tr>
<td>Pseudotsuga menziesii/ Symphoricarpos albus</td>
<td>PSME/ SYAL</td>
<td>Meagher, Gallatin MT</td>
<td>10</td>
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<tr>
<td>Pseudotsuga menziesii/ Physocarpus malvaceus</td>
<td>PSME/ PHMA</td>
<td>Gallatin MT, Park WY</td>
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<tr>
<td>WARM MOIST FORESTS</td>
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<tr>
<td>Populus tremuloides/ Calamagrostis rubescens</td>
<td>POTR/ CARU</td>
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<tr>
<td>Tsuga heterophylla/ Clintonia uniflora</td>
<td>TSHE/ CLUN</td>
<td>Flathead MT</td>
<td>10</td>
</tr>
<tr>
<td>Abies lasiocarpa/ Clintonia uniflora</td>
<td>ABLA/ CLUN</td>
<td>Flathead MT</td>
<td>9</td>
</tr>
<tr>
<td>Abies lasiocarpa/ Xeophyllum tenax</td>
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<td>Abies lasiocarpa/ Arnica cordifolia</td>
<td>ABLA/ ARCO</td>
<td>Teton WY</td>
<td>10</td>
</tr>
<tr>
<td>Abies lasiocarpa/ Vaccinium scoparius</td>
<td>ABLA/ VASC</td>
<td>Teton WY</td>
<td>10</td>
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<td>HIGH GRASSLANDS AND TUNDRA</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Festuca idahoensis/ Agropyron caninum</td>
<td>FEID/ AGCA</td>
<td>Teton WY</td>
<td>10</td>
</tr>
<tr>
<td>Deschampsia caespitosa/ Carex spp.</td>
<td>DECA/ CASP</td>
<td>Park WY, Carbon MT</td>
<td>11</td>
</tr>
</tbody>
</table>

aEnvironmental types are those of Pfister et al. (1977) and Meuggler and Stewart (1980).
bAbbreviations provide a key to Table 3. They represent dominant species by reporting initial letters (2) from genus and species names.
cLocations are specified by county. Glacier and Flathead are in the Glacier National Park area. Broadwater and Meagher are adjacent to the Bridger/Big Belt Mountains. Gallatin, Park, and Carbon are at the north edge of Yellowstone. Teton includes Grand Teton National Park.
dEach environmental type was sampled at 7–11 sites. At each site 5 environments were sampled with 5 parallel quadrats. Of these, those representing roadsides and undisturbed vegetation are discussed here.
sites in the ET). Potential dominance on those sites is indicated by cover (the average cover on sites which are occupied); and current realized success is found by multiplying these entries. Presence in undisturbed vegetation is reported nonquantitatively from plots of the same size and shape. The material in cells having constancies >30% is in boldface because a higher constancy indicates that the plant has established more or less regularly in that environmental type.

The 29 exotic plants occurring in >10% of the sites in at least one environmental type are listed (Table 3, vertically). Ten species have a narrow amplitude; i.e., they have a high constancy in only 1 or 2 types. Ten species have a moderate amplitude, that is, range over 4–8 environmental types, as arranged in Table 3. Four species have a broad amplitude, ranging over 10–14 ETs. The ranges of 5 species of moderate to broad distribution are interrupted; that is, they occupy low and higher sites, but not the intervening environments. Two types of occurrence deserve further comment. First, plants with low constancy in a single ET are ignored because they may occupy microsites in an environmental type; that is, they do not actually occupy the environmental type discussed. Alternatively, they could either be new to the region (Forcella and Harvey 1981) or be the vanguard of a newly adapted ecotype. Second, 7 environmental types contain a species which occurs on undisturbed, but not on non-competitive disturbed, sites. Such species could possibly require a stability not found at roadsides, e.g., lack of erosion or frost action. More likely, these species are “accidentals”; otherwise this pattern would repeat in similar types, as it does for Taraxacum.

On disturbed sites the number of high-constancy (>30%) exotics (Fig. 1, Table 3) was 10–11 in grasslands, 9–12 in dry forests, and 8–10 in warm moist forests and 7–11 in cool forests. Numbers were lower in shrublands (5–7), mountain meadows (5), and alpine (1). Numbers of low-constancy exotics were 3–6 in grasslands, 5–11 in dry forests, 3–6 in warm moist forests, and 2–6 in cool forests. Low-constancy richness was similar in mountain shrublands (2–5) and mountain meadows (7), and low in alpine (2).

The number of exotics entering undisturbed sites (Fig. 1, Table 3) decreased from grasslands (9–13) through aspen forests (8) and shrublands (5–7) to conifer forests (0). It increased again in mountain meadows (7) and alpine tundra (2). While the richness (average number of species per sample) on undisturbed sites is always lower than on disturbed sites, most grassland ETs are occupied by at least one species not found on disturbed sites in it.

**DISCUSSION**

**Exotics in the Northern Rocky Mountains**

We found only 29 exotic species (Table 3) in our sample of major upland environmental types of Glacier National Park, Grand Teton National Park, and little disturbed intervening areas including parts of Yellowstone National Park. Our list does not include species that have invaded since 1986, which occupy heavily grazed areas or uncommon substrates. To
### Table 3. Presence of major exotic species in major environmental types of the northern Rocky Mountains. Code digits indicate constancy and cover on disturbed sites and tendency to invade undisturbed vegetation. Constancies >30% are in boldface to emphasize environments where the species is common.

<table>
<thead>
<tr>
<th>Species with narrow amplitude</th>
<th>STCO</th>
<th>AGSP</th>
<th>ARAR</th>
<th>ARTR</th>
<th>FESC</th>
<th>PSME</th>
<th>POMO</th>
<th>TSHC</th>
<th>CLUN</th>
<th>ABLA</th>
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<tbody>
<tr>
<td>Agropyron cristatum</td>
<td>7CX</td>
<td>X</td>
<td>1A</td>
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<tr>
<td>Alyssum alyssoides</td>
<td>8AX</td>
<td>9BX</td>
<td></td>
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</tr>
<tr>
<td>Camelina microcarpa</td>
<td>4AX</td>
<td>5AX</td>
<td></td>
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<tr>
<td>Bromus japonicus</td>
<td>8BX</td>
<td>6AX</td>
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<td>Descurania pinnata</td>
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<td>5AX</td>
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<tr>
<td>Rumex acetosa</td>
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<tr>
<td>Dactylis glomerata</td>
<td></td>
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<td></td>
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</tr>
<tr>
<td>Festuca pratensis</td>
<td></td>
<td></td>
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<tr>
<td>Verbascum thapsus</td>
<td>2AX</td>
<td>1AX</td>
<td></td>
<td></td>
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<td></td>
<td></td>
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<td></td>
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<tr>
<td>Chrysanthemum leucanthemum</td>
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</tr>
</tbody>
</table>

### Species with moderate amplitude

| Tragopogon dubius           | 4AX  | 8AX  | 1AX  | 5BX  | 4AX  | 2A   | 5BX  | 1A   | 1A   | 2B   |      |      |      |      |      |
| Centaurea maculosa          | 4BX  | 3AX  | 1D   |      |      | 7EX  | 2A   | 7C   | 2B   |      |      |      |      |      |      |
| Mellotus officinalis        | 8BX  | 5BX  |      |      |      | 6BX  | 3B   | 5A   | 9CX  | 2A   | 1A   |      |      |      |      |
| Cirsium arvense             |      | 1A   |      |      |      | 3CX  | 4A   | 1A   | 5CX  |      |      |      |      |      |      |
| Poa compressa               | 1A   | 1A   |      |      |      | 6CX  | 1AX  | 1A   | 8C   | 1A   | 1A   | 3A   | 1A   |      | X    |
| Trifolium procumbens        |      |      |      |      |      | 4BX  |      | 7BX  | 7C   | 5D   | 3B   |      |      |      |      |
| Trifolium pratense          |      |      |      |      |      | 5BX  | 1AX  |      | 7D   | 1C   | 8D   |      |      |      |      |
| Trifolium repens            |      |      |      |      |      | 5DX  | 1A   |      | 8C   | 4B   | 8B   | 1B   | 4B   | 1C   |      |
| Agrostis alba               |      |      |      |      |      |      | 1A   | 6DX  | 6C   | 4A   | 5B   | 2B   | 4B   |      |      |
| Trifolium hybridum          |      |      |      |      |      |      | 2A   | 1AX  |      | 2C   | 9D   | 3D   | 6D   | 5E   | 5E   | 6C   |

### Species with broad amplitude

| Bromus inermis              | 2B   | 5E   | 2B   |      |      | 5D   | 5DX  | 8B   | 2AX  | 5E   | 8E   | 6B   | 7D   | 4D   |      |
| Poa pratensis               | 4EX  | 5EX  | 9EX  | 9EX  | 8DX  | 7CX  | 6CX  | 7BX  | 4B   | 6C   | 7B   | 5C   | 4C   | 7DX  |      |
| Taraxacum officinale        | X    | 2AX  | X    | 5BX  | 3B   | 5CX  | 8BX  | 8BX  | 9C   | 8C   | 5C   | 9E   | 8D   | 9CX  | 3BX  |
| Phleum pratense             |      | 1AX  |      | 9DX  | 7CX  | 8DX  | 9EX  | 9D   | 9C   | 9C   | 8B   | 8C   | 7BX  |      | 0A   |

### Species with interrupted ranges

| Lactuca serriola            | 5AX  | 2BX  |      | 2A   | 1A   | 5A   |      |      |      |      |      |      |      |      |      |
| Bromus tectorum             | 9BX  | 7DX  |      |      |      |      |      |      |      |      |      |      |      |      |      |
| Polygonum aviculare         |      | 1AX  | 9CX  | 4BX  |      |      |      |      |      |      |      |      |      |      |      |
| Madia glomerata             |      | 7AX  | 5CX  |      | 1A   | 3B   |      |      |      |      |      |      |      |      |      |
| Medicago lupulina           |      | 1A   |      |      |      | 4C   | 6C   |      |      |      |      |      |      | 3C   | 4D   | 3A   |

---

*Environmental types are listed from dry to moist, as in Table 1: grasslands (1, 2, 5), shrublands (3, 4), dry forests (6, 7), aspen (8), warm moist forests (9–11), cool forests (12, 13), mountain meadows (14), and alpine (15).

*Codes indicate constancy in roadside sites, cover in occupied roadside sites, and invasiveness. Constancy (= the probability of occurring in a stand in the environment): 0 = 0–9, 1 = 10–19, 2 = 20–29, . . . 9 = 90–100%. Cover classes are A = +, B = 0–1%, C = 1–2%, D = 2–5%, E = 5–25%, F = >25%. Invasion of undisturbed areas in an environmental type is indicated by X.*
illustrate this qualifying statement, we give *Chrysanthemum leucanthemum* as a species underrepresented because its range is expanding, *Centaurea maculosa* as less common than expected because it expands with grazing absent on the sites we studied, and *Euphorbia esula* as a species that is most important in areas moister than we sampled, e.g., riparian sites. Since volcanic materials are uncommon in the region, extrapolation to volcanic parts of Yellowstone National Park must be made with caution.

Exotic Richness Across Environmental Types

The presence of an exotic in an environmental type depends on at least 3 factors. First, the environment must be within the physiologic niche of the species. A species range on disturbed sites across the broad altitudinal gradient suggests the breadth of the physiologic niche. Second, the environment/vegetation must be within the realized niche of the species. Presence in undisturbed vegetation of an environmental type demonstrates presence in the realized niche, with respect to climax (= late seral) vegetation. And third, presence in either disturbed or undisturbed sites demonstrates that the species has dispersed to the site. While proximity to a highway maximized the exotic’s likelihood of arrival at the sites we studied, sites in environmental types in the agricultural zone had far more exposure to invading propagules than did sites in the high mountains.

On disturbed sites the exotic richness (species number) across the environmental gradient seems remarkably constant (Fig. 1), despite changes in its composition (Table 3). Regulars (constancy >30%) were 8–12 except in shrublands (5–7), one conifer forest (7), mountain meadows (5), and tundra (1). While one might argue that incidentals (constancy <30%) indicate microsite effects, numbers of incidentals were also rather constant (2–6), except in the *Pseudotsuga/Symphoricarpos* environment (11). Thus, disturbed sites seem to have a more or less constant “richness capacity,” but filled with species differing among environments. Shrubland environments are slightly species deficient, for no obvious reason. *Pseudotsuga* environments have a small
excess, possibly due to their location at elevations supporting floras from Mediterranean/steppe environments and northern coniferous environments. While we see no corresponding break in environmental rigor (Table 2), the tundra environment is notably exotic poor.

In contrast, numbers of species invading undisturbed vegetation of different environmental types vary greatly (Table 3): grasslands (7–13), aspen (8), dry Pseudotsuga forests (8–10), other conifer forests (0), and alpine (2). This suggests that the undisturbed vegetation of major environmental types differs greatly in competitiveness. In grasslands and dry forests, exotics occupying disturbed sites, i.e., tolerating the physical environments, also colonize adjacent undisturbed vegetation. The open structure of these vegetation types apparently provides non-competitive microsites for these exotics. The exotic deficiency seen in the shrub zone was also seen on disturbed sites and is most likely induced by the physical environment. In contrast, exotics known to tolerate physical conditions in the conifer zone (i.e., disturbed sites) rarely invade adjacent forest. These exotics are probably excluded from forests by heavy competition for water/nutrients (Watt and Fraser 1933) or light. Thus, removal of forest communities, by fire or harvest, should allow plants capable of occupying noncompetitive disturbed sites to colonize more widely in the forest environment, where they may inhibit forest establishment but will finally yield when they are overtopped by tree species.

The low exotic richness of the alpine is probably due in part to environments too rigorous for establishment of opportunists (Billings and Mooney 1968), but this does not explain the sharp decline from the forest and meadows below. It is likely that failure of dispersal also contributes. To illustrate, we contrast the exotic presence in alpine and mountain meadow vegetation. (1) First, while plants adapted to disturbed Old World alpine environments may exist, vectors—crops, animals, machinery—rarely pass directly from these areas to high-altitude areas in the Rockies. Thus, the transfer of potential weeds has been slight. We conservatively suggest that as recreational use grows, managers should minimize introductions (exchanges) of exotics by increasing both quarantine and efforts to detect and eradicate unwanted establishment. (The presumed need for this caution might be tested by showing that alpine opportunists are available in the Old World [Alps, Himalayas, Southeast Asia] flora and that the grazing disturbance has been sufficient and environmental rigor slight enough to induce the evolution of opportunistic species.)

(2) In contrast, while mountain meadows seem almost equally isolated, our culture has provided a stepping stone for exotics to them. The exotics have been introduced to environmentally similar foothill sites through commercial and agricultural activity, have established, and are being transported upward, especially as motorized backcountry use increases. For example, while an experimentally bared portion of a remote mountain meadow (Weaver and Collins 1977) was not infected by Cirsium arvense in the preceding 2 decades, thistle appeared soon after loggers entered nearby forests.

Distribution of Individual Species

Knowledge of the tolerance range of a species tells us where to look for established stands and where to expect establishment. Both are useful in planning control. It may also help us estimate a species’ ability to cross stressful—dry or cold—zones without assistance. The importance of the latter is declining as human transport becomes the dominant dispersal mechanism.

Distribution among Disturbed Sites.—The physiologic niche of a species is suggested by its presence in disturbed sites because open spacing reduces competition. We recognize 4 distribution types (niche types).

First, species with narrow distributions are most important in lower, warmer environments (Table 3). Some occupy dry grasslands (Agropyron cristatum, Alyssum alyssoides, Camelina microcarpa, and Bromus japonicus), shrublands (Rumex acetosa), and warm forests (Dactylis glomerata, Festuca pratensis, Veronica thapsus). None are important in the moist conifer zone, cool conifer zone, or mountain grasslands/tundra. In our data Chrysanthemum leucanthemum seems to have narrow tolerances, but it is spreading rapidly into drier environmental types including those dominated by Pseudotsuga menziesii and Festuca idahoensis.

Second, plants with broader tolerances populate wider zones in the altitudinal gradient (Table 3). Low-site plants (Tragopogon dubius, Centaurea maculosa, and Melilotus officinalis)
may prefer grasslands over shrublands. Exotics dominating near the lower forest margin plants include *Cirsium arvense*, *Poa compressa*, and the most drought tolerant (?) of the clovers (*Trifolium pratense*). *Trifolium pratense* occurs throughout the low/warm conifer zone. *Trifolium repens*, *T. hybridum*, and *Agrostis alba* occur in the moist conifer zone, both low/warm and high/cool.

Third, 2 plants (*Poa pratensis* and *Taraxacum officinale*) have remarkably wide distributions, extending from low grasslands through forests to mountain meadows and even tundra (Table 3). Two others (*Bromus inermis* and *Phleum pratense*) range from moister grassland environments through forest environments to mountain meadow environments. All of these species cover 2–5% (D in Table 3) or 5–25% (E) of the ground surface on disturbed sites in some environments they occupy.

Fourth, 5–6 species representing 2 subgroups have interrupted or bimodal distributions (Table 3). First, *Lactuca serriola* and *Bromus tectorum* were found in dry grasslands (*Bouteloua* and *Agropyron*), were absent from moister grassland environments, and reappeared in dry forests (*Pseudotsuga*). One might speculate that these species tolerate arid environments, cannot compete in moister grassland environments, and become competitive again where precipitation evaporates from treetops before it becomes available to plants in the ground layer. This hypothesis would be more convincing if the interruption occurred in the undisturbed zone, but not in the disturbed zone. The same interruption was reported for 2 native grasses (*Stipa viridula* and *Koeleria nitida*) and 5–10 exotic species (including *Bromus inermis*, *B. tectorum*, *B. japonicus*, 3 annual mustards, and *Kochia scoparia*) that are present in the dry plains of eastern Montana, disapper in the foothills and grasslands, and reappear in the *Pseudotsuga* zone to the west (Weaver and Meier 1997). Second, 3–4 species have modes in both a lower-elevation zone and in the *Abies*/mountain meadow zone. *Descurania* (listed as unimodal) appears in dry grasslands and has a weak high mode. *Polygonum* and *Madia* appear first in moister grasslands and have solid high modes. *Medicago* appears first in the dry forest zone (*Pseudotsuga*) and reappears in the *Abies*/mountain meadow zone. We speculate (hypothesize) that plants of the lower mode occupy a site dry due to lack of precipitation and those of the high mode occupy sites dry due to the high wind flows near mountain ridges (cf. Weaver 2001).

Each altitudinal zone contains species of both narrow and broad environmental amplitudes. This is demonstrated by listing the species within an amplitude group according to their locations on the altitudinal gradient (Table 3). Thus, among species with narrow distribution, *Agropyron cristatum*, important only in the driest environments, appears first. And among species with broad distribution, *Poa pratensis* appears before *Taraxacum officinale* because it becomes important at lower altitudes.

**Distribution among undisturbed sites.** — The tendency of exotics to escape from distribution corridors is inversely related to the penetrability of adjacent vegetation. Thus, while establishment on disturbed sites provides an indication of the physiologic niche, invasion of natural vegetation provides an indication of the realized niche, i.e., performance under competition from natural vegetation.

The escape of species of all amplitudes and gradient segments is proportional to the openness of the adjacent native vegetation. Species of narrow to moderate altitudinal ranges often escape into relatively open grassland or Douglas-fir (*Pseudotsuga*) vegetation, but they are unlikely to escape into denser subalpine fir forests (*Abies*; Table 3). Similarly, species with broad ranges tend to escape into grassland and low forests but are unlikely to escape into dense forest environments (Table 3). Given these observations, we expect bimodal species to escape in their lower, drought-stressed environments, but to be competitively constrained in their upper, moister environments. This is true except where the environment in the upper arm is sufficiently wind-dried to create competitive conditions (and escape) similar to that in the low-elevation mode (Table 3). *Polygonum aviculare* and *Madia glomerata* are bimodal plants illustrating the last point.

While undisturbed vegetation in the center of the forest zone may be impenetrable, segments of the forest zone that have been logged or burned are probably more penetrable, either because competition for light or water/nutrients (*Watt and Fraser 1933*) is reduced or because wind dispersal is facilitated. Analysis of comparable samples (existing data) will eventually test this hypothesis.
We expect the dominance of a species on disturbed sites of an environmental type to indicate its capacity to invade undisturbed sites in that environmental type, both because a species thriving on the disturbed site must be well adapted to the physical environment it occupies and because, as a well-adapted species, it will produce more seed. Our hypothesis is, then, that invading species will be more dominant on adjacent disturbed sites than noninvaders. In fact, the median constancy of invaders usually does exceed the median constancy of noninvaders, and the difference is significant in 70% of the cases (Table 4). When data are pooled across all except the moist conifer types, which show no escape, the difference is significant ($P < 0.0005$). The moist conifer types, PSME/PHMA, TSHE, and ABLA forests are reasonably excluded from this analysis because no exotic species have moved from roadside to forested environments.

### Evaluating Exotics

If public forest and park vegetation is to be managed for “pre-Columbian” condition (cf. U.S. Congress 1872), exotics should be excluded. If this is impossible, managers should strive to prevent exotics from dominating the vegetation because dominants are most likely to affect the success of native plant associates and, through their influence on vegetation composition, animal associates as well (cf. Clinton 1999). In evaluating species, we minimize “breadth of distribution” as a criterion on the assumption that conservationists should equally emphasize preservation of all vegetation types important in the region. Vegetation types rare in the region deserve special attention if they are endemic to it, but they are less critical if they are well represented in other regions. Because our project was designed for generality, we studied no rare types.

Sites undergoing primary succession are rare in the forest and grassland zones (e.g., river deposits or landslides) and more common in ridge sites of the alpine (e.g., undecomposed rock). Although slopes of our roadside sites may be steeper than the average disturbed site, our data (Table 3, cover classes D and E) probably identify the most problematic species of upland sites undergoing primary succession. On disturbed grassland sites (including mountain meadows) the only exotic with 5–25% cover (E) was *Poa pratensis* and exotics having 2–5% cover (D) were *Bromus inermis*, *B. tectorum*, *Phleum pratense*, and *Rumex acetosa*. In dry forests exotics with cover 5–25% (E) were *Dactylis glomerata* and *Phleum pratense*, while those with cover 2–5% (D) were *Agrostis alba*, *Bromus inermis*, and *Trifolium repens*. In moister conifer forests, those with cover 5–25% (E) were *Bromus inermis*, *Melilotus officinalis*, *Taraxacum officinale*, and *Trifolium hybridum*; and 2–5% (D) were *Medicago lupulina*, *Phleum pratense*, *Trifolium pratense*, and *T. procumbens*. No exotic covered as much as 5% of either disturbed or undisturbed sites in the alpine. Ironically, the most aggressive exotics are rarely discussed as problematic, and none of the exotics designated as noxious seem to dominate in the wide range of environments we studied.

Secondary secession sites—such as recent burns, logged areas, or old fields—are more common on public lands than are primary succession sites. Here, the performance of exotics may be similar to their performance on primary succession sites. This expectation may overstate the problem since exotics, mostly dispersing laterally through space, must compete with natives colonizing both from the propagule bank and dispersing laterally. Thus, we expect the grasses (*Agrostis, Bromus, Dactylis, Phleum*, and *Poa*), legumes (*Melilotus, Medicago*, and *Trifolium*), and dandelion, listed above, to be among the most important exotic invaders.

### Table 4

<table>
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<th>Environmental type (HT)</th>
<th>BOGR</th>
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<th>PSME</th>
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* $P = 0.0005^a$  

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$^a$Kruskal-Wallis test (Gibbons 1985)
Late seral sites may be as common as or more common than secondary succession sites in national forests and parks. Later seral vegetation of moister forests is impenetrable, but grasslands, shrublands, and dry forests are invaded by many species (Table 3). However, because dominance of all species falls from disturbed to undisturbed sites, we discount most of the species not listed as invaders of secondary succession sites. This position may underestimate the effects of robust (e.g., Agropyron cristatum or Melilotus officinalis) or very numerous (e.g., Bromus tectorum, B. japonicus, or Alyssum alyssoides) plants of the driest environmental types.

CONCLUSIONS

The number of exotics currently common in vegetation of the northern Rocky Mountains is relatively few, approximately 29 (Table 3). The altitudinal (temperature/moisture) amplitude of each of these species is described by presence in environmental types (HTs) representing segments of the environmental gradient (Table 3). Knowledge of species amplitudes will enable managers to estimate and even map potential distributions of exotics, both in disturbed (primary succession) and undisturbed (late seral) vegetation.

The overall invasibility of major environmental types—in both disturbed and undisturbed conditions—is indexed by tabulating exotic species richness across a broad altitudinal gradient of types. Grasslands and dry forest environments harbor the most exotic species, both in disturbed and undisturbed sites. Moist conifer forests have similar species richness on disturbed sites, but no exotics appear on undisturbed sites. Tundra environments support few exotics on either disturbed or undisturbed sites.

Dominance in vegetation in at least one environmental type is our criterion for recognizing an exotic of special concern, because a dominant is most likely to affect the success of plant associates and, through its influence on vegetation composition, the success of animal associates as well. We minimize breadth of distribution as a criterion on the assumption that conservationists should emphasize equally the preservation of all regionally common and internationally unique ecosystems. Seven species exhibited cover of 5–25% on disturbed sites they occupied in at least one type (Table 3); they include grasses (Agrostis, Bromus, Dactylis, Phleum, and Poa), legumes (Melilotus, Medicago, and Trifolium), Rumex and Taraxacum species. An additional seven species exhibited cover of 2–5% on disturbed sites in at least one environmental type (HT). Most of these plants were introduced intentionally and none of these stealth plants is normally considered a noxious weed.

ACKNOWLEDGMENTS

We thank the University of Wyoming/NPS (Grant #3-10144) and Montana Department of Transport (FHWA/MT 97-8115) for monetary support. B. Wood sampled sites in Glacier and Grand Teton national parks, J. Lichtardt sampled stands in the intervening area, D. Gustafson did most of the mathematical analysis, and T. Weaver did the writing. We thank many colleagues for critical discussion and D. Despain, K. Harper, and R. Sheley for review of the manuscript.

LITERATURE CITED


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More than 100 exotic plant species occur in Yellowstone National Park (Whipple 2001), and others will undoubtedly become established in the future. Many of these are likely to undergo range expansion. An ability to predict the areas threatened by expanding exotics should be of great value to park managers trying to minimize dispersal to susceptible areas and eradicate new colonies of these areas.

Information needed to predict the potential extent of a species includes knowledge of which environments are susceptible to invasion by the species and the location and extent of susceptible environments.

Both are available for Yellowstone National Park. First, we have a map of environmental types (Despain 1990a). Students of vegetation have pointed out that plant communities provide a good indicator for site conditions (Holdridge 1947, Whittaker 1975, Huschle and Hironaka 1980). In our area Daubenmire identified major environmental types (habitat types) for eastern Washington and northern Idaho and demonstrated the relationship of indicator species to both environmental qualities (Daubenmire 1952, 1956) and plant performance (Daubenmire 1976). His environmental types have been extended into southern Idaho, Montana, and Wyoming (Pfister et al. 1977, Mueggler et al. 1980, Hironaka et al. 1983, Steele et al. 1983), and their relationships to environment have been reviewed by Weaver et al. (2001).

Second, exotic species’ potentials to invade environmental types representing segments of the altitudinal gradient of the northern Rocky Mountains have been identified by Weaver et al. (2001). In their treatment the environmental range of a species is expected to be wider in disturbed sites (where competition is less) than in late seral communities (where competition is intense; Daubenmire 1968, Grime 1979, Huschle and Hironaka 1980), and this has been demonstrated (Weaver et al. 2001). Thus, we expect geographic ranges of exotic species in undisturbed vegetation to be narrower than, and nested in, ranges of the same species occupying disturbed vegetation.

This paper has 5 objectives: (1) to demonstrate a method for mapping potential plant distribution, (2) to illustrate it with 4 exotic plant species of Yellowstone National Park, (3) to publicize maps of 24 other exotics, (4) to compare the mapped ranges of each species on undisturbed and disturbed sites, and (5) to...
evaluate the method by comparing predicted distributions with actual distributions recorded by Yellowstone National Park’s weed management staff.

**Methods**

Working in Glacier National Park, Yellowstone National Park, Grand Teton, and areas between, Weaver et al. (2001) studied the distribution of exotic plants in 16 environmental types representing altitudinal zones of the northern Rocky Mountains. To determine which exotics invade disturbed and undisturbed vegetation in these environmental types, they recorded presence at 7–10 sites in each environmental type. To test susceptibility, they examined sites long exposed to diverse seed sources, i.e., sites near major highways. Their inspection of each site was concentrated in two 4 × 25-m plots running parallel to the road. Entry into disturbed sites was examined with a plot on the roadcut (inslope) bordering the highway. Entry into near-climax vegetation was examined with another plot in adjacent undisturbed vegetation. They listed all species present in the plot (and in similar undisturbed vegetation). They listed all species present in the plot (and in similar undisturbed vegetation). They listed all species present in the plot (and in similar undisturbed vegetation). They listed all species present in the plot (and in similar undisturbed vegetation). They listed all species present in the plot (and in similar undisturbed vegetation). They listed all species present in the plot (and in similar undisturbed vegetation). They listed all species present in the plot (and in similar undisturbed vegetation). They listed all species present in the plot (and in similar undisturbed vegetation).

We used Weaver et al.’s (2001) constancy value as a measure of a species’ ability to establish in an environmental type. Our maps indicate areas where a species was present at more than half the sites, at less than half the sites, and where they were capable of invading the climax community.

Two details require elaboration. First, because Weaver et al. (2001) did not encounter all environmental types that occur in Yellowstone National Park, we predicted exotic plant species occurrence, in those Yellowstone National Park types for which they had no data, from the most similar type for which data were available. A type was judged to be similar if it was in a similar moisture range of the same series. Resultant assignments are shown in Table 1. Exotic plant species presence in the known type was assigned to other types in its group.

Second, Despain’s (1990a) habitat type map sometimes uses mosaic mapping units that contain 2 dominant types, such as a matrix of grasslands with numerous islands of trees or

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**Table 1. Environmental types of Yellowstone National Park with Weaver et al. (2001) equivalents.**

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<th>Weaver et al.</th>
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vice versa. In these cases we averaged the constancy values of the 2 component types to derive a value for the mosaic units. If a species could invade the climax vegetation of either of the types, the entire map unit was considered to be susceptible to that species.

The resultant database was combined with the vegetation map using GIS to create 28 maps, one for each species studied. Four species are used as illustrations. Canadian thistle (*Cirsium arvense* [L.] Scop.) and spotted knapweed (*Centaurea maculosa* Lam.) are classed as noxious weeds by the surrounding states. Yellow sweetclover (*Melilotus officinalis* [L.] Lam.) and timothy (*Phleum pratense* L.) are crop plants that have become widely established in nonagricultural areas of the region. All 4 are of special concern to Yellowstone National Park managers.

To evaluate the success of our model, we compared locations we mapped for 3 species with actual locations mapped by Yellowstone National Park’s staff: Canadian thistle, spotted knapweed, and yellow sweetclover (data for timothy were not available).

**RESULTS**

Potential ranges of 28 exotic species found repeatedly in northern Rocky Mountain vegetation (Weaver et al. 2001) were mapped. Maps are available from the Geographic Information and Analysis Center, Montana State University, Bozeman, website (http://www.giac.montana.edu) in raster format at 50-m resolution, which should be useful for field purposes.

*Centaurea maculosa* is classified as a noxious weed in the Greater Yellowstone Ecosystem. The potential range of spotted knapweed mapped for disturbed sites (Fig. 1) includes the drier portions of the park, i.e., dry grasslands/shrublands and drier Douglas-fir forests. We mapped no areas where knapweed would have an expected constancy >50%. It is expected to invade climax vegetation only in dry grasslands/shrublands. In contrast to our predictions, actual Yellowstone National Park data showed many locations along park roads outside our predicted areas. Thus, more data are required to determine how threatening this species is in Yellowstone National Park. Unpredicted locations may be either transient occurrences that would disappear without constant seeding from the outside or an indication that knapweed enters environments not predicted by this model and is thus a serious threat over a much larger area than that mapped. While it does not appear to pose a serious threat to the majority of the park, it should be closely monitored as a potential threat especially in the Yellowstone River valley along the north boundary.

*Cirsium arvense* is a 2nd noxious weed of the Greater Yellowstone Ecosystem. The potential range mapped for it (Fig. 2) includes disturbed areas primarily in sparsely vegetated forest types and montane and subalpine grasslands/shrublands. We map no potential for entry into dry grasslands/shrublands. Because it does not invade climax vegetation, colonies established on disturbed sites are expected to die out as succession progresses to climax. No areas occurred where Canadian thistle would have an expected constancy >50%. Our map is
validated by noting that the majority of locations mapped by the Yellowstone National Park weed management staff are within the areas we mapped as potential habitat. Anomalous colonies in dry grassland/shrubland units may be located within inclusions of wetter environmental types.

*Melilotus officinalis* is a plant of special concern because it tends to dominate grasslands. The potential range mapped for yellow sweetclover on disturbed sites (Fig. 3) includes areas from drier grassland/shrubland sites in the northern part of the park to moist subalpine meadows. Our map predicts that *Melilotus* is capable of invading open climax communities across the same range. In the higher-elevation forest zone it can invade disturbed areas. No areas were mapped where yellow sweetclover would have an expected constancy >50%. Most locations recorded by the weed management staff did not correspond to predicted locations. More data must be gathered to determine the threat posed by yellow sweetclover. This species could become a serious problem if it displaces native climax species in sites to which it is well adapted.

While *Phleum pratense* is less obvious than the forbs just discussed, it has a significant tendency to dominate Yellowstone National Park vegetation (Weaver et al. 2001). The potential range mapped for timothy (Fig. 4) includes disturbed areas in most of the park. The map indicates that it can invade climax communities in a smaller range of environmental types, i.e., moister grasslands/shrublands and lower forest communities. It is more common than spotted knapweed, Canadian thistle, and yellow sweetclover on disturbed sites; i.e., it had a constancy >50% over large portions of the park. Because weed management staff
members do not map it, actual location data for this widespread species are not available for validation of our maps. While it is of little concern in the forested types because it would be greatly reduced at canopy closure, it could be of major concern in moister grassland/shrubland environments, which are the major source of forage for native ungulates.

DISCUSSION

This exercise has demonstrated a method for producing maps showing the potential ranges of exotic plant species in disturbed and undisturbed environments. Some general patterns are seen in the maps: (1) potential ranges of some species are limited while others are extensive; (2) most invader species are adapted to colonize disturbed sites, and thus species ranges are broader on disturbed than undisturbed segments of an environmental type; (3) where colony locations are known, constancies are usually highest in or near the potential range predicted. We attribute near-misses to interfingering of environmental types in ecolonal areas, unmapped islands of one type in a matrix of another, or inexact records of invader colony locations made by the weed team.

The certainty of our maps could be increased by adding more observations, particularly in those types where Weaver et al. (2001) have no data. The most extensive of these in Yellowstone are the wetland types and high-elevation forests.

For simplicity we have mapped ranges in successional extremes of severely disturbed roadside cuts and near-climax conditions. Roadcuts are typically void of developed soil and are usually in the early stages of primary succession. Gathering more data relating to more moderate disturbances, such as wildland fire, could usefully extend the work. For example, while Canadian thistle has been shown to increase after forest fire (Turner et al. 1997), this is not reflected (Fig. 2). The persistence of this species as the community succeeds, after fire, to climax vegetation deserves study. Thus, it would be useful to gather exotic species distribution data across successional stages within each of the environmental types (Despain 1990a) to allow a broader and more accurate evaluation of the threat posed by a particular species.

We recommend that managers gather the data necessary to use this method to further their efforts in monitoring and controlling the establishment and spread of these exotic plants, especially those that are most likely to cause extensive ecological and economic problems.

ACKNOWLEDGMENTS

National Park Service/University of Wyoming Research Center and U.S./Montana Department of Transport supported measurement of exotic presence in major environmental types. Yellowstone National Park supported mapping of the environmental types of the park and provided information about the distribution of exotic plants in the park.

LITERATURE CITED

Cutthroat trout (Oncorhynchus clarki) have been divided into 4 major and 10 minor subspecies by Behnke (1988), based on phylogenetic divergence. Behnke (1992) has described phenotypic differences among these subspecies as well as their geographic distribution, status, life history, and ecology.

Differences among subspecies are of importance to fisheries managers and anglers. For example, Lahontan cutthroat trout (O. c. henshawi) may reach a maximum size twice that of other subspecies (Behnke 1992). In the rainbow trout (O. mykiss) group, redband trout (O. m. subsp.) display an ability to adapt to high temperatures, feeding at temperatures lethal to other subspecies (Behnke 1992). Researchers have also noted differences in feeding habits, susceptibility to various methods of angling, return to the creel, and condition among cutthroat trout stocks (Trojan and Behnke 1974, Nielson and Lentsch 1988, Dwyer 1990, Hepworth et al. 1999).

These genetically based differences among subspecies and stocks are indicators that cutthroat trout have undergone some degree of natural selection, creating adaptations to particular environments. Genetic differences, e.g., as measured by mitochondrial DNA or enzyme proteins, among subspecies of cutthroat trout have been noted and used to differentiate between them (Loudenslager and Gall 1980, Leary et al. 1987, Shiozawa and Evans 1994).

Several stocks of cutthroat trout are available from certified pathogen-free sources for fisheries management in Utah. These include Bear Lake Bonneville (BL), Bear Lake, Utah-Idaho; southern Bonneville (BV) from Manning Meadow Reservoir, Monroe Mountains, Utah; and Electric Lake (EL), Emery County, Utah, stocks. The EL stock is primarily Yellowstone cutthroat trout (O. c. bouvieri), with potential introgression by rainbow trout and Bear Lake Bonneville cutthroat trout while in Strawberry Reservoir before transfer to Electric Lake (Martin et al. 1985). The BL and BV are recognized as O. clarki utah (Behnke 1992). The history of these broodstocks was reviewed by Wagner (1996) and Hepworth et al. (1997).

COMPARATIVE TOLERANCE OF FOUR STOCKS OF CUTTHROAT TROUT TO EXTREMES IN TEMPERATURE, SALINITY, AND HYPOXIA

Eric J. Wagner1,2, Ronney E. Arndt1, and Mark Brough1

ABSTRACT.—Four stocks of cutthroat trout (Oncorhynchus clarki) were exposed to high temperature, high salinity, and low dissolved oxygen to determine inherent differences. The fish tested included 2 stocks of Bonneville cutthroat trout (O. c. utah), a lacustrine stock derived from Bear Lake and a fluvial-origin stock from southern Utah (Manning Meadow Reservoir). The other 2 stocks tested were from Electric Lake (largely Yellowstone cutthroat trout, O. c. bouvieri) and Jackson Hole, Wyoming (fine-spotted Snake River cutthroat trout, O. c. subsp.). Temperature tests were either critical thermal maximum (CTM) or 96-hour trials using juveniles acclimated between 12.5°C and 18.0°C. Two CTM end points were temperature at first loss of equilibrium (CTMeq) and onset of spasms (CTMs). There were no significant differences in CTMeq among test fish acclimated to 18.0°C, but CTMs was significantly higher for Bear Lake Bonneville (30.0°C) than for Snake River (29.6°C) or southern Bonneville (29.7°C) stocks. With fish acclimated at 13.0°C, there were no significant differences among the stocks in CTMeq or CTMs. Differences among stocks varied significantly among nine 96-hour tests. Overall, it appeared that the southern Bonneville stock had slightly better survival at warmer temperatures than other stocks. In 24-hour survival tests at high salinities, the Snake River stock had the lowest tolerance, with significant mortality occurring at 18‰ (29.5 mS · cm⁻¹ conductivity). The southern Bonneville stock had the highest tolerance, with no mortality until 25‰ (38 mS · cm⁻¹). Bear Lake Bonneville and Electric Lake stocks had 60% and 30% mortality, respectively, at 21‰ (36 mS · cm⁻¹). Hypoxia tolerance measured by resistance time, 24-hour mortality, or probit analysis (LEC50) did not differ among stocks. The 24-hour LEC50 was 2.34 mg O₂ · L⁻¹ for all stocks combined.

Key words: temperature, oxygen, conductivity, critical thermal maximum, Bonneville cutthroat trout, Yellowstone cutthroat trout, Snake River cutthroat trout.

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The Snake River stock (O. c. subsp.; SN; Behnke 1992), originating from wild stock in Wyoming via Jackson National Fish Hatchery, was also included in this study for comparison.

Water quality is a critical aspect of the fish’s environment, but how these subspecies differ in water quality tolerances has not been evaluated. Water quality in Utah is as varied as the landscape, ranging from nearly distilled water in granite watersheds of the Uinta Mountains to over 150,000 mg \( \cdot \) L\(^{-1} \) salinity in Great Salt Lake (Gliwicz et al. 1995). Some reservoirs experience low dissolved oxygen during winter ice cover and summer stratification, and others experience high temperature during summer months and irrigation drawdown. Summertime stream temperatures can exceed lethal limits. This study was conducted to determine inherent differences among available cutthroat trout stocks in the ability to withstand water quality extremes, possibly making some stocks more suitable for stocking in harsher environments.

**Methods**

We reared 4 cutthroat trout stocks from wild broodstocks from the sources mentioned above from eggs at the Fisheries Experiment Station, Logan, Utah. Stocks were tested for survival differences at extremes of temperature, dissolved oxygen (DO), and salinity. We divided test fish into 2 groups, one acclimated to 13.6 \( \pm \) 0.6 °C and the other to 18.0 \( \pm \) 0.5 °C. Fish acclimated to 13.6°C had been reared at that temperature since hatching. Fish at 18.0°C were transferred to that temperature on 10 September 1996 and remained there for at least 30 (CTM tests) to 90 days (96-hour tests) prior to tests. Additional 96-hour temperature tests were conducted in January 2000, one with the 4 stocks acclimated to 12.5°C and the other two with fish acclimated to 16.0°C for at least 30 days. The study fish were freeze-branded 1 or 2 weeks prior to testing to identify the stocks. For each test, 20 fish from each stock were put into each of 5 circular tanks, 3 of which had recirculating heaters to control temperature and 2 that served as controls.

Water exchange of half volume was performed once or more (first 2 tests at 18.0°C acclimation temperature), halfway through each test using water of the appropriate temperature. DO was monitored daily with an oxygen meter calibrated with replicate Winkler titrations (APHA et al. 1989) and did not drop below 5.2 mg \( \cdot \) L\(^{-1} \). NH\(_3\)-N was determined by Nesslerization (APHA et al. 1989) at the end of each test, and levels did not exceed increased at a constant rate of 0.2°C \( \cdot \) min\(^{-1} \) on a laboratory hot plate, similar to the rate recommended by Becker and Genoway (1979). Temperature was recorded at 10-minute intervals from a digital probe suspended off the bottom, and change in temperature was calculated for each interval. Time and temperature were recorded at the first loss of equilibrium and at the onset of spasms, whereupon the test was concluded. DO was recorded at the end of the test. We conducted these tests between 25 September and 31 October 1996 using fish of 0.7–2.9 g average weight.

### 96-hour Temperature Tolerance Tests

Eight 96-hour mortality tests (3 February to 7 April 1997) were used to compare the tolerance of the 4 cutthroat trout stocks to high temperature. All tests were conducted in insulated 800-L indoor circular tanks. Airstones in each tank insured that low DO did not compromise survival.

For each 1997 test, we transferred fish directly from acclimation temperatures (13.6 \( \pm \) 0.6°C or 18.0 \( \pm \) 0.5°C) into test tanks. We used 4 cylindrical cages (56-cm diameter) per tank, placing 10 fish of one stock per cage. This insured that all stocks within a tank were exposed to the same water temperature. Test temperatures ranged from 23.0°C to 24.5°C among the 8 tests. Two or 3 tanks per temperature treatment provided the replication for each test.

Three additional 96-hour tests were conducted in January 2000, one with the 4 stocks acclimated to 12.5°C and the other two with fish acclimated to 16.0°C for at least 30 days. The study fish were freeze-branded 1 or 2 weeks prior to testing to identify the stocks. For each test, 20 fish from each stock were put into each of 5 circular tanks, 3 of which had recirculating heaters to control temperature and 2 that served as controls.

Water exchange of half volume was performed once or more (first 2 tests at 18.0°C acclimation temperature), halfway through each test using water of the appropriate temperature. DO was monitored daily with an oxygen meter calibrated with replicate Winkler titrations (APHA et al. 1989) and did not drop below 5.2 mg \( \cdot \) L\(^{-1} \). NH\(_3\)-N was determined by Nesslerization (APHA et al. 1989) at the end of each test, and levels did not exceed increased at a constant rate of 0.2°C \( \cdot \) min\(^{-1} \) on a laboratory hot plate, similar to the rate recommended by Becker and Genoway (1979). Temperature was recorded at 10-minute intervals from a digital probe suspended off the bottom, and change in temperature was calculated for each interval. Time and temperature were recorded at the first loss of equilibrium and at the onset of spasms, whereupon the test was concluded. DO was recorded at the end of the test. We conducted these tests between 25 September and 31 October 1996 using fish of 0.7–2.9 g average weight.

### Critical Thermal Maximum

Fish were selected at random and tested individually; 10 fish were sampled from each stock and acclimation temperature. We placed each fish in a 4.0-L Erlenmeyer flask containing 3.0 L of 13°C water. Temperature was recorded at 10-minute intervals from a digital probe suspended off the bottom, and change in temperature was calculated for each interval. Time and temperature were recorded at the first loss of equilibrium and at the onset of spasms, whereupon the test was concluded. DO was recorded at the end of the test. We conducted these tests between 25 September and 31 October 1996 using fish of 0.7–2.9 g average weight.
0.019 mg · L⁻¹. We weighed each fish after it had died or at the end of the test. Mortality was recorded after 96 hours. Mean weights during the temperature tests were as follows: 4.9–23.7 g, BL; 4.0–23.6 g, BV; 2.4–19.8 g, SN; and 4.5–17.6 g, EL.

**Salinity Tolerance**

Seven salinities were tested in 2 separate 24-hour tests. Salinities of 0.4 (control), 29.6, 32.3, and 33.5 mS · cm⁻¹ (0, 18.0, 19.0, and 20.0‰, respectively) were evaluated in test 1; and salinities of 0, 36.1, 38.2, and 41.6 mS · cm⁻¹ (0, 21.0, 22.0, 23.5‰) were evaluated in test 2. We used 2 replicate 800-L circular tanks per treatment, stocking 10 fish per stock into cylindrical cages in each tank. Salinities were adjusted by adding noniodized rock salt to the water and dissolving it prior to testing. Water between replicate tanks was exchanged prior to adding fish to minimize salinity differences between replicates. Salinity was measured by a specific conductivity probe (Hydrolab, Austin, TX). Other variables measured concurrently included temperature (14.4 ± 0.4°C) and dissolved oxygen (5.7–7.3 mg · L⁻¹, maintained with airstones bubbling compressed air). Un-ionized ammonia nitrogen at the end of the test did not exceed 0.008 mg · L⁻¹. Mortality was recorded after 24 hours. Total body weights of mortalities were recorded and compared to live weights separately for each stock using a t test for paired samples.

**Low Dissolved Oxygen Tolerance**

Between 15 April and 15 May 1997, we conducted 8 tests using fish acclimated to 13°C. By adding nitrogen gas to the water in a flow-through system similar to that described by Cochran and Babcock (1974), we manipulated dissolved oxygen. Two 800-L circular tanks were used for each test, and each received flows of 11 ± 1 L · min⁻¹. Un-ionized ammonia determined by Nesslerization at the end of 2 tests did not exceed 0.001 mg · L⁻¹. Fish were allowed access to the surface to gulp for air. Loss of equilibrium was the end point (resistance time) for each fish in all tests, and most recovered when returned to normoxic water. Weight of each fish was measured after loss of equilibrium to evaluate possible size effects on resistance time. The temperature was 14.7 ± 0.8°C for each test.

We performed 2 tests in which dissolved oxygen (DO) was gradually decreased over 6–7 hours; resistance time (time at which equilibrium was lost) and DO at the time of loss of equilibrium were noted. Ten fish from each stock were maintained in plastic-mesh cages for each test, 4 cages per 800-L tank. Mean weights for these tests were BL, 21.9 g; BV, 15.7 g; SN, 10.0 g; and EL, 22.1 g. Test-1 fish were acclimated to the cages for 40 hours and not fed for 96 hours prior to the test. Test-2 fish were fed until test time and given no acclimation time in the cages. Of interest was the comparative response of the 4 stocks to hypoxia under the varied conditions of the 2 tests, avoiding possible biases due to handling stress and oxygen demand for digestion.

Remaining tests were 24-hour challenges at a given DO; average levels ranged from 1.85 to 3.34 mg · L⁻¹ among the 6 tests. The 4 cutthroat trout stocks were freeze-branded one week prior to tests to identify stocks upon removal from a tank. Fish were transferred from outdoor raceways in which DO ranged from 6.6 to 7.8 mg · L⁻¹. For each test we put 10 fish from each stock into each of 2 circular tanks holding 400 L of water. During each test we monitored DO and removed the fish upon loss of equilibrium, weighed them in water, and noted the time. Mean weights during these tests were 25.2–30.7 g, BL; 16.1–21.6 g, BV; 8.8–11.6 g, SN; and 20.2–32.3 g, EL.

**Statistical Analysis**

LEC₅₀, i.e., the lower limit of dissolved oxygen causing loss of equilibrium within 24 hours, or LT₅₀, the maximum temperature in 96-hour tests that killed half the fish, was calculated for each stock by probit analysis (Newman 1994, SPSS 1994). For DO data we used natural log transformation for probit analysis; we also conducted analysis with stocks pooled. Probit analysis for each acclimation temperature was not possible due to insufficient data, and so data were pooled. Percent mortality was arcsine transformed prior to 1-way analysis of variance (ANOVA) within each test. Normality tests (Kolmogorov-Smirnov) were conducted for each continuous variable, and the data were subsequently analyzed by 1-way ANOVA if the data were normally distributed and, if not, by the Kruskal-Wallis 1-way ANOVA (SPSS
Duncan’s test was used for mean comparisons. Using 1-way ANOVA, we analyzed separately transformed mortality data from the salinity trials for each salt concentration. For DO data analysis, median resistance time (average elapsed time of 5th and 6th fish) and average DO at that time were used to compare stocks in 1-way ANOVA. Simple least-squares regression was used to test the strength of the relationship between total body weight and DO resistance time. To assess total body weight effects on mortality in the temperature tests, we compared average live and dead weights by Wilcoxon matched-pairs and signed-ranks tests for each temperature test (stocks pooled), stock (tests pooled), and for combined data. Differences were considered significant at \( P \leq 0.05 \) for all statistical tests.

**RESULTS**

**Critical Thermal Maximum Tests**

Mean CTMeq and CTMs were significantly higher for fish acclimated at 18.0°C (29.5°C and 29.7°C, respectively) than those acclimated at 13.6°C (28.1°C, 28.6°C). There were no significant differences in CTMeq among stocks acclimated to 18.0°C, but CTMs was significantly higher \( (P = 0.03) \) for BL (30.0) than for SN (29.6) or BV (29.7°C; Table 1). For tests with fish acclimated at 13.6°C, there were no significant differences among the 4 stocks in CTMeq or CTMs.

**96-hour Temperature Tolerance Tests**

In 96-hour tests, differences among stocks varied among the 11 tests (Table 2). For fish acclimated to 13.6°C and challenged at 24.0°C, mortality for BL and SN was significantly higher (100%) than for EL (73%) and BV (13%). At 23.0°C and 23.5°C, results were much different; BV had significantly higher mortality than the other stocks or did not significantly differ (Table 2). When cold-acclimated fish were challenged at 24.0°C with a larger sample size per tank, BV had the lowest mortality (3%) and SN the highest (86.7%; Table 2).

Five 96-hour tests were conducted with fish acclimated to 18.0°C. At 23.2°C, only the EL experienced mortality (3%). At 23.7°C, BV had significantly lower mortality (21%) than SN (95%) or BL (90%). Mortality at 23.9°C was significantly higher for SN (75%) than the other 3 stocks (10–15%). After raising the test temperature half a degree, mortality reached 100% in SN and BL groups, but was less for EL and BV (75% and 65%, respectively). Probably due to having only 2 replicates, these stock differences were not significant \( (P = 0.21, \text{ Kruskal-Wallis test}) \). A repeat of this test resulted in significantly lower mortality for BV (27%) than for SN (87%). Repetition of the tests with another year-class of fish acclimated to 16.0°C provided similar results; BV had significantly lower mortality (1.7%) than EL (30.0%) or SN (68.3%) when challenged at 24.0°C (Table 2). Probit analysis resulted in LT50 values of 23.5°C for SN, 23.9°C for BL, 24.0°C for EL, and 24.3°C for BV (Fig. 1). Overall, BV had slightly better survival at high temperatures than the other stocks, but the difference was small.

Mean weight of mortalities was not significantly different from survivor weight for each stock when all tests were pooled for analysis. Analysis of pooled data combining tests and stocks (49 pairs) similarly resulted in no significant difference.

**Salinity Tolerance Tests**

There were significant differences among stocks in 24-hour survival at high salinities (Table 3). SN had the lowest salinity tolerance, with significant mortality occurring at 29.6 mS \( \cdot \) cm\(^{-1}\) conductivity (18‰); BV had the highest tolerance (<5% mortality up to 38 mS \( \cdot \) cm\(^{-1}\) [22‰]). BL and EL were intermediate, with 60% or 30% mortality, respectively, at 36 mS \( \cdot \) cm\(^{-1}\) (21‰). Size appeared to have little influence on mortality; for only BV, the mean weight of dead fish was smaller than that of survivors (1.8 versus 2.4 g, respectively, \( P = 0.032, \text{ t test for paired samples} \)).

**Dissolved Oxygen Tolerance Tests**

Using the method of gradually decreasing DO over time, resistance times (elapsed time until loss of equilibrium) among the 4 stocks did not significantly differ for either of the 2 trials (Table 4). Similarly, mean DO at the median resistance time did not differ significantly among stocks. A t test for differences in DO between tests (stocks pooled) was not significant, indicating that acclimation to tanks or time off feed had little impact on the lower
lethal limit of DO. Mortality began when DO dropped below 1.9 mg \( \cdot \) L\(^{-1}\) (test 1) or 1.7 mg \( \cdot \) L\(^{-1}\) (test 2). The last fish survived until DO dropped to 1.2 to 1.3 mg \( \cdot \) L\(^{-1}\).

In the 24-hour tests, mortality began when DO dropped below 2.6 mg \( \cdot \) L\(^{-1}\). Least-squares regression for each of these tests indicated no significant relationship or a poor relationship (e.g., \( r^2 = 0.254 \), DO test 8) between individual total body weight and the resistance time to low DO levels for any of the 4 stocks. There were no significant differences in mortality among stocks except for 1 test in which SN experienced higher mortality (30%) than the other stocks (\( \leq 5\% \); Table 5). Resistance time was not significantly different among stocks in most tests, except 1 trial (DO = 2.18 mg \( \cdot \) L\(^{-1}\)) in which BL survived significantly longer than the other stocks (Table 4). Probit analysis of mortality in the 24-hour tests indicated little difference in hypoxia tolerance among stocks (Fig. 1). When stocks were pooled, the LEC50 of DO was 2.34 mg \( \cdot \) L\(^{-1}\) (27% of saturation or PO2 = 35.3 mm Hg).

**DISCUSSION**

Inherent differences in thermal tolerance among the 4 stocks of cutthroat trout were not evident based upon critical thermal maximum.
(CTM) tests. CTM tests conducted by Lee and Rinne (1980) indicated little difference between the native Gila (Oncorhynchus gilae) and Apache trout (O. apache) and introduced trout species such as rainbow, brown (Salmo trutta), and brook trout (Salvelinus fontinalis). Similar to results of this study, Lee and Rinne (1980) and Lohr et al. (1996) also noted an increase in CTM at higher acclimation temperatures. CTM values for cutthroat trout in this study (28.1–29.8°C) were similar to those reported for other salmonids at similar acclimation temperatures (Lee and Rinne 1980, Lohr et al. 1996). Contrary to CTM tests, 96-hour tests generally indicated that BV had a greater thermal tolerance than the other stocks. Given the natural habitats found in the southern Bonneville Basin, this stock would likely have been exposed to selective pressures from high summer temperatures. Duff (1988) reported Bonneville cutthroat trout found in “small headwater streams with degraded habitat and warm summer water temperature (21°C).” Differences in LEC₅₀ values were minor, but stock differences may be accentuated if fish are exposed to daily fluctuating high temperatures instead of constant high temperatures, where fish can recover overnight. For example, Otto (1974) observed higher thermal tolerance in western mosquitofish (Gambusia affinis affinis) exposed to cyclic high temperatures than in those exposed to constant temperatures. Feminella and Matthews (1984) reported similar findings for the orangethroat darter (Etheostoma spectabile). The biological significance of our results still requires field testing, but warm-temperature adaptation might be a useful trait for maintenance of trout populations in shallow reservoirs and streams with high summer temperatures. Intraspecific differences in thermal tolerance have been observed by McCauley (1958) for arctic char (Salvelinus alpinus), but not for brook trout. Bidgood and Berst (1969) did not detect any difference in thermal tolerance among rainbow trout from 4 different Great Lakes stocks.

The upper incipient lethal temperature (UILT) is defined as the upper temperature at which 50% mortality is observed at a given acclimation temperature (Amour 1991). In this study cutthroat trout had UILT limits ranging

### Table 3. Comparison of percent mortality of 4 cutthroat trout stocks after 24-hour exposure to various salinities (presented as specific conductivity and parts per thousand [in parentheses]). Percent mortality is the average of 2 tanks with 10 fish per stock per tank. Stock abbreviations: BL = Bear Lake, BV = Bonneville, SN = Snake River fine-spotted, and EL = Electric Lake stock. A common subscript letter or no letter among means within a given salinity indicates no significant difference (1-way ANOVA, $P \geq 0.05$).

<table>
<thead>
<tr>
<th>Salinity mS⋅cm⁻¹ (‰)</th>
<th>BL</th>
<th>BV</th>
<th>SN</th>
<th>EL</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.4 (0.0)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>29.6 (18.0)</td>
<td>0</td>
<td>0</td>
<td>10</td>
<td>0</td>
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<tr>
<td>32.3 (19.0)</td>
<td>0 a</td>
<td>0 a</td>
<td>40</td>
<td>5 a</td>
</tr>
<tr>
<td>33.5 (20.0)</td>
<td>0 a</td>
<td>5 a</td>
<td>66</td>
<td>b a</td>
</tr>
<tr>
<td>36.1 (21.0)</td>
<td>60</td>
<td>c a</td>
<td>95</td>
<td>d a</td>
</tr>
<tr>
<td>38.2 (22.0)</td>
<td>80</td>
<td>ab</td>
<td>45</td>
<td>100</td>
</tr>
<tr>
<td>41.6 (23.5)</td>
<td>100</td>
<td>a</td>
<td>75</td>
<td>100</td>
</tr>
</tbody>
</table>
from 23.6°C to 24.3°C. Other researchers have indicated that rainbow trout tolerate slightly higher values at similar acclimation temperatures; Bidgood and Berst (1969) and Charlon et al. (1970) both noted UILT values ranging from 25°C to 26°C. Arctic grayling (Thymallus arcticus) in Montana had UILTs of 23.0°C for fish acclimated to 8.4°C or 16.0°C, or 25.0°C for those acclimated to 20.0°C (Lohr et al. 1996).

CTM tests resulted in higher lethal temperature values than 96-hour tests, similar to tests with arctic grayling (Lohr et al. 1996). The 2 methods differ in that CTM is a progressive change in temperature resulting in a “physical disorganization response,” whereas the UILT method is an abrupt change resulting in a lethal response (Becker and Genoway 1979). The CTM method has been useful for comparative studies, such as that of Kowalski et al. (1978) of New York stream fishes. Also, Matthews and Maness (1979) observed significant differences in CTM values among cyprinid species that correspond to fluctuations in fish populations in the South Canadian River in Oklahoma. However, as the 96-hour tests indicated, CTM values should not be regarded as the maximum “safe” temperature for a fish at a given acclimation temperature. Mortality at a given temperature can occur over a much longer period than that allowed in the CTM tests. In this study the 96-hour tests were more sensitive indicators of differences in temperature tolerance, detecting differences where CTM tests did not. Incongruous results were not limited to this study. CTM tests were inconsistent with thermal preference tests for 2 species of darters (Ingersoll and Claussen 1984). The 2 methods measure different responses and thus should both be conducted for future temperature studies.

As in this study, size differences in thermal tolerance were not significant for studies with brook trout and arctic char (McCauley 1958), nor for perch (Perca flavescens; Hathaway 1927, Hart 1952). Smale and Rabeni (1995) similarly found no difference in tolerance related to size in tests of 34 species found in Missouri headwater streams.

Salinity tolerance among salmonids seems to vary considerably with species and age (Clarke 1982, Blackburn and Clarke 1987). For example, salinities causing 50% mortality of coho salmon increased from 33‰ in early February to 41‰ in mid-April as the fish progressed through the parr-to-smolt transformation (Blackburn and Clarke 1987). Varnavskiy and Varnavskaya (1984) reported significant mortality in 28‰ seawater for sockeye and coho salmon. Tolerances are also complicated by the fact that salt in the diet can improve salt tolerance (Basulto 1976). Rainbow trout have been reared in water with salinities of 30‰ after 9 days of acclimation (Murai and Andrews 1973). Salt-tolerant strains of rainbow trout have been developed for marine net pen rearing in Finland (Stickney 1991). Tatum (1973) successfully reared rainbow trout in cages in salinities of 20‰ after a 24-hour acclimation period. We found cutthroat trout tolerated salinities approaching 18–22‰.

Salinity tolerance was quite different among the 4 stocks, with highest to lowest tolerance following the order BV > EL > BL > SN; i.e.,
the southern stock was most tolerant and the northern stocks the least. The Great Basin and Intermountain West have experienced several fluctuations of wetter and drier climatic periods over the last 25,000 years (Bright 1963, Smith 1978), which may have altered ancient lake levels and salinity. Lake Bonneville is reported to have undergone 4 periods of low water levels between 8,000 and 22,000 years ago, including one period of complete dessication followed by refilling that occurred 11,000 years ago (Hickman 1978). Such conditions may have exerted selective pressures on the cutthroat trout. Galat et al. (1985) noted that Lahontan cutthroat trout, which evolved in Pleistocene Lake Lahontan that underwent similar water level fluctuations, have adapted to salinities approaching 11.9‰ (15.1 mS cm⁻¹).

Cutthroat trout subspecies can be divided into 3 major groups: coastal (O. c. clarki) characterized by 68 chromosomes, westslope (O. c. lewisi) characterized by 66 chromosomes, and interior cutthroat trout characterized by 64 chromosomes (Loudenslager and Gall 1980, Behnke 1981, 1988). Using starch gel electrophoresis, Loudenslager and Gall (1980) further subdivided the interior cutthroat trout into 2 additional groups: (1) Lahontan cutthroat trout and (2) those cutthroat trout inhabiting the Colorado, Yellowstone, and Upper Snake rivers, and the Bonneville Basin. Further study of this latter group by Martin et al. (1985) using the same techniques indicated that differences were evident between northern (Bear River drainage) and southern (Sevier River drainage) forms of the Bonneville cutthroat trout; they also suggested that fish from the Wasatch Front streams of Utah may form a 3rd group. We

also found differences between the southern and northern forms of the Bonneville cutthroat trout, particularly in temperature and salt-tolerance limits.

DO limits have been reviewed by Barton and Taylor (1996), Davis (1975), and Doudoroff and Shumway (1970), who summarized that mortality for most fish occurs at concentrations between 1 and 3 mg L⁻¹. Cutthroat trout in this study had lower DO threshold values (1.9 mg L⁻¹ or 22% of saturation or 28.6 mm Hg, PO₂) when DO levels were steadily dropped compared to 24-hour tests (2.3–2.5 mg L⁻¹ or 26–29% saturation). Differences in tolerance to hypoxia were not evident among the 4 stocks, indicating little difference in natural selection for that trait. For rainbow trout in 24-hour tests, Alabaster et al. (1957) reported a median tolerance level of 2.6–2.7 mg L⁻¹. Steelhead (O. mykiss) at 16–20°C died at 1.6–1.7 mg L⁻¹ in tests by McNeil (1956, cited by Warren and Bouck 1973). The discrepancy between these 2 studies may be stock related since intraspecific differences in DO tolerance have been observed in rainbow trout (Klar et al. 1979). The 4 cutthroat trout stocks in this study had incipient lethal limits that fell between these 2 reported ranges. Hepworth et al. (1999) indicated that cutthroat trout survived overwinter in a reservoir whereas rainbow trout did not. Controlled studies comparing rainbow trout and cutthroat trout stocks are needed to better define these DO tolerance differences.

In DO studies with other salmonids, Katz et al. (1959) noted that resting juvenile chinook salmon (Oncorhynchus tschawytscha) mortality at 20°C occurred at 1.4–1.9 mg L⁻¹ in 24-hour tests. At 10°C, Klyashtorin (1975) reported

<table>
<thead>
<tr>
<th>Dissolved oxygen (mg · L⁻¹)</th>
<th>BL</th>
<th>BV</th>
<th>SN</th>
<th>EL</th>
<th>Test</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.85 ± 0.16</td>
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<td>100</td>
<td>100</td>
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<td>100</td>
<td>95</td>
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<tr>
<td>2.18 ± 0.11</td>
<td>90</td>
<td>95</td>
<td>90</td>
<td>100</td>
<td>6</td>
</tr>
<tr>
<td>2.29 ± 0.10</td>
<td>67</td>
<td>82</td>
<td>75</td>
<td>80</td>
<td>8</td>
</tr>
<tr>
<td>2.40 ± 0.15</td>
<td>5 a</td>
<td>0 a</td>
<td>30 b</td>
<td>5 a</td>
<td>7</td>
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<tr>
<td>3.34 ± 0.71</td>
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<td>0</td>
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<td>0</td>
<td>3</td>
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</tbody>
</table>
lower threshold values for chinook salmon (1.6 mg L\(^{-1}\), 19.5 mm Hg), sockeye salmon (O. nerka), 1.4 mg L\(^{-1}\), 19.0 mm Hg), coho salmon (O. kisutch), 1.4 mg L\(^{-1}\), and arctic char (Salvelinus alpinus; 1.4 mg L\(^{-1}\)). Burdick et al. (1954) noted mortality of individual brook trout occurred at 1.15–3.40 mg O\(_2\) L\(^{-1}\) and individual rainbow trout occurred at 0.81–2.47 mg O\(_2\) L\(^{-1}\), depending upon the temperature. Tests by Burdick et al. (1954) and Klyashtorin (1975) were conducted using the sealed-vessel method, which can lead to underestimation of actual lethal levels (Doudoroff and Shumway 1970). Shepard (1955) noted that brook trout held at 9°C all survived 1.9 mg L\(^{-1}\) (17% saturation) for 5 days, but died at concentrations below this.

The literature on the effect of size upon tolerance to low DO has been contradictory. Shepard (1955) reported that small fish died more quickly than large fish. Wells (1913) and Keys (1931) observed similar results, but it was not evident in our study. Similarly, no correlation between size and resistance time to low DO was observed by Alabaster et al. (1957) in studies with rainbow trout and perch (Perca fluviatilis). Doudoroff and Shumway (1970) reviewed several studies and also found inconsistencies in the effect of size upon DO tolerance.

Overall, results indicated differences in water quality tolerance among the cutthroat trout stocks tested, especially to high temperature and salinity. These differences accentuate the importance of preserving the genetic diversity of the individual stocks for greater flexibility in fisheries management and stock survival. These adaptations may make the southern Bonneville stock a better candidate for stocking in waters of marginal temperature or salinity than the other stocks tested.

ACKNOWLEDGMENTS

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The stonefly genus *Isoperla* is widely distributed throughout the Holarctic region and contains approximately 131 species worldwide (Illies 1966, Zwick 1973). It represents the largest stonefly genus in North America, with 57 documented species. Szczytko and Stewart (1979a) provided a revision of 20 western North American species (except *I. decolorata* Ricker), including descriptions of the eggs and nymphs of 19 and 12 species, respectively. Three western species have subsequently been discovered (Szczytko and Stewart 1984, Bottorff et al. 1990a).

The large eastern fauna has remained a problematic group taxonomically and biologically because of the cryptic external morphology of adults and poorly known eggs and nymphs; it is currently under revision by S.W. Szczytko (personal correspondence) and contains substantially more than the currently recognized 33 species. Definitive separation of most *Isoperla* species requires aedeagal eversion and its description in males, and description of associated eggs, nymphs, and females.

Despite the diversity and importance of this large group as lotic food web components and generally biological indicators of good water quality, relatively little is known about their behavior, life history, and ecology. Their drumming behavior, which can be a useful line of evidence for delineating species (Stewart et al. 1988), has been described for only 19 North American *Isoperla* species (Szczytko and Stewart 1979b, Maketon and Stewart 1984, Stewart et al. 1988), and detailed life histories have been published for only 13 of them (Stewart and Stark 1988, Sandberg and Szczytko 1997) largely because nymphs have not been correlated with adults and therefore are unknown for most species.

*Isoperla petersoni* is a widely distributed western species, from Alaska where it is common in most clearwater streams (Stewart et al. 1990) southward to Utah. It was included for Colorado in a later electronic list of Stark et al. (1973), but that record has been deleted since no literature record can be substantiated. Its adult emergence and nymphal growth have been described only from eastern Alaskan North Slope populations (Stewart et al. 1990), and its drumming behavior has not been studied. In its southernmost range in Colorado, it occurs...
at high elevations between 3109 and 3444 m and is one of the last regional *Isoperla* species to emerge (Baumann et al. 1977). This research was conducted on a population in Boulder County, Colorado, which we discovered in 1998.

**SITE DESCRIPTION**

This study was conducted on an *I. petersoni* population from a northern unnamed tributary of the North Fork Middle Boulder Creek, Boulder County, Colorado. The study reach is a 1st-order stream located approximately 40°00′27″N, 105°39′56″W, and is about 2 km east of Arapaho Pass (3629 m) on the Arapaho Glacier Trail near the abandoned Fourth of July Mine (elevation 3414 m). The study site is in the Hudsonian life zone dominated by trees with stunted growth. The alpine zone begins approximately 100 m north and 50 m west of the study site. The stream flows through a wet meadow near scattered clusters of blue spruce (*Picea pungens* Engelman), Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.), and Engelman spruce (*Picea engelmannii* Parry ex Engelman), most of which have been stunted by high winds and snow. The riparian vegetation consists of short stands of willow (*Salix* sp.) and alder (*Alnus* sp.), which are more prevalent at the lower tributary reaches, and herbaceous annuals and perennials including elephants head (*Pedicularis* sp.), gentian (*Gentiana* sp.), Indian paintbrush (*Castilleja* sp.), fireweed (*Epiobium* sp.), and short grasses and sedges along the stream margins.

The tributary flows 1.5 km before joining with the North Fork Middle Boulder Creek. The water source of the seeps and flowing springs forming the tributary consists of nearby permanent snowfields and the South Arapaho Glacier. Typical stream substrates include gravel, cobble, and boulders that form alternating riffles, small waterfalls, and pools. Areas that include cobble substrate are tightly embedded and limit the effectiveness of kicknet sampling. However, much of the study reach substrate is covered with aquatic moss (*Hygrohypnum* sp.) that provides cover for nymphs and emerging adults. Other stoneflies collected in the tributary include *Sweltsa borealis* (Banks), *Plumiperla diversa* (Frison), *Zapada haysi* (Ricker), *Megarecsis signata* (Hagen), and *Kogotus modestus* (Banks). Mayflies collected include *Drunella coloradensis* (Dodds), *Cinygmula rameleyi* (Dodds), and *Cinygmula par* (Eaton).

**METHODS AND MATERIALS**

We collected late instar nymphs qualitatively at approximately weekly intervals from 26 July to 26 September 1998 with a triangular-frame kicknet fitted with a 600-µm-mesh bag. Stream temperature during this period ranged from 3.3° to 8.9°C. Access by foot to the study site was delayed until July due to extended presence of deep snow well into June 1998 that limited ability to sample through the nymphal growth period. Senior author Sandberg traveled to Colorado in mid-December 1999 to attempt collection of nymphs for winter growth determination. Avalanches in the area caused trail closure and prevented access to the study tributary. Typically, <33 nymphs were sampled from this sparse population and preserved weekly; they were handpicked from each kicknet sample that also contained moss and debris. Additional late instar nymphs were transported live to the laboratory for rearing. These we maintained in styrofoam cups containing stream water from the North Fork Middle Boulder Creek, Buckingham Campground (elevation 2896 m). Temperature and photoperiod were adjusted in a refrigerator to simulate stream environmental conditions, and cups were checked twice daily for emergence. Reared adults were preserved in 80% ethanol.

We determined nymphal growth by interocular distance (IOD) measurements made with a calibrated ocular micrometer fitted to a stereo-dissection microscope. The IOD is the shortest distance between the eyes. Sex was determined using the presence (female) or absence (male) of a gap in the posterior setal row of the 8th abdominal sternite (Stewart and Stark 1988). Food habit was determined from midgut and hindgut contents, removed by dissection and identified to the lowest practical taxonomic level.

Adult presence data and sex ratios were determined from weekly beating sheet samples of adults taken from riparian vegetation within 1 m of the stream margins. Collecting effort on each sampling date was duplicated as closely
as possible and consisted of beating riparian vegetation for about 3 hours within 1 m of the stream margin. Emergence timing and sex ratios of laboratory-reared adults were compared with presence and sex ratios of field-collected adults.

On 21 August 1999 we collected late instar nymphs at the study site for rearing. Eight virgin males and 6 virgin females were successfully reared in a Fridgid Units Living Stream™, and drumming signals from pairings of these were recorded at room temperatures of 20–24°C, under fluorescent room light of about 70 foot candles. Digital sound recordings were made with a Sony MiniDisc (model MZ-R37) and Optimus Electret omnidirectional condenser microphones in a sound-dampened, partitioned recording chamber described by Stewart and Zeigler (1984). We made digital, computer-generated graphic facsimiles from recorded signals played into a computer and translated with the sound editing and analyzing software Audiowave (Voyetra-Turtle Beach Inc.) and Acid WAV (Polhedric Software). The latter program displayed each stereo channel (male-left, female-right) with unique colors, assisting in the determination of signal characteristics. Clear, well-defined signals of both males and females were measured to determine number of drum beats, beat intervals to nearest 1 ms, duet duration, and for overlapped duets the interval between the 1st female response beat and the male beat immediately before it. For nonoverlapped duets, the male-female interval (interval between end of male call to start of female answer) was also measured.

Drumming amplitude of all recorded signals was low; this complicated identification of specific male call and female answer drumbeats. We attempted audiocassette recordings made with a Marantz (model PMD 340) recorder early in the recording sessions but abandoned them due to noise obliteration of the low-amplitude drum beats, and therefore poor generation of graphic facsimiles. Digital recordings provided increased discrimination between drumbeats and noise interference. In some instances the beat(s) of the overlapped female answer fell at the exact time of male call beat(s). These duets were not included in the analysis because the resolution power of the signal analysis software did not allow definitive measurement of these “masked” events.

**RESULTS AND DISCUSSION**

Emergence was not observed in the field; however, we collected several exuviae using the beating sheet or hand-picked them from exposed, moss-covered rocks. Adults reared in the laboratory emerged both during the day ($N = 33$) and evening ($N = 27$) throughout the emergence period and ecdysis required 20–30 minutes. In the field adults were found in low vegetation along the stream margin where they had crawled up to seek cover as has been demonstrated for other *Isoperla* (Hynes 1967, Jop and Szcztyko 1984, DeWalt and Stewart 1995).

The presence of adults at North Fork Middle Boulder Creek from early August through the 1st half of October indicated that *I. petersoni* has an extended emergence. *Isoperla petersoni* adults ($N = 18$) from eastern Alaska North Slope streams also emerged over an extended period, from June to mid-August (Stewart et al. 1990). Therefore, in terms of length of adult presence, this southern-latitude Hudsonian zone population is similar to the Alaskan population, but the onset of presence is later by 2 months (June vs. August). The 1st adult male was collected on 8 August 1998 when stream temperature was 7°C (Fig. 1). The field sex ratio (male:female) of 225 adults was 1.1:1. A substantially lower sex ratio of 0.4:1 was observed for the 67 individuals reared in the laboratory. Adult field presence lasted 68 days and was assumed complete when the last adult was observed on 10 October. Although 0.6 m of snow had fallen on 1 October, several adults were collected from willow brush after snow was carefully removed. The last 3 nymphs were collected in the field on 26 September (Fig. 2), 2 weeks before the end of adult field presence.

Mean fecundity of field-collected adult females was 92.9 $\pm$ 46.44 eggs ($N = 94$), but decreased slightly over time from 94.1 $\pm$ 45.15 in September ($N = 81$) to 85.2 $\pm$ 57.63 in October ($N =12$). This may have been due to the small number of females remaining late in the emergence cycle for analysis, or to the possibility that later-emerging females were smaller. Smaller females late in the emergence cycle have been noted for other stoneflies (Khoo 1968, Schwarz 1970, Sheldon, 1972, Cather and Gaufin 1975, Orberndorfer and Stewart 1977, Snellen and Stewart 1979), even
though we did not measure *I. petersoni* females. Laboratory-reared females produced 6 egg masses with average egg counts increasing slightly from 92.5 ± 58.69 in late September (*N* = 2) to 119.5 ± 14.25 in early October (*N* = 4).

Winter growth of nymphs was not documented due to inaccessibility of the study site from November to June. However, the absence of early instars at the end of the snow-free season in mid-October and again in early July when nymphs had attained maximum size (Fig. 2) suggested a univoltine cycle. We assume the eggs hatched over a short period and that the majority of nymphal growth occurred over winter, presumably under an insulative snow cover. Our nymph collections late in the growth cycle did not include a wide size range; however, the Alaskan population (Stewart et al. 1990) did have a wide range in monthly size of nymphs from fall through spring, suggesting a flexible life cycle that ranged from univoltine-slow to semivoltine. The latter was represented by a slow, winter-growing portion of the cohort that was recruited in late summer, or possibly by an egg diapause.

Sexual size dimorphism of 127 nymphs was observed throughout the sampling period, with average IOD for males and females of 1.11 ± 0.06 and 1.36 ± 0.09, respectively. Maximum average size was attained first by male nymphs (1.16 ± 0.04 mm) on 8 August (*N* = 7), followed by female nymphs (1.40 ± 0.09 mm, *N* = 15) on 22 August (Fig. 2). Mean IOD for both sexes then decreased for the remaining sample dates.

*Isoperla petersoni* was carnivorous from late July to mid-September. Chironomidae (91.4%) and Ostracoda (5.6%) formed the majority of food items ingested (Table 1). The highest frequency of empty midguts and hindguts was observed during the onset of emergence between late August and early September. The predominance of chironomid larvae as the prey of *I. petersoni* is consistent with observations for other *Isoperla* (Frison 1935, Minshall and Minshall 1966, Richardson and Gauvin 1971, Fuller and Stewart 1977, 1979, Sandberg and Szczytko 1997).

Vibrational communication signals were recorded from 8 males and 6 females from 3 to 13 September 1999. Duets consisted of simple monophasic male calls (5–19 beats) and female responses (1–14 beats). Females varied their responses from nonoverlapped (Fig. 3A) to overlapped (Fig. 3B); when overlapped, they began answering after the 7th male call beat (Fig. 3C). We analyzed a total of 228 signals; 134 were overlapped, 55 nonoverlapped, and 39 were lone male calls (Table 2). Male calls had 11 mode beats (̅ = 11.1 ± 2.09) with average beat intervals of 118 ± 9 ms. The mean number of call beats increased slightly for overlapped duets (11.6 ± 1.32) and decreased slightly to 11.0 ± 1.48 for nonoverlapped duets. The average number of answer
Table 1. Taxa found in the midgut and hindgut of 124 *Isoperla petersoni* nymphs collected July to September 1998 from a high-altitude stream in Colorado.

<table>
<thead>
<tr>
<th>Sample date (1998):</th>
<th>07/26</th>
<th>08/08</th>
<th>08/16</th>
<th>08/22</th>
<th>08/29</th>
<th>09/06</th>
<th>09/19</th>
<th>% of total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number dissected :</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plecoptera</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>6.3%</td>
</tr>
<tr>
<td>Zapada sp.</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>4.2%</td>
</tr>
<tr>
<td>Baetidae</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>2.1%</td>
</tr>
<tr>
<td>Chironomidae</td>
<td>10</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>16.7%</td>
</tr>
<tr>
<td>Orthocladiinae</td>
<td>56</td>
<td>17</td>
<td>49</td>
<td>86</td>
<td>14</td>
<td>1</td>
<td>1</td>
<td>46.55%</td>
</tr>
<tr>
<td>Cricotopus/Orthocladius sp.</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0.21%</td>
</tr>
<tr>
<td>Diplocladius sp.</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0.21%</td>
</tr>
<tr>
<td>Paraorthocladius sp.</td>
<td>6</td>
<td>1</td>
<td>2</td>
<td>7</td>
<td>8</td>
<td>5</td>
<td>5</td>
<td>5.01%</td>
</tr>
<tr>
<td>Parametriocnemus sp.</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1.04%</td>
</tr>
<tr>
<td>Rheocricotopus sp.</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0.63%</td>
</tr>
<tr>
<td>Diamesinae</td>
<td>9</td>
<td>2</td>
<td>2</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>3.55%</td>
</tr>
<tr>
<td>Diamesa sp.</td>
<td>12</td>
<td>53</td>
<td>34</td>
<td>30</td>
<td>10</td>
<td>4</td>
<td>4</td>
<td>29.02%</td>
</tr>
<tr>
<td>Psuedodiamanesa sp.</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1.04%</td>
</tr>
<tr>
<td>Pagastia sp.</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>3.55%</td>
</tr>
<tr>
<td>Prosinillum sp.</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1.04%</td>
</tr>
<tr>
<td>Ostracoda</td>
<td>14</td>
<td>7</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>5.64%</td>
</tr>
<tr>
<td>Hydrachnidia</td>
<td>1</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2.1%</td>
</tr>
<tr>
<td>Total</td>
<td>117</td>
<td>85</td>
<td>95</td>
<td>137</td>
<td>42</td>
<td>0</td>
<td>3</td>
<td>100%</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Number of midguts/hindguts containing</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chironomidae parts</td>
</tr>
<tr>
<td>Unidentified insect parts</td>
</tr>
<tr>
<td>Unidentified insect eggs</td>
</tr>
<tr>
<td>Unidentified insect eggs</td>
</tr>
<tr>
<td>Ostracoda</td>
</tr>
<tr>
<td>Sand</td>
</tr>
</tbody>
</table>

Table 2. Drumming signal statistical characteristics of *Isoperla petersoni* recorded from 8 males and 6 females between 3 and 13 September 1999 at 20–24°C.

<table>
<thead>
<tr>
<th>Total calls, answers, duets and intervals</th>
<th>Nonoverlapped duets</th>
<th>Overlapped duets</th>
</tr>
</thead>
<tbody>
<tr>
<td>8♂</td>
<td>6♀</td>
<td>5♂</td>
</tr>
<tr>
<td>Beats</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number</td>
<td>228</td>
<td>189</td>
</tr>
<tr>
<td>Mean ± s</td>
<td>11.1 ± 2.09</td>
<td>6.2 ± 2.99</td>
</tr>
<tr>
<td>Mode</td>
<td>11</td>
<td>4</td>
</tr>
<tr>
<td>Range</td>
<td>5–19</td>
<td>1–14</td>
</tr>
<tr>
<td>Duet duration (ms)</td>
<td>1458 ± 163 (N = 189)</td>
<td>1483 ± 170</td>
</tr>
<tr>
<td>Mean ± s</td>
<td>1490</td>
<td>1610</td>
</tr>
<tr>
<td>Range</td>
<td>1070–1930</td>
<td>1080–1800</td>
</tr>
<tr>
<td>Beat intervals (ms)</td>
<td>118 ± 9 (N = 2307)</td>
<td>58 ± 22 (N = 1785)</td>
</tr>
<tr>
<td>Mean ± s</td>
<td>118 ± 9 (N = 551)</td>
<td>59 ± 27 (N = 292)</td>
</tr>
<tr>
<td>Mode</td>
<td>120</td>
<td>50</td>
</tr>
<tr>
<td>Range</td>
<td>90–160</td>
<td>10–290</td>
</tr>
<tr>
<td></td>
<td>9–160</td>
<td>10–290</td>
</tr>
</tbody>
</table>
beats increased from $5.3 \pm 2.56$ when duets were nonoverlapped to $6.6 \pm 3.08$ when overlapped. The rhythm of male calls was uneven and had gradual interval transitions, which began long ($131 \pm 9$ ms), then decreased to $113 \pm 5$ ms for beats 7 and 8, and then returned up to 130 ms for the final intervals.

*Isoperla petersoni* belongs to the *I. sordida* Banks species complex (Szczytko and Stewart 1979b, 1984, Bottorff et al. 1990a) that includes 8 western Nearctic species. Drumming is known for only 3 of them (Bottorff et al. 1990b): *I. adunca* Jewett, *I. bifurcata* Szczytko and Stewart, and *I. miwoc* Bottorff and Szczytko. *Isoperla petersoni* male calls had nearly twice as many mode and average number of beats as other species within the complex. The average male call interval was closest to *I. adunca* (138 ms). *Isoperla petersoni* male and female signals generally fit the ancestral *Isoperla* pattern (Stewart and Maketon 1991) in being monophasic and involving 2-way vibrational communication with or without overlap of call-answers. The drumming evolution paradigm of Stewart (2001) indicates that all of these *Isoperla* have achieved specificity from ancestral Plecopteran signals by slight modification of numbers of beats and beat intervals (rhythm). *Isoperla petersoni* average call beat intervals are about median to those of the 24.5 to 356.8 ms range of other known western *Isoperla* species signals. Only a few *Isoperla* species have derived, and more complex, grouped or phased calls (Stewart and Maketon 1991).

**Literature Cited**


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Studies in plant physiological ecology strive to provide an understanding of the diversity of plant physiological functions and how such diversity allows plants to interact favorably with their changing environment (Jacquard and Urbanska 1988). Many of these environmental changes eventually impose selection that acts on plants functioning as physiological units (Chapin and Oechel 1983). The end result of selection varies depending upon the nature of environmental change and the concomitant plant response. Variation among populations in their abilities to respond to environmental change is important in understanding the result of ecosystem perturbations and in our ability to predict a population’s ability to adapt and survive. Therefore, it is ecologically and evolutionarily important to study the amount and direction of physiological variation in natural plant populations that experience environmental changes.

The riparian ecosystem along the middle Rio Grande and its major tributaries in New Mexico is an ideal model for studying physiological plant response to environmental change. In the last 80 years, this ecosystem has experienced dramatic hydrologic perturbations that, in turn, may have induced physiological and morphological variation among these riparian populations. Construction of dams and extensive channelization of this river system have increased salinization of soil and groundwater, eradicated most flood events, and decreased water availability (Crawford et al. 1993). With the control of flooding and the construction of a system of drains paralleling the river through most of the middle Rio Grande basin in the 1930s, the water table was lowered by 1.5 m and the periodic, evenly distributed recharge of groundwater by flood events was virtually eliminated (Crawford et al. 1993). Even now, the storm-water conveyance system along a large portion of the Rio Grande surrounding Albuquerque, New Mexico, delivers most of the water runoff directly to the river channel.
thereby effectively bypassing the recharge of groundwater (Crawford et al. 1993). In addition, the low mean annual rainfall and high summer temperatures of the desert Southwest likely exacerbate these hydrologic impacts. All 3 likely sources of water in these riparian ecosystems, i.e., surface rainfall, channel flow, and groundwater stores, can be highly variable and are often relatively scarce. The effects of low precipitation and flow are exaggerated by the sandy alluvium in the middle Rio Grande valley, which cannot provide a suitable substrate for groundwater storage (Crawford et al. 1993). One might expect, therefore, that geographically separated plant populations within this system are likely to experience differing degrees of water availability. If so, separation by distance combined with changes in the hydrological environment may be driving differential physiological and morphological plant responses to lowered water availability in New Mexico riparian ecosystems.

One species likely to be acutely affected by these hydrologic changes is New Mexico’s native cottonwood, *Populus deltoides* var. *vislizenii*. Although primarily phreatophytic, *P. deltoides* relies secondarily on precipitation and stream flow for its water resources (Leffler and Evans 1999). Dams have not only impacted stream flow and groundwater levels, but they have also virtually eliminated germination sites in most *P. deltoides* populations along the Rio Grande. It is therefore expected that these populations will be replaced by exotic plant species within the next 50 years (Howe and Knopf 1991). This is not an uncommon phenomenon; in parts of western Canada, cottonwood forests downstream from dams have virtually been eliminated due to imposed water stress (Rood and Heinze-Milne 1989, Rood and Mahoney 1990). Therefore, studies that examine the physiological-morphological responses of riparian tree populations to imposed changes in water regime provide new insights and predictions about how dams contribute to the decline of downstream ecosystems (Tyrree et al. 1994).

To gauge the degree of variation among *P. deltoides* cottonwood populations in New Mexico in both environmental conditions and possible physiological responses to differences in hydrology, we quantified variability among 4 study sites in both soil and groundwater conditions and examined physiological and morphological characters on trees at these sites. We chose physiological traits that can be indicators of water stress including photosynthesis, water vapor exchange, and water potential (Buxton et al. 1985, Baldocchi et al. 1987, Iacobelli and McCaughey 1993). We also examined several morphological traits that are indicators of changes in water availability, i.e., traits that significantly affect gas exchange characteristics including leaf area, specific leaf weight, and chlorophyll content.

**Methods**

**Study Sites**

Four study sites were established to sample the relatively contiguous cottonwood forest along the middle Rio Grande basin of New Mexico. In New Mexico cottonwood forests are found from just below Taos Gorge south to Elephant Butte Reservoir. Populations south of the reservoir have been reduced to isolated patches due to a variety of anthropogenic impacts. The study sites are located along an approximately 250-km expanse of the Rio Grande watershed in New Mexico (Fig. 1). The northernmost site is Abiquiu (36°12′30″N, 106°19′06″W, elevation 1507 m) on the Rio Chama (a major tributary of the Rio Grande). Along the Rio Grande there are 3 additional study sites: 1 each at Corrales (35°14′16″N, 106°36′22″W, elevation 1552 m), Bernardo (34°25′06″N, 106°50′06″W, elevation 1444 m), and San Antonio (33°55′06″N, 106°52′06″W, elevation 1380 m).

For a previous study, ten 10-m-wide randomly located study plots were established within an approximately 0.5-km section of forest at each study site (Rowland et al. 2000). Each plot is perpendicular to the river and extends from the river’s edge to the end of the riparian forest. At 3 of the sites, the forest edge coincides with a levee road and water diversion channel that both parallel the river. At Abiquiu the river and an abandoned agricultural field border the forest. Thirty trees at each site were randomly chosen for measurements. Cottonwood stands sampled tended to be continuously mature throughout each site, and tree age averaged 30–40 years (unpublished data). However, minor recruitment was observed at Corrales and San Antonio. At these latter sites the gallery forest ended abruptly at a 50-m (Corrales) or 200-m (San Antonio) stretch.
of floodplain inhabited by younger trees between the forest edge and the river. These trees were sampled at Corrales and averaged 10–15 years of age, but trees at San Antonio were not measured because they were too small to tag without causing damage and possible mortality.

Measurements

SOIL SITE CHARACTERISTICS.—Soil, physiological, and morphological measurements were made during the same sampling period, June and July 1995. At each of the 4 sites, we randomly chose 30 trees for soil and physiological measurements. Soil samples were taken from the north side of each tree at either 2/3 of the canopy width from the trunk or 1.6 m from the trunk if the canopy was not even; this distance ensured that samples were taken from the active root zone. Samples were taken with a 2-inch (5.08-cm) PVC pipe sharpened at one end. After removing overlying organic material, the PVC pipe was driven into the ground to a depth of 20 cm and withdrawn. We then removed core samples, placed them in plastic bags, and refrigerated them at 4°C until processed. Soils were air-dried and homogenized using a #10 sieve (2.00-mm sieve opening) before analysis.

Following procedures outlined by Black et al. (1965), we prepared saturation paste extracts and analyzed them for salinity by the electrical conductivity (EC) method using an Accumet model 50 pH/ion/conductivity meter. We determined total nitrogen and phosphorus on 10 random samples per site using the Kjeldahl digestion method (Black et al. 1965). Soil texture from 8 randomly chosen samples per site was analyzed by the hydrometer method (Black et al. 1965). After percentages of sand, silt, and clay were calculated, we used a Soil Survey Staff chart to apply textural classifications (e.g., clay, loam, sandy loam).

GROUNDWATER SITE CHARACTERISTICS.—After taking physiological and morphological measurements, we established 3 groundwater wells at each site in a stratified random manner in December 1995. At each site 3 plots were chosen randomly and single wells were installed 20 m from the edge of the river, 20 m from the edge of the forest near the levee road (or near the agricultural field at Abiquiu), and at the center of the plot. All wells were hand-augered to groundwater. Three-inch (7.62-cm) PVC pipe was used for the well body, and approximately 1 m of screened PVC tube was inserted into each well at groundwater. Measurements were taken monthly during the cottonwood growing season from May 1996 until December 1996. Depth to groundwater (m) from the soil surface was measured using a meter tape to the nearest cm. Dissolved oxygen was measured with a YSI dissolved oxygen meter (Yellow Springs Instrument Co., Inc.), and water samples were taken for electrical conductivity measurements (samples were stored in a refrigerator at 4°C until conductivity measurements were made). Conductivity, a measure of salinity, was determined with an Accumet model 50 pH/ion/conductivity meter.

MORPHOLOGICAL AND PHYSIOLOGICAL MEASUREMENTS.—In mid-June 1995 we took morphological and physiological measurements at the southernmost population (San Antonio). Because of seasonal changes in flower production, the delay in leaf development between successively more northern sites was approximately 1 week. To compensate for this seasonal difference, each successive northern site was sampled 1 week later than the previous site. At each of the 4 sites, the same 30 individuals chosen randomly for soil samples were
used for gas exchange, morphological, and water potential measurements. To minimize light-induced developmental differences, we collected 3 shade leaves near the tree bole from the lower canopy of each tree. Branch apices were excised with an extendable pole-cutter and leaf samples analyzed immediately for gas exchange. Although measuring gas exchange, especially photosynthesis, on excised tissue may be problematic (Slavik 1974, Lakso 1982), others have found no appreciable effects (Barden et al. 1980). In this study, measurement of intact leaf tissue was not possible due to inaccessibility of the canopy. Therefore, measurements were standardized across all sites by equalizing time between excision and gas exchange analysis. One fully expanded leaf per cut branch was selected for measurement; selected leaves had blade lengths between 6 and 7 cm, which standardized leaf developmental stage based on the plastochron index for *Populus* (Dickmann 1971, Larson and Isebrands 1971, Isebrands and Larson 1973, Lamoreaux et al. 1978). Gas exchange measurements were made in full sun. Photosynthesis, stomatal conductance, and transpiration were measured with an ADC infrared gas analyzer (The Analytical Development Company Ltd., England; LCA model 3). Water-use efficiency (WUE) was calculated as the ratio of photosynthesis:transpiration. To ensure that gas exchange was measured at maximum levels, all such measurements were taken between 0900 and 1130 hours MDT at all sites. This time interval was previously determined to be within the period of peak gas exchange for *P. deltoides* at the New Mexico sites (unpublished results).

Immediately after the gas exchange measurements, chlorophyll content was estimated with a Minolta SPAD chlorophyll meter (Minolta Corp., Ramsey, NJ). The SPAD chlorophyll meter measures absorbance by plant tissues of a particular range of wavelengths in the visible spectrum; this is a relative measure of the internal concentration of chlorophyll a and b. Three SPAD measurements were taken per leaf and then averaged to correct for possible non-homogeneous distribution of chlorophyll throughout the leaf (Monje and Bugbee 1992). SPAD measurements were then converted to chlorophyll content using the equation:

\[
\text{chlorophyll (µg ⋅ cm}^{-2}) = (\text{SPAD} – 8.1095)/0.855
\]

developed for *Populus deltoides* trees in New Mexico (J. Leffler personal communication).

After field measurements of gas exchange and chlorophyll, leaves were placed in plastic bags and kept on ice or refrigerated at 4°C until leaf area and stomatal density measurements were completed. Hence, leaf morphological characters were measured on the same leaves measured for gas exchange. Leaf area was measured to the nearest square centimeter with a model CI-201 leaf area meter (CID, Inc.). For each leaf, 3 area measurements were taken and averaged. Leaves were then dried in a drying oven at 60°C for 5 days and, after drying was complete, leaf mass (g) was determined using an analytical balance. Specific leaf weight (SLW) was calculated for each leaf (i.e., mean leaf area/leaf mass).

Leaf xylem pressure potentials were measured in the field with a pressure bomb (PMS Instrument Company, Corvallis, OR). Using a polecutter, we excised 1 branch from each of the same 30 trees measured for gas exchange. Branches were placed in plastic bags and measured within 15 minutes after excision in a Scholander-style pressure chamber (Scholander et al. 1965). Water potential measurements were taken between 1200 and 1500 hours MDT, the hours of greatest water loss. Predawn measurements were not taken because previous results at the Corrales site indicated no significant differences among individuals for predawn water potentials; therefore, we concluded that midday water potentials would provide a relative index of water stress among sites.

At each site we measured stomatal density on 10 trees randomly selected from the same 30 trees measured for physiology. One branch per tree was collected and frozen at 0°C. One leaf was removed from each branch for stomatal density measurement. For each leaf, we cut 2 samples from the center of the leaf blade, on either side of the midrib, and mounted them on glass microscope slides with distilled water. Because *Populus* is amphistomatous, stomatal density was counted on both the adaxial and abaxial surfaces of each leaf sample. Samples were observed and stomata counted with a Zeiss Axioskop light microscope at 20× magnification. For each mounted sample, stomata were counted in 4 arbitrary fields (right adaxial, right abaxial, left adaxial, left abaxial).
**Statistical Analyses**

For environmental variation among sites, 1-way fixed model ANOVAs (SAS Institute 1989), with SITE as a fixed factor, were used to assess possible differences in salinity, total nitrogen, total phosphorus, ratio of nitrogen to phosphorus, and soil texture among sites. Repeated-measures ANOVAs (SAS Institute 1989) were used to assess differences in groundwater depth, dissolved oxygen, and salinity among sites. Physiological and morphological variation both among and within sites was examined with individual mixed-model nested univariate ANOVAs with SITE as a fixed factor and TAG(SITE) or tree nested within site as a random factor (Sokal and Rohlf 1995). Scheffe’s multiple range tests were used to determine where differences existed among sites. Pearson correlations (SYSTAT 1996) were used to relate the environmental parameters to physiological and morphological characteristics within a given site. Within each of the 4 sites, we correlated soil salinity and distance to the river of a measured tree with its average measured physiological characters of photosynthesis, stomatal conductance, transpiration, water-use efficiency, chlorophyll content, and water potential.

**Results**

**Environmental Variation**

Significant variation was evident among the 4 sites for all soil characteristics (Table 1). Soil salinity showed a wide range among sites. Abiquiu had the highest mean salinity, followed by Bernardo; whereas San Antonio and Corrales had similarly low soil salinity. Total nitrogen and soil phosphorus content was highest at Abiquiu and lowest at Corrales (Table 1). The nitrogen-to-phosphorus ratio was highest at Bernardo and lowest at Corrales, while San Antonio had an intermediate value. Soil textures ranged widely among sites as well (Table 1). Analysis of variance showed significant differences among sites for both sand and clay. Mean percentages for sand ranged from 11.8 at San Antonio to 57.2 at Corrales; for clay, mean percentages ranged from 19.9 at Corrales to 56.3 at San Antonio. However, silt content did not differ among sites; mean percentages ranged from 22.9 at Corrales to 36.5 at Abiquiu. Corrales samples were extremely sandy (57%), San Antonio was mostly clay (57%), and Bernardo soil was 43% clay. Abiquiu soils were more equally partitioned among 3 soil particle classes (31% clay, 36% silt, 32% sand), i.e., a texture of loam.

<table>
<thead>
<tr>
<th>Trait</th>
<th>AB</th>
<th>CO</th>
<th>BE</th>
<th>SA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Salinity (dSiemens (\cdot) m(^{-1}))</td>
<td>1.33 (0.11) a</td>
<td>0.10 (0.02) c</td>
<td>0.92 (0.05) b</td>
<td>0.18 (0.02) c</td>
</tr>
<tr>
<td>Nitrogen ((\mu)g (\cdot) g(^{-1}))</td>
<td>1132.9 (142.7) a</td>
<td>331.4 (138.8) b</td>
<td>1010.3 (141.8) a</td>
<td>808.3 (71.0) ab</td>
</tr>
<tr>
<td>Phosphorus ((\mu)g (\cdot) g(^{-1}))</td>
<td>350.0 (22.8) a</td>
<td>208.9 (29.1) b</td>
<td>292.4 (18.2) ab</td>
<td>328.1 (16.5) a</td>
</tr>
<tr>
<td>Nitrogen / phosphorus ratio</td>
<td>3.2 (0.3) a</td>
<td>1.2 (0.3) b</td>
<td>3.3 (0.3) a</td>
<td>2.5 (0.2) ab</td>
</tr>
<tr>
<td>Sand</td>
<td>32.3 (5.2) ab</td>
<td>57.2 (8.2) a</td>
<td>33.0 (9.5) ab</td>
<td>11.8 (7.5) b</td>
</tr>
<tr>
<td>Clay</td>
<td>31.2 (2.3) b</td>
<td>19.9 (1.5) b</td>
<td>42.6 (8.1) ab</td>
<td>56.3 (6.5) a</td>
</tr>
<tr>
<td>Silt</td>
<td>36.5 (3.1) a</td>
<td>22.9 (6.9) a</td>
<td>24.4 (3.8) a</td>
<td>31.9 (4.4) a</td>
</tr>
</tbody>
</table>
Groundwater measures varied significantly among sites. Distance to groundwater (df = 2, SS = 11.317, MS = 5.658, F = 12.65, P < 0.0186), conductivity (df = 2, SS = 527048, MS = 527048, F = 394.82, P < 0.0002), and dissolved oxygen content (df = 2, SS = 0.69, MS = 0.69, F = 15.84, P < 0.0126) were all significantly different among sites. Depth to groundwater was greatest at Corrales and least at Abiquiu throughout the sampling period (May–December; Fig. 2a). However, Abiquiu groundwater was highly saline and lower in dissolved oxygen content than Bernardo and Corrales for most months during the measurement period (Figs. 2b, 2c). Bernardo groundwater was higher in dissolved oxygen than the other 2 sites for every month except June 1996 (Fig. 2c).

### Physiological and Leaf Morphological Variation

Individual nested ANOVAs, using a significance level of P < 0.0125, adjusted for multiple tests (Sokal and Rohlf 1995), showed signifi-
significant variation among and within populations for specific physiological and morphological characters. Photosynthesis was significantly different among and within populations and ranged from 7.2 μmol C \cdot m^{-2} \cdot s at San Antonio to 12.2 μmol C \cdot m^{-2} \cdot s at Corrales (Table 2). However, there was no clear geographical (i.e., north–south) pattern for photosynthetic levels, with the northernmost site (Abiquiu) not significantly different from the southernmost site (San Antonio). Nonetheless, stomatal conductance, transpiration, and midday xylem pressure potentials did show geographical trends. Stomatal conductance was significantly different among and within populations (Table 2) and decreased with each site from north to south; Abiquiu had the highest stomatal conductance, while San Antonio had the lowest value. Transpiration also showed significant differences among and within populations and a similar decreasing trend to the south (Table 2); however, the 2 middle geographic populations (Corrales and Bernardo) were not significantly different from one another. Midday xylem pressure potentials were significantly different among populations and showed a geographic trend of increasing xylem pressure potentials to the south (Table 2). The greatest water stress was noted at Abiquiu (–1.9 MPa), the lowest at San Antonio and Bernardo (–1.7 MPa). Although water-use efficiency showed no strong geographic trend, differences among and within populations were significant. All populations were significantly different from one another, with the highest WUE occurring at Corrales (1.8 mmol C \cdot mol H_{2}O^{-1}) and the lowest at Abiquiu (0.8 mmol C \cdot mol H_{2}O^{-1}; Table 2). Water-use efficiency was also significantly negatively correlated with soil salinity at Abiquiu, the site with highest soil salinity (Table 3), but it was not correlated with distance to the river. No other physiological or morphological variables were significantly correlated with these 2 environmental parameters within individual sites.

Leaf morphological traits were also significantly different among and, in most cases, within populations (Table 4). Mean chlorophyll content (converted values, μg \cdot cm^{-2}) showed significant differences among and within populations and ranged from 28.1 at San Antonio to 23.6 at Abiquiu. Chlorophyll levels showed a geographic trend of increasing to the south; like transpiration, chlorophyll levels were not significantly different between Corrales and Bernardo. Leaf area also showed significant variation among and within populations. Leaf area was largest at the 2 southernmost populations, Bernardo (31.7 cm²) and San Antonio (29.5 cm²), while leaves were smallest at Corrales (20.1 cm²; Table 4). Specific leaf weight (SLW) differed among and within sites; it was highest at Corrales (100.0 g \cdot m^{-2}) and lowest at San Antonio (62.9 g \cdot m^{-2}; Table 4). Although leaves were smaller at Corrales, they were thicker, thus contributing to high SLW. Adaxial (upper) stomatal density did not significantly differ among sites; however, abaxial (lower) density approached significance (Table 4). Abiquiu had the lowest mean values for both adaxial stomatal density (67.2 \cdot mm^{-2}) and abaxial (53.4 \cdot mm^{-2}). A paired t-test across populations showed that the adaxial surface had a significantly higher stomatal density than the abaxial surface (df = 39, tcrit = 2.02, P < 0.0001).

**Discussion**

Our study provides evidence of considerable variation in environmental, physiological, and morphological characteristics within and among natural riparian populations of *Populus deltoides* in the New Mexico Rio Grande basin. While many studies have addressed physiological variation among and within *Populus* species, most were conducted on limited, clonal material (e.g., Ceulemans and Impens 1980, 1983, 1987, Blake et al. 1984, Liu and Dickmann 1992, Dunlap et al. 1993, Donahue et al. 1994). Those studies comparing the degree and type of physiological differences among natural *Populus* populations of contrasting environments, as in our study, are quite scarce (see McGee et al. 1981). Our study is ecologically important for detecting and describing the partitioning of physiological and morphological variation among populations. These descriptions assist us in predicting future population survival because variability among populations in physiological and morphological characteristics will eventually impact their ability to respond to these environmental differences. In addition, studies that examine variation within natural populations are a mainstay of silviculture research for screening and identifying new candidate genetic stock (Bassman and Zwier 1991). Because *Populus* is
being studied for energy plantations (Schulte et al. 1987) and for wood and fiber production (Ceulemans and Impens 1980, 1987), identifying genotypes in natural populations with drought-adaptive traits would be extremely beneficial (Bassman and Zwier 1991). We know that plants coming from arid environments generally are better adapted for survival under low water conditions (Gurevitch et al. 1986); therefore, genotypes from these populations might be useful for introduction to plantations under arid and low watering regimes.

Water availability, as reflected in soil and groundwater parameters, differed significantly among separate, cottonwood-dominated sites in the Rio Grande basin. At the northern site at Abiquiu, there were high levels of salt in both the soil and groundwater, presumably reducing the water available to *P. deltoides* trees at this site. High salinity and nitrogen levels at Abiquiu may be due to the extensive agricultural fields that are directly adjacent to the forest. Leaching and runoff of salts and fertilizer into the cottonwood forest from agricultural fields could cause elevated salinity and nitrogen levels at this site; abandoned agricultural fields can be extremely saline (Hendrickx et al. 1992). The Bernardo site also had high salt levels, but these may be due to increased abundance of salt cedar. Salt cedar was much more abundant at Bernardo than at the other 3 sites; and, as Busch and Smith (1995) have shown, salt cedar, because of its high salt content in leaf litter, tends to salinize soil. Corrales showed a relative deficiency in soil nitrogen and very low soil salinity, both of which might be a result of its extremely sandy soil texture. These environmental differences, both in soil and groundwater, may be factors contributing to the physiological and morphological variation we found among these populations.

Large variation in many physiological traits and leaf morphological traits related to water use was evident among the New Mexico populations and appears to be somewhat influenced by environmental differences among populations. With high soil and groundwater salinity levels at Abiquiu, we expected cottonwoods there to be water stressed. That is precisely

<table>
<thead>
<tr>
<th>Trait</th>
<th>Source of variation</th>
<th>AB</th>
<th>CO</th>
<th>BE</th>
<th>SA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Photosynthesis (µmol C ⋅ m⁻² s⁻¹)</td>
<td>Site: df = 3, MS = 455.3, F = 42.7, P-value = 0.0001; Tag(Site): df = 116, MS = 10.7, F = 2.3, P-value = 0.0001</td>
<td>7.8 (0.3) c</td>
<td>12.2 (0.3) a</td>
<td>9.0 (0.2) b</td>
<td>7.2 (0.2) c</td>
</tr>
<tr>
<td>Stomatal conductance (mmol H₂O ⋅ m⁻² s⁻¹)</td>
<td>Site: df = 3, MS = 468899.6, F = 68.5, P-value = 0.0001; Tag(Site): df = 116, MS = 6869.4, F = 3.8, P-value = 0.0001</td>
<td>265.8 (7.8) a</td>
<td>225.0 (6.9) b</td>
<td>165.3 (4.2) c</td>
<td>102.6 (5.0) d</td>
</tr>
<tr>
<td>Transpiration (mmol H₂O ⋅ m⁻² s⁻¹)</td>
<td>Site: df = 3, MS = 430.0, F = 123.7, P-value = 0.0001; Tag(Site): df = 116, MS = 3.5, F = 4.0, P-value = 0.0001</td>
<td>9.8 (0.1) a</td>
<td>6.7 (0.1) b</td>
<td>6.8 (0.2) b</td>
<td>4.5 (0.1) c</td>
</tr>
<tr>
<td>Water-use efficiency (mmol C ⋅ mol H₂O⁻¹)</td>
<td>Site: df = 3, MS = 18.4, F = 62.6, P-value = 0.0001; Tag(Site): df = 116, MS = 0.3, F = 6.2, P-value = 0.0001</td>
<td>0.8 (0.0) d</td>
<td>1.8 (0.0) a</td>
<td>1.4 (0.0) c</td>
<td>1.7 (0.0) b</td>
</tr>
<tr>
<td>Xylem pressure potential (MPa)</td>
<td>Site: df = 3, MS = 30.3, F = 6.7, P-value = 0.0003</td>
<td>−1.9 (0.0) c</td>
<td>−1.8 (0.0) bc</td>
<td>−1.7 (0.0) ab</td>
<td>−1.7 (0.0) a</td>
</tr>
</tbody>
</table>
what we found, with Abiquiu cottonwoods experiencing higher transpiration levels and lower midday water potentials than cottonwoods at the other sites. In fact, midday water potentials of –1.8 MPa suggest that cavitation stress may be high in these trees because cavitation is known to occur in *Populus* at water potentials of –1.7 MPa (T yree et al. 1994). The negative correlation of water-use efficiency and soil salinity at Abiquiu appears to support the conclusion that environment is influencing cottonwood physiology to some extent.

Environmental differences among cottonwood populations related to the geography of the Rio Grande basin are indicated by the north–south trends in physiological and morphological variation. The 2 middle sites, Bernardo and Corrales, are separated by 60 miles and are isolated from the other 2 sites by natural constrictions in the river north of Corrales and south of Bernardo. Hence, these 2 middle populations may be more environmentally similar. This is certainly true for our measurements of soil nitrogen and nitrogen:phosphorus ratio. Further, we found that transpiration, water potential, and chlorophyll content did not differ between these 2 sites. Nonetheless, there are important environmental parameters, such as soil salinity, which did differ between them and may explain tree-response differences in other physiological traits (e.g., water-use efficiency) and morphological traits (e.g., specific leaf weight). We found a strong geographic trend in stomatal conductance that was greatest at Abiquiu and decreased to the south. Geographic trends in physiological traits are not uncommon. For example, Dang et al. (1994) found that photosynthesis, midday water potentials, and transpiration in red alders (*Alnus rubra*) have a geographic trend increasing from southeast to northwest in British Columbia, Canada.

Morphological variation among sites suggests that some populations are better able than others to respond favorably to water stress conditions. For example, at Corrales, cottonwoods had higher specific leaf weights than did cottonwoods at other sites, indicating that Corrales leaves were smaller but thicker (Busch and Smith 1995). This type of leaf morphology is adaptive in relatively dry habitats. Leaf morphology may explain the ability of Corrales trees to maintain higher water-use efficiencies than trees in the other populations. Geber and Dawson (1990) provided evidence that small-leafed populations in certain plants have high gas exchange rates, low water-use efficiencies, and maximum vegetative yields, all leading to a highly cost-efficient photosynthetic system. This appears to be the case for cottonwoods in Corrales, since they have relatively small leaves and high photosynthetic rates. Other morphological traits, such as stomatal frequency, can be linked to gas exchange characteristics that are positively correlated with photosynthesis (Paul and Eagles 1988). Although we found no significant variation in stomatal density among studied populations, a trend toward high stomatal density was noted in Corrales trees, which may be another factor explaining their high photosynthetic rates.

In addition to the variation among populations, we also found significant variation within populations of *P. deltoides* for several physiological and morphological traits. This is not an uncommon finding since individual plants within populations can respond differently to stress, and recent studies have shown considerable microscale environmental variation within populations. What is important about this intrapopulation variation in physiological response is that it may lead to small-scale genetic variation within populations (Perry and Knowles 1991, Young and Merriam 1994, Loisell et al. 1995). Because our study spanned only a single growth season, long-term predictions about the continued direction of inter- and intrapopulation variation are limited. Long-term monitoring of these populations is necessary as well as determining the genetic basis of the physiological and morphological traits for a full understanding of any possible adaptive responses to environmental stress.

<table>
<thead>
<tr>
<th>Population</th>
<th>Salinity (dSiemens · cm⁻¹)</th>
<th>Distance to river (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abiquiu</td>
<td>-0.523*</td>
<td>-0.272</td>
</tr>
<tr>
<td>Corrales</td>
<td>0.146</td>
<td>0.284</td>
</tr>
<tr>
<td>Bernardo</td>
<td>0.088</td>
<td>0.080</td>
</tr>
<tr>
<td>San Antonio</td>
<td>0.019</td>
<td>-0.005</td>
</tr>
</tbody>
</table>

*P ≤ 0.05
ACKNOWLEDGMENTS

The Research Experience for Undergraduates Program provided field and monetary assistance for this study; LB, AC, and LG were supported by NSF Grant #BIR-9424121. The Graduate Research Allocations Committee at UNM and the LTER Sevilleta provided monetary support for DR. We thank P. Kelley, J. Leffler, M. Healey, L. LaBong, D. Wheeler, and R. Cabin for field assistance. We especially thank D.P. Rowland, Dr. D.T. Jennings, and N. Jennings for field support and design consultation. We gratefully thank M. Mason for the use of the property and trees at Abiquiu. We also thank Dr. E. Bedrick of UNM and Dr. I. Harris of Northern Arizona University for statistical consultation, and Dr. D. Marshall for use of the Zeiss microscope. Drs. D. Natvig, G. Johnson, C. Crawford, M. Lechowicz, N. Johnson, and D. Jennings provided helpful and constructive comments on an earlier draft.

LITERATURE CITED


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Increasing atmospheric carbon dioxide concentration is expected to increase global temperatures and thereby alter the amount, seasonality, and intensity of precipitation on global to regional scales (Houghton et al. 1996, Mahlman 1997, Giorgi et al. 1998). Although considerable research has described the effects of increasing atmospheric carbon dioxide concentration (e.g., Koch and Mooney 1996, Körner and Bazzaz 1996) and expected increase in temperature (e.g., Chapin et al. 1995, Harte and Shaw 1995, Beerling and Woodward 1996) on ecosystems, little research has focused on potential changes in precipitation regimes, which embodied 50% changes to quantities of summer and winter precipitation, and encompassed a continuum of precipitation from 359 mm · year⁻¹ to 846 mm · year⁻¹. However, survival and physiological performance of seedlings were negatively impacted by seasonal environmental conditions common to all treatments, especially during the annual pre-monsoon drought. Seedling predawn leaf water potentials, net CO₂ assimilation, and stomatal conductance indicate that growing conditions for Q. emoryi seedlings at this site are generally restricted to periods with adequate soil moisture (i.e., April and August). Results contrast with an assumption implicit to the “two-layer” soil water resource partitioning hypothesis that woody plants in all life history stages are more dependent upon winter than summer precipitation. In fact, summer precipitation appears more important than winter precipitation for Q. emoryi seedling recruitment and growth.

Key words: Quercus emoryi, precipitation seasonality, seedling recruitment, population demographics, carbon isotope discrimination, leaf gas exchange.

We investigated how amount and seasonality of precipitation affect the physiologic and demographic performance of oak \textit{(Quercus L.)} seedlings in oak savannas of the southwestern United States (Brown 1982, McClaran and McPherson 1999). This region is characterized by a bimodal precipitation regime, with peaks in amount of precipitation in both summer (52% of annual precipitation) and winter (29% of annual precipitation). This regional precipitation regime is likely to change within the next century as atmospheric CO2 concentration increases (Houghton et al. 1996, Giorgi et al. 1998), although the extent and direction of these changes are difficult to predict (Mahlman 1997).

We used a manipulative field experiment to simulate potential scenarios of precipitation redistribution that southwestern oak savannas may experience by the mid- to late 21st century. Recruitment and production of seedlings of the dominant savanna tree, \textit{Quercus emoryi} Torr. (Emory oak), are described in Weltzin and McPherson (2000). The objectives of this study were to (1) assess physiological performance of these seedlings and (2) compare measures of seedling physiology with seedling demographic responses.

**MATERIALS AND METHODS**

**Study Site**

We conducted research between 1994 and 1996 at the lower (and drier) margin of temperate, evergreen oak woodland at the base of the Huachuca Mountains in southeastern Arizona, USA. The ecotone between oak woodland and adjacent semidesert grassland is characterized by \textit{Q. emoryi}–dominated savannas bordered by semidesert grassland dominated by \textit{C}4 perennial bunchgrasses (Brown 1982, McClaran and McPherson 1999).

The study site is located in lower Garden Canyon (31°29’N, 110°20’W) on Fort Huachuca Military Reservation (FHMR) near Sierra Vista, Arizona. During the study period overstory tree cover within the savanna was 11%, as estimated from aerial photographs (Haworth and McPherson 1994). Herbaceous vegetation was dominated by the perennial bunchgrass \textit{Trachyopogon montufari} (H.B.K.) Nees. The site is 1550 m in elevation with a 5% slope on a northeastern aspect. Soils developed from gravelly alluvium. Climate is semiarid, with an average annual temperature of 20°C. Average annual precipitation of 602 mm is bimodally distributed, with peaks during the summer ‘monsoon’ (July–September) and during winter (December–February; NOAA 1996). Weltzin and McPherson (2000) provide further details on climate, vegetation, and soils at this site.

**Experimental Design**

In June 1994 we initiated a field experiment consisting of 5 simulated precipitation treatments applied to plots isolated from ambient precipitation and soil moisture. The 1st treatment received simulated precipitation equivalent to the long-term (30-year) mean annual precipitation for the site (602 mm \textit{year}–1; Table 1). The other 4 treatments received all possible combinations of 50% additions and reductions of summer (July–September) and winter (December–February) precipitation relative to the long-term seasonal mean. Treatments received equal amounts of precipitation in spring (defined herein as March–June) and autumn (October–November).

This experimental design incorporated changes to both seasonal and total precipitation because changes in atmospheric circulation that will accompany climate change will produce regional changes in both the amount and seasonality of precipitation (Houghton et al. 1996, Mahlman 1997, Giorgi et al. 1998). Because effects of interannual variation in total precipitation on plant communities have been well studied (e.g., Weaver and Clements 1929, Stephenson 1990), we focused on the little-studied component of precipitation seasonality (see Neilson 1986, Neilson et al. 1992).

Treatments were arranged within a randomized complete block design \(n = 4\). Blocks
were established within homogeneous stands of perennial bunchgrasses. Within each block, we linearly arranged five 1.2 m × 1.5 m-plots at 1.5-m spacing. The perimeter of each plot was trenched to 1-m depth and lined with polyethylene film to prevent lateral movement of soil water. The edge of each plot was bordered to prevent lateral movement of surface water. Vegetation in each plot was left intact. A permanent precipitation shelter (16 m × 4 m) constructed of steel tubing, clear polyethylene film, and fence posts was erected over each block to exclude ambient precipitation (Fig. 1). The pitched roof of each shelter was 2.2 m aboveground at its apex and 1.5 m high along the sides and ends. Poultry netting (2.5-cm mesh) was wired to fence posts and rebar stakes around each block to form a 60-cm-tall vertebrate exclosure.

We kept the shelters open-sided to minimize microclimatic impact. Shelters reduced photosynthetically active photon flux density by 29% ± 10% (mean ± 1 sx) at solar noon on a clear, midsummer day. Although shelters likely altered other, unquantified microenvironmental variables (e.g., ambient temperature, relative humidity), experimental units were affected equally.

Precipitation collected and stored on-site was applied to plots according to a randomly generated precipitation regime that simulated natural precipitation patterns (Nicks and Lane 1989; CLIGEN, USDA-ARS Southwestern Watershed Research Center, J. Stone, personal communication). Simulated precipitation events, ranging from 1 mm to 120 mm, were applied by hand-watering 57 times annually (Table 1). Additional details of the experimental design are in Weltzin and McPherson (2000).

On 17 July 1995 we collected Q. emoryi acorns from trees on-site, sorted them by visual examination and flotation (Nyandiga and McPherson 1992), and planted 49 acorns at 10-cm spacing into each plot. Survival of emerged seedlings was monitored throughout the experiment. When seedlings were about 8 months old, we started our assessments of leaf water potential and leaf gas exchange. *Quercus emoryi* are evergreen and accumulate little aboveground biomass during the first several years after germination (Weltzin and McPherson 2000). Because seedlings in this experiment developed few, if any, new leaves in 1996, we sampled leaves initiated in 1995.

We determined *Q. emoryi* predawn leaf water potential (Ψ) with a Scholander-type pressure chamber (PMS Instrument Company, Corvallis, OR) on 20 April, 30 June, 22 August, and 17 October 1996. In particular, on each date we selected one seedling at random from each plot. During a period of 1–3 hours before the beginning of the daily photoperiod, we collected one leaf at random from near the top of the seedling canopy for determination of Ψ (n = 4). On each date we also used a portable open-loop photosynthesis system (CIRAS-1 CO2/H2O Infrared Gas Analysis System, PP Systems, Haverhill, MA) to determine midday net CO2 assimilation (A), the ratio of leaf intercellular to ambient CO2 concentration (ci/ca), and stomatal conductance (gs) (n = 4) of randomly selected seedlings other than those used for assessment of Ψ.

*Quercus emoryi* leaves used for Ψ were retained for carbon isotope (δ13C) analysis (Brugnoli and Farquhar 2000). We measured δ13C on finely ground, oven-dried (70°C for 48 hours) samples using an isotope ratio mass spectrometer (delta S, Finnigan MAT, San Jose, CA) at the University of Utah Stable Isotope Ratio Facility for Environmental Research.
\begin{align*}
\Delta &= (\delta_a - \delta_p)/(1 + \delta_p) \\
\delta_p &= \delta^{13}C_{\text{leaf}} \quad \delta_a &= \delta^{13}C_{\text{air}} = -8\%e \quad \text{Farquhar et al. (1989)}
\end{align*}

where $\delta_p$ is $\delta^{13}C$ of leaves and $\delta_a$ is that of the air ($-8\%e$) according to Farquhar et al. (1989). $
\Delta$ during photosynthesis is directly related to $c_i/c_a$ as

$$\Delta = a + (b - a)c_i/c_a \quad (2)$$

where $a$ and $b$ represent fractionations associated with CO$_2$ diffusion into the leaf (4.4\%e) and carboxylation (27\%e), respectively. The $\Delta$ value forms the basis of a flux integrated estimate of $c_i/c_a$ in C$_3$ plants (Farquhar et al. 1989) and reflects the balance between biochemical demand for CO$_2$ by the chloroplasts and CO$_2$ supply through stomata. $\Delta$ integrates $c_i/c_a$ over the active periods of photosynthesis and leaf formation and is frequently correlated to stomatal conductance and drought stress (Ehleringer 1990, Meinzer et al. 1992).

To assess relationships between seedling physiology and demography by assessing correlations between $\Delta$ and seedling survival rates. Seedling survival rates were calculated as the change in percentage survival divided by the number of days within a given time period, and are expressed as \% day$^{-1}$. Seedling survival rates were determined for 4 time periods: 60 and 30 days before determination of $\Delta$ (PRE60 and PRE30, respectively), and 30 and 60 days after determination of $\Delta$ (POST30 and POST60, respectively). These 30- and 60-day time periods do not correspond exactly with monthly and bimonthly assessment of seedling survival and $\Delta$, respectively, because survival and $\Delta$ were not necessarily determined on the same date of the month. POST30 and POST60 were not determined for the October sample date because the experiment was terminated shortly thereafter.

**Statistical Analyses**

For each sample date we used analysis of variance (ANOVA; SAS procedure GLM, SAS Institute 1989) to evaluate random and fixed effects of block and treatment, respectively, on seedling survival, $\Delta$, $c_i/c_a$, $g_s$, $\Psi$, and $\Delta$. We used Fisher’s protected LSD (Fisher 1960) a posteriori mean separation tests for significant treatment effects ($P < 0.05$ unless otherwise indicated). In addition, we compared summer-

Fig. 1. Experimental system for capturing and redistributing precipitation. Each of 4 precipitation shelters (16 m $\times$ 4 m) was covered with clear polyethylene film to exclude ambient precipitation from experimental plots. Ambient precipitation was stored in on-site tanks for later application to plots.
wet vs. summer-dry and winter-wet vs. winter-dry treatments using single-degree-of-freedom contrasts (Zar 1996; P-values are for ANOVAs unless otherwise indicated).

We used Pearson and Spearman rank correlation procedures (SAS procedure CORR, SAS Institute 1989) to assess correlations between percent seedling survival and $A$, $c_i/c_a$, $g_s$, $Ψ$, and $Δ$ for each sample date ($n = 20$) and for all sample dates combined ($n = 80$). Spearman rank correlation coefficients for $Δ$ vs. PRE60, PRE30, POST30, and POST60 were determined for all treatments at each sample date ($n = 20$ except POST30 and POST60 in October), and for all sample dates combined ($n = 80$ except POST30 and POST60 where $n = 60$). For each correlation analysis, we performed sequential Bonferroni corrections to control the group-wide type I error rate (Rice 1989). We used least-squares regression analysis (SAS procedure REG, SAS Institute 1989) to investigate the relationship between $c_i/c_a$ and $Δ$ for all treatments for each date ($n = 20$), and for all dates combined ($n = 80$).

Prior to analysis, all data were tested for normality with the Shapiro-Wilk W-statistic (Shapiro and Wilk 1965). Data not normally distributed ($P < 0.05$) were transformed or ranked as appropriate. Percent seedling survival data were arcsine-transformed prior to analysis (Zar 1996).

**Results**

Seedling survival rates ranged from 76–90% in April to 38–58% in October (Table 2). Survival rates differed between treatments only in June ($P = 0.06$), when survival was greater in the summer-dry/winter-dry treatment than in the summer-wet/winter-wet and long-term mean treatments. Additional details of seedling survival are in Weltzin and McPherson (2000).

Seedling predawn leaf water potentials ($Ψ$) differed ($P = 0.002$) between treatments only in October, when $Ψ$ was lower in summer-dry ($–4.8$ MPa) than summer-wet plots ($–1.9$ MPa), and long-term mean plots were intermediate ($–3.5$ MPa; Table 2). $Ψ$ did not differ ($P > 0.05$) between treatments in April ($–1.6$ MPa) or August ($–0.8$ MPa). $Ψ$ in June were less than $–6$ MPa (i.e., the lower limit of the pressure chamber) for all sample units.

Net CO$_2$ assimilation ($A$) and $c_i/c_a$ at midday did not differ between treatments on any date (Table 2). Stomatal conductance ($g_s$) differed between treatments only in April, when $g_s$ was about 2.5 times higher in winter-wet than winter-dry treatments (Table 2). On all sample dates carbon isotope discrimination ($Δ$) was greater (contrast $P < 0.06$) for seedlings in wet summer treatments than seedlings in dry summer treatments (Table 2).

Percent seedling survival was positively correlated with $Δ$ when all dates were considered collectively ($r = 0.28$, $P = 0.01$, $n = 79$) and in August ($r = 0.50$, $P = 0.02$, $n = 20$). Percent survival and $c_i/c_a$ were negatively correlated only when all dates were considered ($r = –0.29$, $P = 0.01$, $n = 77$). Percent survival was not correlated with $A$, $g_s$, or $Ψ$ for any given sample date or when all dates were considered ($P > 0.16$, data not shown).

Carbon isotope discrimination ($Δ$) was not correlated with rates of seedling survival either 30 or 60 days before or after assessment of $Δ$ when sample dates were considered collectively (Table 3). In contrast, PRE60 and POST60 were positively correlated with $Δ$ determined in August and June, respectively. Although variations in $Δ$ explained only about 38% of the variation in survival rates, survival rates between June and August were greater in summer-wet plots, where seedlings had higher $Δ$ values, than in summer-dry plots, where seedlings had lower $Δ$ values (Fig. 2).

The ratio of intercellular to ambient CO$_2$ concentration ($c_i/c_a$) was a poor predictor of $Δ$ across the growing season, and for most dates within the growing season. In particular, $c_i/c_a$ and $Δ$ were correlated only in August ($r = 0.51$, $P = 0.03$) and, to a lesser extent, in April ($r = 0.45$, $P = 0.06$) and October ($r = 0.40$, $P = 0.09$), $c_i/c_a$ and $Δ$ were uncorrelated in June ($r = 0.02$, $P = 0.94$) and when all dates were considered ($r = 0.05$, $P = 0.67$).

**Discussion**

*Q. emoryi* Demography and Physiology

Surprisingly, seedling survival differed little between treatments, which embodied 50% changes in quantities of summer and winter precipitation and represented a continuum of precipitation from 359 mm ⋅ year$^{-1}$ to 846 mm ⋅ year$^{-1}$ (Table 1). There were also few treat-
ment effects on point measures of leaf gas exchange (A, gs, ci/ca, Ψ), net CO2 assimilation (Δ; µmol m-2 s-1), and carbon isotope discrimination (Δ) of Q. emoryi seedlings (n = 4).

Table 2. Mean (±sx–) survival (%), predawn leaf water potential (Ψ; MPa), net CO2 assimilation (A; µmol m-2 s-1), ci/ca, stomatal conductance (gs; mol m-2 s-1), and carbon isotope discrimination (Δ) of Q. emoryi seedlings (n = 4).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Variable</th>
<th>Date</th>
<th>Long-term mean</th>
<th>Summer dry/ winter wet</th>
<th>Summer dry/ winter dry</th>
<th>Summer wet/ winter wet</th>
<th>Summer wet/ winter dry</th>
</tr>
</thead>
<tbody>
<tr>
<td>Survival (%)</td>
<td>April</td>
<td>79 (2)1</td>
<td>76 (6)</td>
<td>90 (4)</td>
<td>85 (4)</td>
<td>85 (6)</td>
<td></td>
</tr>
<tr>
<td>June</td>
<td>52 (11) a</td>
<td>70 (7) ab</td>
<td>87 (5) b</td>
<td>66 (17) a</td>
<td>69 (13) ab</td>
<td></td>
<td></td>
</tr>
<tr>
<td>August</td>
<td>39 (9)</td>
<td>58 (7)</td>
<td>41 (19)</td>
<td>58 (18)</td>
<td>59 (14)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>October</td>
<td>38 (6)</td>
<td>58 (7)</td>
<td>40 (20)</td>
<td>58 (18)</td>
<td>57 (14)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ψ (MPa)</td>
<td>April</td>
<td>-1.5 (0.2)</td>
<td>-1.1 (0.1)</td>
<td>-2.0 (0.2)</td>
<td>-1.4 (0.5)</td>
<td>-2.0 (0.7)</td>
<td></td>
</tr>
<tr>
<td>June</td>
<td>-0.9 (0.4)</td>
<td>-1.4 (0.6)</td>
<td>-0.6 (0.1)</td>
<td>-0.6 (0.1)</td>
<td>-0.6 (0.2)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>August</td>
<td>-3.5 (0.2) a</td>
<td>-4.2 (1.2) ab</td>
<td>-5.4 (0.7) b</td>
<td>-1.6 (0.2) c</td>
<td>-2.1 (0.2) c</td>
<td></td>
<td></td>
</tr>
<tr>
<td>October</td>
<td>-1.9 (1.4)</td>
<td>-0.9 (0.8)</td>
<td>-0.5 (0.6)</td>
<td>-0.2 (1.6)</td>
<td>-0.1 (0.8)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>A (µmol m-2 s-1)</td>
<td>June</td>
<td>6.2 (0.0)</td>
<td>4.6 (1.7)</td>
<td>4.4 (1.2)</td>
<td>8.9 (3.3)</td>
<td>3.5 (1.4)</td>
<td></td>
</tr>
<tr>
<td>October</td>
<td>0.91 (0.14)</td>
<td>1.01 (0.03)</td>
<td>0.79 (0.01)</td>
<td>0.74 (0.04)</td>
<td>0.74 (0.04)</td>
<td>0.81 (0.04)</td>
<td></td>
</tr>
<tr>
<td>ci/ca</td>
<td>April</td>
<td>0.13 (0.08)</td>
<td>0.40 (0.15)</td>
<td>0.15 (0.15)</td>
<td>0.44 (0.09)</td>
<td>0.44 (0.09)</td>
<td></td>
</tr>
<tr>
<td>June</td>
<td>1.18 (0.14)</td>
<td>1.02 (0.09)</td>
<td>0.97 (0.04)</td>
<td>1.00 (0.21)</td>
<td>0.96 (0.17)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>August</td>
<td>0.79 (0.04)</td>
<td>0.73 (0.01)</td>
<td>0.74 (0.04)</td>
<td>0.74 (0.04)</td>
<td>0.81 (0.04)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>October</td>
<td>0.91 (0.14)</td>
<td>1.01 (0.03)</td>
<td>0.79 (0.01)</td>
<td>0.74 (0.04)</td>
<td>0.74 (0.04)</td>
<td>0.81 (0.04)</td>
<td></td>
</tr>
<tr>
<td>gs (mol m-2 s-1)</td>
<td>June</td>
<td>0.041 (0.009) a</td>
<td>0.079 (0.023) a</td>
<td>0.036 (0.006) a</td>
<td>0.063 (0.014) a</td>
<td>0.016 (0.007) b</td>
<td></td>
</tr>
<tr>
<td>August</td>
<td>0.059 (0.024)</td>
<td>0.025 (0.003)</td>
<td>0.061 (0.021)</td>
<td>0.040 (0.014)</td>
<td>0.014 (0.003)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>October</td>
<td>0.016 (0.008)</td>
<td>0.084 (0.026)</td>
<td>0.093 (0.011)</td>
<td>0.191 (0.067)</td>
<td>0.090 (0.026)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Δ</td>
<td>April</td>
<td>18.1 (0.8)</td>
<td>18.5 (0.5)</td>
<td>17.3 (1.0)</td>
<td>19.4 (0.4)</td>
<td>19.3 (0.4)</td>
<td></td>
</tr>
<tr>
<td>June</td>
<td>19.0 (0.2) ac</td>
<td>18.2 (0.4) ab</td>
<td>17.7 (0.06) b</td>
<td>19.2 (0.3) c</td>
<td>19.3 (0.4) c</td>
<td></td>
<td></td>
</tr>
<tr>
<td>August</td>
<td>17.3 (0.4)</td>
<td>17.5 (1.0)</td>
<td>17.2 (0.9)</td>
<td>19.7 (0.6)</td>
<td>18.7 (0.4)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>October</td>
<td>18.3 (0.1) a</td>
<td>18.1 (0.4) a</td>
<td>16.7 (0.8) b</td>
<td>19.0 (0.4) a</td>
<td>19.4 (0.3) a1</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

1Means in rows with different lowercase letters differed (ANOVA, P < 0.05).

Although data presented herein represent only a single growing season, survival rates for a separate Q. emoryi seedling cohort in this same experiment differed little between treatments after 3 growing seasons (Weltzin and McPherson 2000). In contrast, Q. emoryi seedling recruitment rates (i.e., the number of individuals added to the population) for both cohorts were as much as 300% greater in summer-wet than summer-dry treatments. Recruitment was more directly attributable to treatment effects on emergence of seedlings from acorns planted during the summer monsoon.

In contrast to point measures of leaf gas exchange, seedling survival rates could roughly be predicted from Δ, which is an integrated
measure of leaf gas exchange. Generally, seedling survival was positively correlated with \( \Delta \), which is consistent with the expectation that metabolic activity is coupled with population demographics. Correlations between \( \Delta \) and seedling survival were greatest during the annual summer monsoon, which suggests that the demographics of these stress-tolerant seedlings can best be predicted from \( \Delta \) when environmental conditions are suitable for extended periods of carbon assimilation.

However, observed differences in \( \Delta \) between summer-wet and summer-dry treatments in April and June 1996 (i.e., prior to experimental application of summer precipitation in 1996) suggest that carbon fixed during summer 1995 was retained in the evergreen leaves of these seedlings into the next year. This could reduce the sensitivity of \( \Delta \) to environmental conditions in other seasons when resource gradients are less intense, and constrains the usefulness of whole evergreen leaves as measures of plant response on relatively short (i.e., a single season) temporal scales.

### Seasonal Precipitation and Q. emoryi Demographics

Seedling predawn leaf water potentials, net CO\(_2\) assimilation, and stomatal conductance indicate that growing conditions for *Q. emoryi* seedlings at this site are generally restricted to periods with adequate soil moisture (i.e., April and August). This conclusion supports observations that 1- and 2-year-old *Q. emoryi* seedlings at this same research site use soil water derived from both winter and summer precipitation (Weltzin and McPherson 1997).

### Table 3. Pearson correlation coefficients (top) and associated *P*-values (bottom) for \( \Delta \) vs. integrated seedling survival (PRE60, PRE30, POST30, POST60).

<table>
<thead>
<tr>
<th>Sample date</th>
<th>PRE60</th>
<th>PRE30</th>
<th>POST30</th>
<th>POST60</th>
</tr>
</thead>
<tbody>
<tr>
<td>All dates</td>
<td>0.08</td>
<td>-0.06</td>
<td>-0.03</td>
<td>-0.002</td>
</tr>
<tr>
<td>20 April</td>
<td>0.46</td>
<td>0.61</td>
<td>0.83</td>
<td>0.99</td>
</tr>
<tr>
<td>30 June</td>
<td>-0.26</td>
<td>-0.32</td>
<td>-0.36</td>
<td>-0.34</td>
</tr>
<tr>
<td>22 August</td>
<td>0.28</td>
<td>0.19</td>
<td>0.13</td>
<td>0.16</td>
</tr>
<tr>
<td>0.14</td>
<td>0.05</td>
<td>0.11</td>
<td>0.005</td>
<td></td>
</tr>
<tr>
<td>22 August</td>
<td>0.62</td>
<td>0.34</td>
<td>0.25</td>
<td>0.23</td>
</tr>
<tr>
<td>0.004</td>
<td>0.14</td>
<td>0.30</td>
<td>0.34</td>
<td></td>
</tr>
<tr>
<td>17 October</td>
<td>0.25</td>
<td>-0.04</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>0.29</td>
<td>0.87</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>

\( \text{PRE60} \text{ and PRE30} = \text{slope of seedling survival over 60- and 30-day period (\% day\(^{-1}\)) before determination of \( \Delta \), respectively, and POST30 and POST60 =}
\text{slope of seedling survival over 30- and 60-day period (\% day\(^{-1}\)) after determination of \( \Delta \), respectively. Significant coefficients after sequential Bonferroni correction (Rice 1989) are in boldface.}

Fig. 2. Relationship between \( \Delta \) for *Q. emoryi* leaves sampled 22 August and seedling survival rate (\% day\(^{-1}\)) for 60-day period before (PRE60) determination of \( \Delta \) (\( r^2 = 0.38, P = 0.004 \)).

However, carbon isotope discrimination values (\( \Delta \)) and \( c_i/c_a - \Delta \) relationships suggest that summer precipitation is more important than winter precipitation for *Q. emoryi* carbon accumulation in leaves. This conclusion is supported by recent research which indicates that recruitment of *Q. emoryi* seedlings was positively correlated with the quantity of summer precipitation but was independent of quantity of winter precipitation (Weltzin and McPherson 2000). Other empirical studies further indicate the importance of summer precipitation to *Q. emoryi* seedling recruitment (Pase 1969, Neilon and Wullstein 1983, McPherson 1992, Germaine and McPherson 1999, Weltzin and McPherson 1999, 2000).

Although changes in regional precipitation regimes are not well predicted by general circulation models, particularly for topographically complex regions such as the southwestern United States, predicted changes in atmospheric circulation and surface temperatures are likely to affect the amount and seasonality of precipitation and soil moisture in this region (e.g., Kattenberg et al. 1996, Giorgi et al. 1998). Results from this study and Weltzin and McPherson (2000) indicate that changes in summer precipitation regimes would likely constrain Q. emoryi population dynamics through changes in seedling recruitment rates. Further, although adult and sapling (ca 1 m tall) Q. emoryi and coexisting grasses at this savanna site access water from relatively deep and shallow in the soil profile, respectively. Q. emoryi seedlings are unable to access deep sources of soil water for at least the first 3 growing seasons after germination (Weltzin and McPherson 1997, 2000). These results contrast with an assumption implicit to the "two-layer" hypothesis (Walter 1954, 1979) that woody plants in all life history stages are more dependent upon winter precipitation than summer precipitation. Thus, models developed to predict the effect of changing climates on the abundance and distribution of woody plants (e.g., Emanuel et al. 1985, VEMAP Members 1995, Iverson and Prasad 1998) should consider spatial and temporal processes that constrain the establishment of individuals (Grubb 1977, Harper 1977, McPherson 1997, Scholes and Archer 1997). This should be facilitated by the development of dynamic global vegetation models (e.g., Foley et al. 1998, Neilson and Drapek 1998) that incorporate such transient processes as emergence and recruitment.

ACKNOWLEDGMENTS

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LITERATURE CITED


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Accepted 24 August 2000*
For several years we and our colleagues have collected occasional specimens of a *Sweltsa*-like stonefly in the Coast Range of northern California. A small series of adults taken from the Willow Creek drainage near Berry Summit during the 1998 field season allowed a more comprehensive examination and confirmed that males could not be identified using existing literature (Surdick 1985, Stewart and Harper 1996). Preliminary results suggested this species might require a new generic name, thus prompting K.W. Stewart and B.P. Stark to search for and rear the nymph in order to include the prospective genus in a forthcoming revision of their nymphal monograph (Stewart and Stark 1988). Although the nymph is very similar to *Sweltsa* and is identified to that genus in Stewart and Stark (1988) and Stewart and Harper (1996), several diagnostic characters separate the nymph from known Nearctic *Sweltsa*. The evolution of nymphal morphology is conservative within the Chloroperlidae; therefore, we consider these nymphal characters and the formation of the male genitalia sufficient for recognition of a new genus.

METHODS

Specimens were collected using beating sheets and aquatic kicknets and by hand-picking from vegetation, rocks, and debris; a few preemergent nymphs were maintained in iced styrofoam coolers during transport until they emerged. Specimens were preserved in 80% ethanol; those examined with scanning electron microscopy were dehydrated through 10-minute washes in 90%, 95%, and 100% ethanol, followed by two 30-minute washes in hexamethyldisilazane. Specimens were attached to specimen stubs with double-stick copper tape, sputter-coated with gold-palladium, and examined with an 1810D Amray scanning electron microscope. Specimens examined during this study are deposited in the following museums or collections:

- B.P. Stark Collection, Clinton, MS (BPS)
- Monte L. Bean Museum, Brigham Young University, Provo, UT (BYU)
- University of North Texas, Denton, TX (UNT)
- United States National Museum of Natural History, Washington, DC (USNM)

*Sasquaperla*, new genus

**TYPE SPECIES.**—*Sasquaperla hoopa*, new species, by monotypy.

**ADULTS.**—Body pale yellow with black and brown markings. Wings transparent, veins pale; anal area of hindwing with 3 anal veins; forewing 2nd anal vein forked. Pale brown mesal area covers ocelli and extends forward over clypeus. Pronotum with black margins and irregular brown areas near median suture (Fig. 1). Meso- and metascutellar U-sutures black. Abdomen with dark mesal pigment band extending to tergum 8 or 9; narrow lateral pigment bands extend through segment 4.

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Mesosternal Y-arms obsolete; dark pigment surrounding Y-stem projects forward beyond stem apex (Fig. 5). Cerci of 9–10 segments.

**MALE GENITALIA.**—Epiproct unhinged, reduced to a small, tablike structure embedded in upturned membrane of tergum 10, which bears a narrow band of stiff hairs around the posterior margin (Figs. 9–10). Basal bar short and wide; paragenital plates obsolete, anterior transband of segment 10 wide and heavily pigmented (Fig. 3). Aedeagus membranous and sparsely armed with microtrichia (Fig. 2).

**FEMALE GENITALIA.**—Subgenital plate a short, entire flap extending over about one-third of sternum 9 (Fig. 4), forming a blunt point medially.

Figs. 1–4. Sasquaperla hoopa adult structures: 1, head and pronotum; 2, aedeagus, ventral; 3, male terminalia, dorsal; 4, female terminalia, ventral.
NYMPH.—Mature nymph brown with obscure darker pattern on dorsum of head and thorax; abdominal terga with narrow, transverse apical bands. Head with a few long setae near eyes, at antennal bases, and anterior corners of frons. Pronotum heavily setose around anterior and posterior margins; mesonotum with strong bristle row along lateral margins. Apical abdominal terga with a few intercalary bristles and an apical fringe of bristles (Fig. 6). Thorax, abdomen, and legs covered with reddish-brown clothing hairs; tibial and femoral silky fringe hairs sparse (Fig. 7). Mesosternal Y-arms obsolete (Fig. 8); strong, erect bristles located lateral to clothing hairs on thoracic sterna. Cerci of about 18 segments; cercal segments with well-developed apical whorls of bristles (Fig. 6).

DISTRIBUTION.—Coast Range of northern California from the greater Trinity River drainage.

DIAGNOSIS.—Adult Sasquaperla are characterized by a dark middorsal stripe, by narrow lateral stripes on anterior abdominal segments, and by dark pronotal margins. The male epiproct consists of a small, upturned, unhinged sclerotized tab arising from a short, wide basal bar (Figs. 3, 9–10). Males cannot be resolved in existing keys by Surdick (1985) and Stewart and Harper (1996), but females and nymphs key to Sweltsa in these publications. Sasquaperla nymphs and adults have the mesosternal Y-arms obsolete (Figs. 5, 8), although in fully pigmented adults the mesosternal Y-region is dark except for a pair of irregular pale spots near the furcal pits (Fig. 5); nymphs have the tibial fringes poorly developed (Fig. 7) and have a few erect bristles located lateral to the mesosternal clothing hair patches (Fig. 8).

Nymphal morphology would suggest that Sasquaperla belongs in the tribe Alloperlini, since it bears large patches of clothing hairs on the meso- and metathorax. Since the male epiproct is unhinged, generic placement according to Surdick (1985) would seem to fall in the Chloroerlini. However, the actual sister genus is obviously Sweltsa, so Sasquaperla would need to have possessed a hinged epiproct and then secondarily lost it. This explanation would be stronger if the present condition of the male genitalia were described in a positive way as an apomorphous state, instead of simply as a lack of a hinged epiproct, which is plesiomorphic.

KEY MODIFICATIONS.—Modifications are provided for keys to adults or nymphs given in Surdick (1985), Stewart and Harper (1996), and Stewart and Stark (1988).

Surdick (1985)

Adult Male Key

7. Aedeagus terminating in pair of thin, feathery processes; hammer absent.

7A. Terminal abdominal segments lacking hair brushes; small median hammer on abdominal sternum 7; aedeagus armed with conspicuous basal band of scale-like spines.

Stewart and Harper (1996)

Adult Key

Males

119 (118'). Epiproct large, its tip hinged and elaborate; epiproct set in a deep groove in tergum 10; brushes of close-set setae on lateral margins of terminal abdominal segments.

119'. Epiproct small, about as wide as long, tergum 10 entire or slightly depressed; brushes of close-set setae present or absent on lateral margins of terminal abdominal segments.

119A (119'). Brushes of close-set setae on lateral margins of terminal abdominal segments; aedeagus without dense basal bands of...
Figs. 6–8. *Sasquaperla hoopa* nymphal structures: 6, partial habitus; 7, right foreleg; 8, mesosternum.
Figs. 9–10. Sasquaperla hoopa male terminalia: 9, terga 9 and 10, Ep = epiproct; 10, epiproct apex, anterodorsal aspect.

dark scale-like armature (Fig. 2); epiproct tip scarcely projecting forward from posterior margin of tergum 10 (Fig. 3).

119A’. Brushes of close-set setae absent from lateral margins of terminal abdominal segments; aedeagus with dense basal bands of dark scale-like armature; epiproct tip projecting forward from posterior margin of tergum 10.

Sasquaperla

125 (124’). Size small (4–6 mm); mesosternal Y-ridge with median branch extending cephalad; subgenital plate scalloped with long hairs restricted to scalloped margins.

Bisancora

125’. Size larger (8–18 mm); mesosternal Y-ridge without anterior extension of median branch; subgenital plate variable, if scalloped, hairs arranged otherwise.

125A (125’). Mesosternal Y-arms obsolete; subgenital plate with slightly projecting mesal lobe covered with short setae (Fig. 4).

Sasquaperla

Stewart and Stark (1988)

Nymphal Key

5. Thick, depressed black clothing hairs laterally on all thoracic sterna.

5A. Thick, depressed black clothing hairs absent from lateral thoracic sterna; sternal hairs erect, light-colored.

6. Mesosternum without erect bristles lateral to clothing hair patch; tibial fringes of silky setae well developed; mesosternal Y-arms well developed.

Sucelsa

Stewart and Harper (1996)

Nymphal Key

63 (62’). Thick, depressed black hairs present inside coxae on thoracic sterna; both pairs of wing pads divergent from body axis; long pronotal fringe hairs except on side.

63’. No black hairs inside coxae on thoracic sterna; wing pads variable in divergence.

63A (63). Mesosternum without erect bristles lateral to depressed hair patches; tibial fringes of silky setae well developed; mesosternal Y-arms well developed.

Sucelsa

Stewart and Harper (1996)

Nymphal Key

63A’. Mesosternum with several erect bristles lateral to clothing hair patch (Fig. 8); tibial fringes of silky setae sparse; mesosternal Y-arms obsolete.

Sasquaperla
ETYMOLOGY.—Sasquaperla occurs in small streams that contain other stoneflies with restricted distributions such as Salmoperla sylvanica (Baumann and Lauck 1987) and Capnia fiali (Nelson and Baumann 1990). The prefix, sasqua, was chosen to honor this region that provides habitat for so many biological treasures, including “Bigfoot”!

Sasquaperla hoopa, new species

MALE.—Forewing length 9–10 mm. General color pale yellow marked with brown and black. Dorsal abdominal band consists of dark brown quadrangular and triangular segmental median patches and extends to tergum 9; anteriorly located patches (terga 3–4) are quadrangular, whereas those on terga 5–8 are triangular; all patches through tergum 8 include a pair of pale mesal spots. Tergum 9 with small posteromesal indentation (Fig. 3); tergum 10 with broadly rounded hemiterga. Epiproct complex greatly reduced; basal bar expanded laterally but not reaching anterior margin of tergum 10; unhinged apex embedded in membrane and sparsely armed with setal-like spines and a narrow band of hairs (Figs. 3, 9–10). Aedeagus membranous and sparsely armed with pale microtrichia (Fig. 2); apex with small ventrolateral lobes.

FEMALE.—Forewing length 11–12 mm. Dorsal abdominal stripe extends through tergum 8. Subgenital plate short; mesal lobe slightly developed beyond lateral margins and armed with short setae; longer submarginal setae located lateral to expanded mesal lobe (Fig. 4).

NYMPH.—Preemergent nymph 9–11 mm. General color brown with obscure darker pattern on head and pronotum, mesosternum bearing several erect bristles lateral to depressed clothing hair patches. Abdominal terga with transverse posterior pigment bands. Abdominal terga with conspicuous intercalary bristles through segment 8, but reduced on segments 9 and 10. Red-brown clothing hairs conspicuous over most of body (Fig. 6).


ETYMOLOGY.—The species name honors the Hoopa people who live in the Willow Creek area of the Trinity Alps, California.

ACKNOWLEDGMENTS

We thank our colleagues C.R. Nelson, I. Sivec, K.W. Stewart, S.W. Szczytko, and M.F. Whiting for assistance in fieldwork and in sharing specimens with us. D.R. Lauck and P. Wilkinson made the first specimens of this interesting species available from their study on the Willow Creek drainage and also shared their data on the original collecting localities.

LITERATURE CITED


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Pygmy rabbits (*Brachylagus idahoensis*) are restricted to sagebrush-steppe areas of the Great Basin and adjacent intermountain regions. Within this area their distribution is further limited by the availability of “suitable” habitat for the construction of burrow systems. Several studies have attempted to describe characteristics of this suitable habitat for pygmy rabbits. These studies generally concluded that pygmy rabbits tend to prefer taller and denser stands of big sagebrush (*Artemisia tridentata*) within sagebrush-dominated areas (Grinnell et al. 1930, Orr 1940, Severaid 1950, Green 1978, Green and Flinders 1980, White et al. 1982, Gahr 1993, Katzner 1994, Katzner and Parker 1997). Weiss and Verts (1984) found shrub cover was the best of 10 variables for distinguishing sagebrush sites occupied by pygmy rabbits. Mean shrub cover in areas occupied by pygmy rabbits ranged from 29% in Oregon (Weiss and Verts 1984) to 43–46% in Idaho and Wyoming (Green 1978, Green and Flinders 1980, Katzner and Parker 1997). These values were in contrast to 16% (Green 1978, Green and Flinders 1980, Weiss and Verts 1984) to 26% cover (Katzner and Parker 1997) for nonuse areas. Possible reasons for the preference for greater sagebrush cover are that it constitutes a large portion of their diet (Green and Flinders 1980) and may offer better protection from predators. Compared to larger leporids, pygmy rabbits are relatively slow and may better elude predators when under a shrub canopy (Orr 1940, Wilde 1978).

Other factors that may define pygmy rabbit habitat are soil depth and texture (Weiss and Verts 1984). Kehne (1991) found 96% of pygmy rabbit burrow sites in Washington in soils at least 51 cm deep, and 72% of burrow sites had either coarse silty, ashy, or coarse loamy soils, all with <18% clay.

Beyond the general preference of pygmy rabbits for taller and denser sagebrush cover and deep, sandy soils, little more is known of their specific habitat requirements. Additionally, there are often areas with appropriate looking woody vegetation and physiognomy that are not necessarily suitable pygmy rabbit habitat (Green and Flinders 1980). Green and Flinders (1980) hypothesized that subtle variations other than sagebrush density in the vegetative component make an area appropriate for pygmy rabbits. This hypothesis has not yet been tested and the question remains: How specific is habitat selection by pygmy rabbits?

Given the pygmy rabbit’s restriction to sagebrush-steppe, loss of this habitat type could impact the species’ survival. This is increasingly so if only a subset of the habitat is suitable. If there is indeed a unique and identifiable subset of habitat factors pygmy rabbits are selecting, this information could be used...
to develop a predictive habitat suitability model. This model could then be used to assess the suitability of specific areas for pygmy rabbits and help develop sound conservation management plans for the species.

We investigated habitat requirements of pygmy rabbits in a 2305-km² area of sagebrush-steppe in southeastern Idaho. Given what is known of pygmy rabbit habitat, we generated and tested 3 predictions. First, habitat characteristics between areas of use and non-use have the largest differences across several vegetal axes. Second, if rabbits are selecting on a finer scale, then there are significant differences in characteristics between actual burrow sites and surrounding areas. Third, if some burrow sites are better than others, there are differences in habitat characteristics between occupied and unoccupied or abandoned burrow sites. The support or refutation of these predictions will help determine the scale of habitat selection by pygmy rabbits and contribute to the development of a predictive habitat model for assessing the suitability of a given area for pygmy rabbits.

**STUDY AREA**

The study was conducted on the Idaho National Engineering and Environmental Laboratory (INEEL). The INEEL is located on the Snake River plain in southeastern Idaho (Fig. 1). Mean annual precipitation at the INEEL is 22 cm, most of which falls from winter to early summer. Snowcover usually persists for at least 2–3 months. Temperature ranges from –9°C to 35°C. Prevailing winds over much of the INEEL come from the southwest (Yanskey et al. 1966).

The surface of the INEEL is relatively flat with some basalt flows and a few volcanic buttes. The subsurface is made up of basalt from past lava flows. Most of the soil is derived from older silicic volcanic and Paleozoic rocks from the surrounding mountains (McBride et al. 1978). In the southern portion of the INEEL, soils tend to be gravelly, while in the northern portion the soil is made up of lake and aeolian deposits composed mainly of unconsolidated clay, silt, and sand (Kramber et al. 1992). Soil depth on the INEEL typically varies from a few centimeters on the more recent or exposed flows to several meters in low-lying areas. Accumulation is also greater on leeward sides of lava ridges and on alluvial fans. The native vegetation at the INEEL consists of a shrub overstory with an understory of perennial grasses and forbs (Anderson et al. 1996).

**METHODS**

**Sampling Habitat Characteristics**

We measured habitat characteristics on plots within 5 different pygmy rabbit use categories (Fig. 2) defined as follows:

1. *Occupied burrow site*: a 40 × 40-m plot centered on an occupied pygmy rabbit burrow discovered during road surveys of the study area (Gabler 1997).
2. *Unoccupied burrow site*: a 40 × 40-m plot centered on an inactive burrow discovered within areas of predicted habitat as defined by GIS analysis (Gabler 1997).
3. *Active area*: a 360 × 360-m plot centered on occupied burrow sites.
4. *Inactive area*: a 360 × 360-m plot centered on an unoccupied burrow site.
5. *Nonuse area*: a 360 × 360-m unoccupied plot in areas of predicted nonuse habitat as defined by GIS analysis (Gabler 1997).
Habitat characteristics were measured within 10 occupied burrow sites, unoccupied burrow sites, inactive areas, and nonuse areas. Because occupied burrow sites were clustered such that 360 x 360-m plots around each site overlapped, only 3 active areas were defined in which habitat characteristics were measured.

We measured habitat characteristics at each sample point within the study plots. In the occupied and unoccupied burrow site plots, habitat variables were measured at 17 sampling points. These variables were sampled at the point centered directly at the burrow system entrances (Fig. 2) and at the surrounding 16 points formed by the 30 x 30-m grid (Fig. 2A). In the active, inactive, and nonuse area plots, the 360 x 360-m sampling grid was divided into 10-m intervals along the east-west axis. Four random points were chosen to serve as the origin of north-south oriented transects (Fig. 2), and 6 random points were sampled along each transect for a total of 24 sample points per grid (Fig. 2B). Mean measurements of each habitat variable ($N = 17$, occupied and unoccupied burrow sites; $N = 24$, active, inactive, and nonuse areas) were used to compare the 5 use categories.

We used 2 techniques to measure the habitat characteristics, point-quarter sampling (Brower et al. 1990) and point interception (Floyd and Anderson 1982). For the point-quarter method, distance to the nearest tall shrub (>50 cm) and distance to the nearest short shrub (<50 cm) were measured in each quarter. A height of 50 cm was arbitrarily chosen to separate the tall shrub community from the short shrub community. Distance measurements were then used to calculate total shrub density (TD)/100 m$^2$ and relative density (RD) for major shrub species in the tall and short categories according to Brower et al. (1990). The major shrub species measured were big sagebrush, green rabbitbrush (*Chrysothamnus viscidiflorus*), and gray rabbitbrush (*C. nauseosus*). In addition, we estimated shrub cover for the 2 height classes by measuring the longest diameter of live canopy and the perpendicular diameter. These 2 measurements were then used as the X and Y diameters of an ellipse to estimate cover area.

The point-frame method (Floyd and Anderson 1982) was used to estimate relative cover (RC) for various vegetation and habitat classes, including microbiotic crust, individual shrub species, total dead shrubs, individual grass species, total forbs, bare ground, litter, and rock. These classes were then lumped into larger coverage categories: total live shrubs, total grasses, and total groundcover excluding vascular vegetation and rocks. Relative coverage was calculated as:

$$RC_i = n_i/s * 36,$$

where $n_i$ is the number of “hits” (Floyd and Anderson 1982) of cover type $i$, $s$ is the number of sample points (17 or 24), and 36 is the number of sample points within the frame.
Diversity for each site was also calculated using the Shannon-Weiner index (Zar 1984).

In addition to vegetation measurements, we collected surface soil samples from 3 points directly next to burrow entrances and from 5 randomly selected points within each 360 × 360-m plot. Particle size analysis was conducted for each sample. The hydrometer method described by Palmer and Troeh (1995), with modifications as described in Gabler (1997), was used.

Data Analysis

Means of habitat characteristics were compared among occupied burrow sites, unoccupied burrow sites, active areas, inactive areas, and nonuse areas. We used univariate comparisons to first identify which individual habitat characteristics might differ among the various sites, followed by multivariate analysis (principal components analysis [PCA]; Morrison et al. 1992) to determine if the collective composition of the various sites differed. We then compared the outcome of each to help identify which habitat variables likely were most important relative to selection of habitat by pygmy rabbits.

A 1-way analysis of variance (ANOVA) was used for the univariate analysis to test the null hypothesis that no difference existed among the 5 plot types for any of the habitat variables. Alpha levels were adjusted for multiple comparisons using the Bonferroni method. If the null hypothesis was rejected in an ANOVA, a Tukey multiple-comparisons test was performed to determine differences among treatments. All variables measured as percentages were arcsine transformed.

For the PCA analysis, we generated standardized Z_1 and Z_2 principal component loadings for each variable. After the 1st pass, variables with low loadings (<0.1) were eliminated. The remaining variables were reanalyzed and their loadings were used to generate Z_1 and Z_2 scores for each plot type. Z_1 and Z_2 scores for the 5 plot types were compared with the ANOVA design described above. Separate PCA analyses and statistical tests were conducted for each vegetation characteristic and soil texture. The 2 resulting predictive equations were used as the predictive model for pygmy rabbit habitat. All statistical analyses were conducted using Systat for Windows (Wilkinson et al. 1992).

RESULTS

Of the 30 ANOVA tests performed for the different habitat characteristics measured, 13 indicated significant differences among the 5 plot types (Fig. 3). Range tests detected differences most often between nonuse areas and 3 of the 4 other plot types (occupied burrow sites, unoccupied burrow sites, and inactive areas). The separation between nonuse areas and occupied burrow sites was seen most often. In 11 cases in which significant differences were detected, nonuse areas had maximum mean values in 3 cases while occupied burrow sites had maximum values in 6 cases. Of the same 11 cases, there were 8 and 2 minimum mean values for nonuse areas and occupied burrow sites, respectively. Among the 4 plot types of actual use (occupied burrow sites, unoccupied burrow sites, active areas, and inactive areas), range testing detected significant differences only for relative cover of big sagebrush, green rabbitbrush, and squirreltail grass (Sitanion hystrix; Fig. 3). Of the 4 actual use categories, nonuse areas differed statistically the least often with active areas.

Soil Texture Analysis

At occupied burrow sites and active areas, mean percent sand was 81.0% and 87.5% while mean percent clay was 5.1% and 5.0%, respectively. The mean sand component at inactive areas and unoccupied burrow sites was 66.9% and 69.6%, respectively, with a mean clay component of 8.7% and 7.3%, respectively. The portion of sand and clay at nonuse areas was 51.6% and 14.4%, respectively. No univariate comparisons among treatments were made on the soil variables (% sand, % silt, and % clay) because they were all correlated.

Principal Component Analysis

Seventeen vegetation variables were used in a PCA. The number of variables chosen was based on their presence at all or most of the 43 plots. Variables used in the PCA included shrub height, canopy cover per shrub, and total density for both tall and short shrub communities; relative density of big sagebrush >50 cm tall; relative densities of big sagebrush and green rabbitbrush ≤50 cm tall; relative cover of bare ground, litter, forbs, dead shrubs, big sagebrush, total live shrubs, and total grass; and diversity index of shrub and grass species, relative
Fig. 3. Results of 1-way analysis of variance tests for those variables with significant $F$-values at the 5 sample site types. The means of groups within a variable that did not differ significantly in a Tukey multiple-comparison test are indicated by bars with the same fill pattern.
coverage of total forbs and total dead shrubs, and relative coverage of big sagebrush.

After calculating the first PCA, we deleted 7 of 17 variables from the analysis because they generated small component loadings relative to the other variables. A PCA of the remaining 10 variables defined the first 2 components, which accounted for 63% of variation among plots (Table 1). Six of these variables also differed significantly among plot types in univariate analysis.

From the first component, mean $Z_1$ scores for each plot type were significantly different (Table 2). This indicates a difference among plot types for the collective description of variables. Nonuse areas had a significantly negative $Z_1$ mean compared to occupied burrow sites, inactive sites, and unoccupied burrow sites (Table 2). The negative $Z_1$ mean for nonuse areas corresponded to high negative loadings in mean canopy cover per shrub for the tall shrub community, relative coverage of litter, and height of the tall shrub community (Table 1). These variables contributed inversely to the $Z_1$ score; therefore, higher values for these variables resulted in a lower $Z_1$ score.

Occupied burrow sites, inactive areas, and unoccupied burrow sites all had significantly positive $Z_1$ means. These corresponded to high positive loadings of relative big sagebrush density within the tall shrub community, relative coverage of total live shrubs, relative coverage of big sagebrush, relative coverage of forbs, total density of tall shrubs, and, to a lesser extent, total density and height of the short shrub community (Table 1). These variables contributed positively to the $Z_1$ score; therefore, higher values for these variables resulted in a larger $Z_1$ score. Because active areas had a mean $Z_1$ score that did not differ significantly from the other 4 plot types, active areas were assumed to be intermediate for $Z_1$.

$Z_2$ scores were calculated from the 2nd component and a 1-way ANOVA was performed on mean $Z_2$ scores. Significantly different $Z_2$ scores were detected only between nonuse

Table 1. Two 1st principal components derived from principal components analysis of 10 vegetation variables and the 2 components for soils in active pygmy rabbit (Brachylagus idahoensis) sites, occupied burrow sites, predicted pygmy rabbit sites, predicted (inactive) burrows, and nonuse sites on the Idaho National Engineering and Environmental Laboratory.

<table>
<thead>
<tr>
<th>Latent roots (eigenvalues)</th>
<th>Vegetation</th>
<th>Soils</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>3.58</td>
<td>2.76</td>
</tr>
<tr>
<td>VARIABLESa</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Sagebrush tall</td>
<td>0.833</td>
<td>0.141</td>
</tr>
<tr>
<td>Total live shrub</td>
<td>0.784</td>
<td>−0.117</td>
</tr>
<tr>
<td>Sagebrush</td>
<td>0.737</td>
<td>0.482</td>
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<tr>
<td>Cover tall</td>
<td>−0.655</td>
<td>0.331</td>
</tr>
<tr>
<td>Forbs</td>
<td>0.625</td>
<td>0.171</td>
</tr>
<tr>
<td>Litter</td>
<td>−0.593</td>
<td>0.472</td>
</tr>
<tr>
<td>Total density tall</td>
<td>0.562</td>
<td>0.584</td>
</tr>
<tr>
<td>Height short</td>
<td>0.132</td>
<td>0.855</td>
</tr>
<tr>
<td>Total density short</td>
<td>0.190</td>
<td>−0.813</td>
</tr>
<tr>
<td>Height tall</td>
<td>−0.438</td>
<td>0.633</td>
</tr>
<tr>
<td></td>
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<td></td>
</tr>
<tr>
<td>Percent of total variance explained</td>
<td>35.8</td>
<td>27.6</td>
</tr>
</tbody>
</table>

aSagebrush tall = relative density of A. tridentata >50 cm tall
Sagebrush = relative coverage of A. tridentata
Cover tall = mean cover per shrub for shrubs >50 cm tall
Forbs = relative coverage of forbs
Litter = relative coverage of litter
Total density tall = total density of shrubs >50 cm tall
Total density short = total density of shrubs ≤50 cm
total density of shrubs ≤50 cm
Height short = height of shrubs ≤50 cm
Height tall = height of shrubs >50 cm tall
areas and occupied burrow sites (Table 2). Nonuse areas had a significantly negative Z₂ score, which mainly corresponded to negative loadings in total density of short shrubs (Table 2). The significantly positive mean for occupied burrow sites corresponded with high positive loadings in height of both tall and short shrubs, total density of tall shrubs, and coverage of big sagebrush and litter (Table 2). Z₁ and Z₂ scores were plotted against each other (Fig. 4A).

For the PCA of the 3 soil texture variables, the 1st principal component accounted for 89.5% of overall variation between sites (Table 1). The 2nd component explained only 10.5% of the variability and therefore was not analyzed. Loadings for the 1st component were used to calculate Z₁ scores for occupied burrow sites, unoccupied burrow sites, active areas, inactive areas, and nonuse areas. Nonuse areas had a significantly positive Z₁ mean compared to the other 4 plot types (Table 2). This positive mean corresponded to high positive loadings for silt and clay (Table 1). Active areas and occupied burrow sites, however, had negative means, corresponding to high sand values. These 2 site types did not differ significantly from each other and thus were assumed to have a similarly high sand content. The inactive areas and unoccupied burrow sites were more intermediate, with a greater sand component at the unoccupied burrow sites. Unlike inactive areas, unoccupied burrow sites did not differ significantly from occupied burrow sites and active areas (Table 2).

A plot of the vegetation and soil Z₁ scores (Fig. 4B) produced distinct separations among the 5 different plot types, with occupied burrow sites and nonuse areas the most separated from the other 3.

Habitat Suitability Model

Based on results of the vegetation and soil PCA, we formulated the following equations from the Z₁ scores for use as a habitat suitability model:

Vegetation Z₁ = (0.833)(ST) + (0.784)(TLS) + (0.737)(SB) + (–0.655)(CT) + (–0.593)(L) + (0.625)(TDT) + (0.132)(HS) + (0.190)(TDS) + (–0.438HT)

Soil Z₁ = (–0.994)(%SAND) + (0.948)(%SILT) + (0.893)(%CLAY)

where:

ST = relative density of A. tridentata >50 cm tall
TLS = relative coverage of live shrubs
SB = relative coverage of A. tridentata
CT = mean cover per shrub for shrubs >50 cm tall
L = relative coverage of litter
F = relative coverage of forbs
TDT = total density of shrubs >50 cm tall
TDS = total density of shrubs ≤50 cm

Table 2. Results of 1-way analysis of variance tests on Z₁ and Z₂ vegetation scores and Z₁ soil scores among active pygmy rabbit (Brachylagus idahoensis) sites, occupied burrow sites, nonuse areas, predicted pygmy rabbit sites, and unoccupied burrows on the Idaho National Engineering and Environmental Laboratory. Means ± standard errors are listed and sample sizes are included in parentheses. Means of groups that did not differ significantly in a Tukey multiple-comparisons test are indicated by the same letter in superscript.
HS = height of shrubs ≤50 cm
HT = height of shrubs >50 cm tall

**DISCUSSION**

Results of our study suggest that pygmy rabbits select burrow sites based on a fairly unique, and thus identifiable, combination of vegetation variables and soil characteristics (prediction 1). This was indicated by both the comparisons of individual habitat variables and PCA score differences between the 4 use categories and the nonuse areas. One of the major contributing factors to the observed differences among use categories was the relative cover of big sagebrush; relative cover at use areas ranged from 3 to 10 times greater than at nonuse areas. This result corresponds with findings of others (Grinnel et al. 1930, Orr 1940, Severaid 1950, Green and Flinders 1980, Weiss and Verts 1984, Gahr 1993, Katzner and Parker 1997). Because 51–99% of pygmy rabbit diet consists of big sagebrush (Green and Flinders 1980), greater sagebrush cover would represent greater food resources for the pygmy rabbit. Greater shrub cover may also represent better protection from predators. Pygmy rabbits move more slowly and are more vulnerable in open habitats than are other leporids (Orr 1940) and therefore are thought to better elude predators while under a shrub canopy (Orr 1940, Wilde 1978). In addition to big sagebrush, our results indicate other vegetal variables, such as ground litter, relative coverage of forbs, and characteristics of the short (<50 cm) shrub community, also likely play a role in the suitability of an area for pygmy rabbits. The inability of multiple range tests to distinguish between active areas and nonuse areas likely is due to the small sample size (3) for active areas.

A 2nd result of our study was that, within use areas, there were identifiable differences in vegetation characteristics between occupied burrow sites and the surrounding (360 × 360-m) active areas (prediction 2). It is not clear, however, whether those differences were caused by detailed selection by pygmy rabbits or modifications of the burrow area. For example, increased activity at burrows by pygmy rabbits may prevent new shrubs from establishing, allowing the existing shrubs to grow larger (Wilde 1978, Gahr 1993). Differential consumption of grasses and forbs by the pygmy rabbit may decrease grass biomass and allow forbs a competitive advantage (Green and Flinders 1980). It also may explain the higher forb density found in this study at occupied burrow sites. However, neither we nor Weiss and Verts (1984) detected any difference in grass cover among sites; thus, whether pygmy rabbits have an effect on forb and grass densities is not completely known. Pygmy rabbits may in fact modify the environment surrounding their burrows; however, indications are that they also select for subtle vegetation differences for the placement of their burrows.

![Fig. 4. Plots of mean Z1 and Z2 vegetation scores (±SE) (4A) and mean Z1 vegetation and Z2 soil scores (±SE) (4B) for the 5 pygmy rabbit use site types on the INEEL.](image-url)
within what could be considered acceptable habitat. Last, we also found differences between occupied burrow sites and unoccupied burrow sites (prediction 3). This suggests that pygmy rabbits are not only selecting specific habitat characteristics within the “acceptable” range, but they also may be making distinctions among various usable burrow sites. Although both occupied and unoccupied burrow sites are considered suitable pygmy rabbit habitat, when pygmy rabbit populations are low, as they appeared to be during this study (Gabler 1997), populations may shrink back into more optimal burrow habitat. Occupied burrow sites may represent this optimal habitat by providing more sagebrush cover. Unoccupied burrow sites may represent secondary habitat that is utilized only when pygmy rabbit densities are higher. Again, pygmy rabbits may be modifying the environment around their burrows. Then, once the burrows are abandoned, the area reverts back to conditions similar to the surrounding areas. There is some support for this explanation, as little difference was observed between unoccupied burrow sites and inactive areas. These 2 contradicting hypotheses could be tested by a temporal study of burrow systems as they change from occupied to unoccupied. Such data could also give more insight into whether pygmy rabbit population density affects habitat selection. Factors other than habitat differences could also explain why pygmy rabbits abandon burrows, e.g., depletion of food resources, predator avoidance, etc. Again, a temporal study of burrow systems would help clarify the possible role of these factors.

If pygmy rabbits select for burrow locations on such a fine scale within suitable habitat, as inferred by this study, the implications could be considerable. For example, although 23.4% of the INEEL contains areas most likely to contain pygmy rabbit burrows within predicted habitat (Gabler 1997), a much smaller portion of those areas may actually be suitable for burrow locations. Therefore, even slight habitat changes within these smaller areas could render some areas unsuitable for burrow construction.

Habitat Suitability Model

Given the measured vegetation and soil differences among the different use categories, the proposed habitat suitability models could be used to (1) determine suitable pygmy rabbit areas and nonuse areas and (2) possibly rank sites within suitable areas. If the recommended variables for vegetation and soil are collected at a location and the values are standardized, resulting $Z_1$ scores can be compared to those from different use categories in this study (Fig. 4). For example, if a $Z_1$ vegetation score for an area is around $-4$ and the $Z_1$ soil score is about $+2$, then it is likely a nonuse area (Fig. 4B). If a $Z_1$ vegetation score for an area is around $+3$ and the $Z_1$ soil score is less than zero, then it has the potential of a highly preferred burrow site (Fig. 4B). An area that has more intermediate $Z_1$ vegetation scores and $Z_1$ soil scores that are close to zero (Fig. 4B) may be usable but would not be a preferred site.

Conclusions

Evidence from other studies (Weiss and Verts 1984, Washington Department of Fish and Wildlife 1995) suggests that pygmy rabbits have declined within their range over this last century. Their numbers are also susceptible to rapid declines (Janson 1946, Bradfield 1975, Weiss and Verts 1984), and population recovery may be very slow (Wilde 1978). The loss of suitable sagebrush habitat to agriculture and the conversion of these lands to accommodate grazing appear to be extensive. These factors, coupled with an increase in fire frequency within this century, pose serious threats to pygmy rabbit habitat (Chapman et al. 1990, Gabler 1997).

This study has found that variables important to pygmy rabbit critical habitat are identifiable. Pygmy rabbits appear to select suitable habitat based on a complex of vegetation and soil characteristics. By incorporating these variables, the habitat suitability model provides an excellent tool for identifying nonuse areas and is a fairly good indicator of potential use areas. As such, the habitat suitability model may help land managers identify potential pygmy rabbit habitat and thereby prevent further loss and degradation of pygmy rabbit habitat when making land-use decisions. This model has great potential for use throughout the pygmy rabbit’s range to aid in the conservation of pygmy rabbit habitat and, ultimately, to aid in the conservation of this species.
ACKNOWLEDGMENTS

The Environmental Science and Research Foundation (ESRF), under contract #DE-AC07-94ID13268 with the U.S. Department of Energy, Idaho Field Office, and the U.S. Bureau of Land Management Cost Share program, provided funding for this project. We thank O.D. Markham, R. Morris, and R. Warren, and Tim Reynolds from the ESRF for their help. Many thanks are due to the ESRF technicians for their assistance with fieldwork. Thanks are also due to M. Gabler and D. Johnson for their assistance with various aspects of this project.

LITERATURE CITED


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Beetle (1960) estimated that sagebrush (Artemisia L.) taxa occur on as much as 109 million ha in the western United States. While developments, management, and fire in the region have considerably reduced this area, the importance of sagebrush taxa and the communities in which they occur is obvious for natural resource management (Wambolt 1998). Wambolt (1996) stated, “Consideration of sagebrush ecology, including forage values, is a necessity for judicious range management.”

Several studies have reported preference ratings of herbivores for various sagebrush taxa (Scholl et al. 1977, Sheehy and Winward 1981, Welch et al. 1981, 1983, Welch and McArthur 1986, Wambolt 1996). With the exception of Wambolt (1996), these studies based their conclusions on short-term projects with small numbers of tame animals under unnatural circumstances. Wambolt (1996) attempted to avoid anomalies that might occur under the previously described conditions by conducting a 10-year study under natural conditions to determine preferences of wild mule deer (Odocoileus hemionus hemionus) and elk (Cervus elaphus nelsoni) for 4 sagebrush taxa.

The purpose of this study was similar to that of Wambolt (1996). Similarities included conducting the study over a 10-year period to determine the preference of wild mule deer for sagebrush taxa under natural conditions. Several differences also exist. This study does not have the complication of elk browsing along with mule deer. Also, the sagebrush taxa are somewhat different. This study examines Artemisia tridentata Nutt. ssp. tridentata (basin big sagebrush), A. t. ssp. wyomingensis Beetle and Young (Wyoming big sagebrush), A. t. ssp. vaseyana [Rydb.] Beetle (mountain big sagebrush), A. tripartita ssp. tripartita (tall threetip sagebrush), and A. arbuscula ssp. arbuscula (low sagebrush). Possible mule deer preferences were determined each year individually for the 2 sites. Utilization was high enough to conclude all taxa are important forage, but not excessive enough to mask preference. Artemisia tridentata ssp. vaseyana (34.4%) and A. arbuscula ssp. arbuscula (35.6%) were preferred over A. t. ssp. wyomingensis (10.9%) and A. t. ssp. tridentata (6.8%) at the Ashbough site. At the Scudder site there were few differences in preference for A. t. ssp. vaseyana (32.1%), A. t. ssp. wyomingensis (28.8%), and A. tripartita ssp. tripartita (32.0%). While ungulates often demonstrate a preference among taxa, all sagebrush taxa are a potentially valuable forage source.

Key words: Artemisia, forage preference, Montana, mule deer, sagebrush.

METHODS

Study Area

The Ashbough and Scudder study areas are located approximately 86 km apart on Bureau of Land Management land in Beaverhead County, Montana. The Ashbough site (44°47’N, 112°38’W) is 50 km south of Dillon, and the
Scudder site (45°18'N, 113°5'W) is 40 km west of Dillon. Both are at elevations of 1980 m, which is typical of elevations used by mule deer on winter range in southwestern Montana. Mule deer were the only ungulate of any significance to use these sites during the winters of the study. Average annual precipitation at the sites is approximately 380 mm, with half received as snow, although the peak occurs in May and June. Vegetative composition on both sites is dominated by an overstory of sagebrush taxa. At the Ashbough site Artemisia tridentata ssp. vaseyana, A. t. ssp. wyomingensis, A. t. ssp. tridentata, and A. arbuscula comprise the overstory. At the Scudder site A. t. ssp. vaseyana, A. t. ssp. wyomingensis, and A. tripartita ssp. tripartita are dominants. The understory at both sites is dominated by Agropyron spicaturn [Rydbl.] Scribn. (blue-bunch wheatgrass) and Festuca idahoensis Elmer (Idaho fescue). The sagebrush taxa at both study sites are present in nearly equal quantities (Table 1) and intermixed as a natural cafeteria for wintering mule deer due to a mosaic of microsites.

Sampling and Analysis

The preference of mule deer among the sagebrush taxa for use as winter forage was evaluated on the 2 deer winter ranges. The portions of the 2 winter ranges measured were confined to areas of 30 × 60 m that comprised each natural cafeteria. Sampling was conducted by establishing eight 1 × 30-m belt transects located parallel to each other at 8.6-m intervals within each browse cafeteria. All sagebrush plants rooted within the belt transects were permanently located and identified by taxon. Thus, the same plants were measured for winter utilization throughout the study.

Sagebrush plants that have been browsed develop a very twisted growth form. This was the situation on the 2 study sites, where a relatively high level of browsing had occurred in the past. Therefore, it was determined that an adequate sample of leaders measured for length, before and after browsing, could not be obtained. Because the study purpose was to determine relative preference of mule deer for the sagebrush taxa, it was decided to compare the proportion of leaders browsed among the taxa at each site. This procedure was not affected by the gnarled sagebrush crowns. A previous study (Guenther 1989) determined that the number of browsed leaders and total utilization obtained by measuring leader lengths were highly correlated ($r = 0.94, P \leq 0.0001$) for Purshia tridentata [Pursh] D.C. (bitterbrush). The percentage of P. tridentata leaders Guenther (1989) found removed by browsing at 18 locations was adequately predicted (±10%) by the proportion of leaders browsed. Because sagebrush leaders are shorter than those of P. tridentata, it is logical that results between the 2 methods for sagebrush would be similar.

Preceding the winter use period, each autumn between 1982 and 1991, a total of approximately 1350 and 1400 available leaders were tagged on 103 and 131 plants at the Ashbough and Scudder study sites, respectively. Sagebrush plants were each divided into segments from which randomly selected leaders were tagged. This procedure insured all portions of the sagebrush crown were sampled. The tagged leaders were reexamined each spring to determine the percentage of total leaders browsed the preceding winter.

The statistical analysis followed Wambolt (1996) and is repeated here for explanatory purposes:

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Ashbough</th>
<th>Scudder</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. tridentata ssp. vaseyana</td>
<td>7.2</td>
<td>7.5</td>
</tr>
<tr>
<td>A. tridentata ssp. wyomingensis</td>
<td>7.9</td>
<td>8.0</td>
</tr>
<tr>
<td>A. tridentata ssp. tridentata</td>
<td>6.9</td>
<td>—</td>
</tr>
<tr>
<td>A. tripartita ssp. tripartita</td>
<td>—</td>
<td>8.3</td>
</tr>
<tr>
<td>A. arbuscula ssp. arbuscula</td>
<td>6.4</td>
<td>—</td>
</tr>
<tr>
<td><strong>Total Artemisia</strong></td>
<td>28.4</td>
<td>23.8</td>
</tr>
</tbody>
</table>

Table 1. Percent canopy cover of 5 sagebrush (Artemisia) taxa at 2 study sites in 1982 at the beginning of the study. Data were determined by the line-intercept method on eight 30-m lines established along each of the belt transects used to sample sagebrush preference.
denominators. The Least Significant Difference (LSD) method ($P \leq 0.05$) protected by a prior F-test ($P \leq 0.05$) was used for comparing treatment means (Snedecor and Cochran 1980).

**Results and Discussion**

Browsing levels (Tables 2, 3) at both sites were in the utilization range considered desirable to detect possible foraging preferences (Wambolt 1996). Utilization was high enough to conclude that the taxa are important forage sources at the 2 sites. At the same time utilization was not so heavy that possible preferences might have been masked. During periods of deep snow accumulation, the availability of taxa might vary from normal and mask preferences. In the same manner, prolonged periods of severe temperatures, snow accumulation, and snow crusting might necessitate higher than normal consumption of all taxa that would have the same result. Because the study was conducted during a decade of below-average snowfall, no severe winters occurred that would have minimized preference differences. The 2 study sites should be considered individually because the sagebrush taxa present varied between the 2 locations.

The 4 taxa at the Ashbough site fell distinctly into 1 of 2 preference classes for mule deer (Table 2). *Artemisia tridentata* ssp. *vaseyana* and *A. arbuscula* ssp. *arbuscula* were clearly preferred over *A. t. ssp. wyomingensis* and *A. t. ssp. tridentata*. *Artemisia tridentata* ssp. *vaseyana* and *A. a. ssp. arbuscula*, with average utilization levels of 34.4% and 35.6%, respectively, were statistically the same 8 of 10 winters. The 2 winters that the taxa were not utilized equally were 1984–85, when browsing on *A. a. ssp. arbuscula* exceeded that on *A. t. ssp. vaseyana*, and 1991–92, when just the opposite occurred.

*Artemisia tridentata* ssp. *wyomingensis*, with a 10-year average utilization of 10.9%, and *A. t. ssp. tridentata*, with 6.8%, were distinctly less preferred than the other 2 taxa. On only 3 occasions (of 20 opportunities: 2 taxa × 10 years), all during winters of light utilization, did the utilization level for either one of these taxa equal the browsing received by either *A. t. ssp. vaseyana* or *A. arbuscula* ssp. *arbuscula*.

Mule deer browsing at the Scudder site provided somewhat different results with the comparison between *Artemisia tridentata* ssp. *vaseyana* and *A. t. ssp. wyomingensis*. In this case the 2 taxa were used at similar average levels of 32.1% and 28.8% during the entire study for *A. t. ssp. vaseyana* and *A. t. ssp. wyomingensis*, respectively (Table 3). The range of utilization levels of 9–59% for *A. t. ssp. vaseyana* and 10–52% for *A. t. ssp. wyomingensis* were also similar. Statistically over the study, the 2 taxa were browsed equally at the Scudder site. During the 4 winters a statistical difference ($P \leq 0.05$) was found; in 2 winters *A. t. ssp. vaseyana* was preferred over *A. t. ssp. wyomingensis*, while in the other 2 winters the opposite was true.

These data for *Artemisia tridentata* ssp. *tripartita* provide the 1st reported utilization levels for the taxon in a forage preference trial. *Artemisia tridentata* ssp. *tripartita* received an average utilization of 32.0% over the study. Interestingly, over that period *A. t. ssp. tripartita* had the greatest range of utilization values, from 8% to 74%. During the 10 years, browsing of *A. t. ssp. tripartita* significantly ($P \leq 0.05$) exceeded that of *A. tridentata* ssp. *vaseyana* 1 winter and was browsed less in 2 winters. Compared to *A. tridentata* ssp. *wyomingensis*, *A. t. ssp. tripartita* was twice used more and twice used less. Overall, little difference was found among utilization levels for the 3 taxa at the Scudder site; all taxa were browsed at similar levels to the preferred taxa at the Ashbough site.

Perhaps the greatest anomaly found in this study when results are considered with previous investigations (Scholl et al. 1977, Sheehy and Winward 1981, Welch et al. 1981, 1983, Welch and McArthur 1986, Wambolt 1996) of herbivore preferences for sagebrush taxa would be the acceptance by mule deer of *Artemisia tridentata* ssp. *wyomingensis* at the Scudder site. If the previous studies had a single point of agreement, it was that *A. t. ssp. vaseyana* was the preferred taxon. At the Scudder location browsing on the 2 taxa was essentially the same throughout the study.

This finding is also made relevant by the fact that the 3rd taxon at Scudder was *Artemisia tridentata* ssp. *tripartita*. Indeed, this taxon was preferred equally to the other 2 taxa by mule deer at the site. That implies that there was no shortage of preferred forage available that would lead to higher than usual consumption of *A. tridentata* ssp. *wyomingensis*. Also, the overall utilization levels were not
high enough to result in less selectivity by mule deer as found in another Montana study (Wambolt 1996). Utilization levels were often considerably higher on the northern Yellowstone winter range (Wambolt 1996), thereby tending to equalize the intakes of taxa during years of high ungulate populations or severe periods of weather.

Other investigators have determined that ungulate acceptance of a taxon for browsing varies among accessions (Welch et al. 1981, 1983, Welch and McArthur 1986, Welch et al. 1994). Thus, it seems likely that under natural conditions a given taxon might be more desirable to mule deer at one location than another. It appears that was the situation at the Scudder site when results there are compared to the Ashbough site and results of Wambolt (1996).

The variation in desirability of Artemisia tridentata ssp. wyomingensis as mule deer forage found at different locations emphasizes the importance of careful interpretation of limited information. This may be relevant to A. tripartita ssp. tripartita studied at the Scudder site. My data show that this taxon was utilized by mule deer to the same degree as A. tridentata ssp. vaseyana, a highly preferred taxon in all studies. However, it is reasonable to assume that this might vary at other locations, just as preference for A. t. ssp. wyomingensis has been found to vary between locations.

Both study sites are at elevations that in western Montana offer prime wintering opportunities for mule deer. They are high enough that conifer forest and topographical security and thermal cover are usually not far away. At
the same time they are low enough that snow depth usually does not significantly affect deer foraging. This is also the topographic position that generally has the most diversity of sagebrush taxa in western Montana. Thus, mule deer often have foraging options among sagebrush taxa on their western Montana winter ranges.

These results should improve understanding of sagebrush-ungulate relationships. Observed differences in foraging patterns are often questioned in making management decisions. This study and the others discussed lead to the general conclusion that while ungulates will demonstrate a preference among taxa, all sagebrush taxa are a potentially valuable forage source (Welch and McArthur 1979, Striby et al. 1987, Welch and Wagstaff 1992, Wambolt 1998).

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Sclerocactus wrightiae Benson (Wright fishhook) is a small, white-flowered barrel cactus endemic to the San Rafael Swell in south central Utah. It grows in salt desert shrub and pinyon juniper communities at 1460 to 1865 m (Welsh et al. 1993). Populations are typically small, consisting of 50–100 individuals, and restricted to fine-textured soils derived from the Mancos Shale, Morrison, Summerville, Curtis, Entrada, and Carmel formations.

Sclerocactus wrightiae was listed as an endangered species by the U.S. Fish and Wildlife Service on 11 October 1979 (USFWS 1979). It was listed based on its narrow distribution, small population size, and threats from mining and natural gas development (Mutz et al. 1985). Past inventories (Welsh 1980, Neese 1987, Kass 1989) have extended its distribution from approximately Ferron in Emery County southwest to Hanksville in Wayne County, Utah (Fig. 1).

Long-term demographic monitoring plots were established throughout the range of S. wrightiae to assess various aspects of its life history and reproductive biology. During the 1993–2000 field seasons, a small, white beetle larva was discovered infesting cacti at all 3 plots. Upon close examination, cacti were often found with external chew marks, pronounced constrictions between growth segments, and a spongy and chlorotic appearance. These abnormalities led to decreased vigor, lower fecundity, and eventual death in the same or subsequent years. Beetle larvae were captured and reared in captivity and later identified as the Opuntia-borer beetle (Cerambycidae: Moneilema semipunctatum LeConte). This is the first published report of M. semipunctatum infesting the genus Sclerocactus.

Six species of Moneilema are recognized in North America and restrict feeding to the Cactaceae, preferring the genus Opuntia as a host (Crosswhite and Crosswhite 1985). Moneilema semipunctatum’s range is the Great Basin in Nevada and western Utah, south to northern Baja California, and east to the Colorado Plateau in Utah, southwestern Colorado, northwestern New Mexico, and northern Arizona (Linsley and Chemsak 1984).

Linsley and Chemsak (1984) discussed feeding and mating habits of the genus Moneilema. Adult beetles are large, black, nocturnal, and flightless. They become active at dusk and climb up and down the cactus stem, feeding at the base or in the stem crown. Mating occurs at night on top of the plant and may continue throughout the night. Females choose a suitable ovipositor site near the base of the plant and deposit eggs. After hatching, the larvae attempt to enter the plant, and during the second or third instar the larvae begin to tunnel into the plant. A pupal cell is constructed in the fall either in soil or within hollowed-out stems.

During the 1993–2000 monitoring period, M. semipunctatum accounted for 23% of the combined mortality at all 3 plots. Similar percentages have been observed throughout the remaining range of S. wrightiae (Kass personal observation). Size class analysis of beetle-killed stems ($n = 25$) indicated 16% mortality in size class 2 (2–4 cm wide), 44% mortality in size class 3 (4–9 cm wide), and 40% mortality in size class 4 (cacti $> 9$ cm wide; Table 1). Beetles did not infest the smallest size class (0–2 cm wide), and so mortality in size class 1

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1Intermountain Ecosystems, L.C., 270 East 1230 North, Springville, UT 84663.
was generally the result of dessication or cattle trampling.

Other mortality sources recorded during monitoring include blister beetles (*Epicauta* sp.), Ord kangaroo rats (*Dipodomys ordii*), and white-tailed antelope ground squirrels (*Ammospermophilus leucurus*). Reports from other researchers indicate *Moneilema* infestations on the federally listed Uinta Basin hookless cactus (*Sclerocactus glaucus*) in Utah (USFWS personal communication) and Mesa Verde cactus (*Sclerocactus mesae-verde*) in Colorado and New Mexico (Naumann 1989).

*Moneilema semipunctatum* appears to infest larger individuals possibly because large individuals are better host plants. Additional declines in larger individuals have been observed range-wide since inventories for *S. wrightiae* began in 1986. Some of these declines are the results of amateur and commercial collecting (BLM personal communication). It is possible that continued beetle mortality may cause a shift in population structure: larger cacti with higher reproductive rates may be replaced with smaller cacti with lower reproductive rates. Kass (2000) reports a mortality-to-recruitment ratio of approximately 2.5 to 1 since monitoring began in 1993. Menges (1991) recommends that recruitment be greater than mortality per year to maintain population viability. These observed mortality rates, coupled with increasing anthropogenic threats of commercial collecting and habitat degradation, indicate a slow decline for *S. wrightiae*.

I thank Steve Wood (Brigham Young University) for identifying the beetles and extend appreciation to Ron Bolander and Lori Armstrong of the Bureau of Land Management for funding the project.
Table 1. Size-specific mortality by beetles. Values indicate numbers and percent of cacti killed by beetles compared to overall percent size class distribution.

<table>
<thead>
<tr>
<th>Size class</th>
<th>N</th>
<th>% beetle killed</th>
<th>% size class</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0</td>
<td>0</td>
<td>8</td>
</tr>
<tr>
<td>2</td>
<td>4</td>
<td>16</td>
<td>23</td>
</tr>
<tr>
<td>3</td>
<td>11</td>
<td>44</td>
<td>63</td>
</tr>
<tr>
<td>4</td>
<td>10</td>
<td>40</td>
<td>6</td>
</tr>
<tr>
<td>Total</td>
<td>25</td>
<td>100</td>
<td>100</td>
</tr>
</tbody>
</table>

LITERATURE CITED


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The biology of temperate North American lizards of the genus *Sceloporus* is relatively well known. We know substantially less about the majority of Mexican and Latin American *Sceloporus* species. Indeed, for too many species we know only what has been published in the original descriptions. Recently, herpetologists have begun to recognize the importance of studying the biology of tropical reptiles (see Vitt and Zani 1996). In some cases studies on tropical species have obtained results counter to those obtained in temperate systems that were sometimes thought to pertain to all reptiles (e.g., Shine and Madsen 1996). Thus, it is important to study the general biology and ecology of previously unstudied species, especially those from tropical or subtropical regions. Such information hopefully can serve as the basis of future syntheses on the biology of lizards. This note concerns the sexual dimorphism and body temperature of *Sceloporus siniferus*, a relatively unstudied species from the seasonal semiarid tropics of México.

The study population was located in a tropical deciduous forest located near the Bahía Papanoa (Km 161, Highway Mex 200 Acapulco-Zihuatanejo: 17°2’0.4”N, 101°3’0.0”W). Lizards were collected by rubber band during May 1996. We measured snout-vent length (SVL; to nearest mm) in the field. In addition, we took body temperatures (Tb; nearest 0.1°C) with a quick-reading cloacal thermometer immediately upon capture. We also measured air temperature (Ta; shaded thermometer 1 cm above substrate where individual first observed) and substrate temperature (Ts; shaded thermometer touching substrate where individual first observed). We also made various morphological measurements to analyze sexual dimorphism. We measured head width (HW; at the widest point), head length (HL; from anterior edge of ear to tip of snout), and femur length (FL; from knee to middle of pelvic region) using calipers.

Mean SVL was 51.2 ± 0.8 mm (N = 56; range = 38–62 mm). For all morphometric variables, the relationship with SVL was highly significant (all $r^2 > 0.80; P < 0.0001$); thus, we used ANCOVA to analyze for sexual dimorphism (on log-transformed data; after assumptions checked).

Males were larger on average than females (Table 1; df = 59, $t = 4.37$, $P < 0.0001$). Males had relatively wider heads than females (Fig. 1; Table 1; ANCOVA with SVL as covariate: $F_{1,58} = 7.6$, $P = 0.008$). The interaction between sex and the covariate was not significant and was not included in the final model.

Males and females did not differ in the length of their heads after the effects of SVL were removed using ANCOVA (Table 1; ANCOVA with SVL as covariate: $F_{1,58} = 1.61$, $P = 0.21$). The interaction between sex and the covariate was not significant and was not included in the final model. The length of a male’s femur was, on average, the same as the length of a female’s femur (Table 1; ANCOVA with SVL as covariate: $F_{1,58} = 0.47$, $P = 0.50$). The interaction between sex and the covariate was not significant and was not included in the final model.
Mean $T_b$ was 36.2 ± 0.3°C ($N = 64$; range 27.6–39.4°C). Mean $T_a$ was 30.4 ± 0.2°C ($N = 64$; range 25.9–36.8°C), and mean $T_s$ was 34.0 ± 0.7°C ($N = 64$; range 27.1–49.6°C). Body temperatures were significantly influenced by both $T_a$ ($N = 64$, $r^2 = 0.42$, $P < 0.0001$; $T_b = 13.10 + 0.76T_a$) and $T_s$ ($N = 64$, $r^2 = 0.28$, $P < 0.0001$; $T_b = 28.2 + 0.24T_s$). Body temperatures showed some diel fluctuations, as did $T_a$ and $T_s$ (Fig. 2). Body size did not influence $T_b$ ($N = 56$, $r^2 = 0.02$, $P = 0.36$). Males and females had the same mean $T_b$ (36.2°C; ANCOVA with $T_a$ as covariate; $F_{1,61} = 0.12$, $P = 0.72$).

Sceloporus siniferus are sexually dimorphic in both body size and head width, but not in head length or length of femur. Males were larger and had wider heads than females. Several other Sceloporus species are sexually dimorphic, with males larger than females; however, not all Sceloporus species are sexually dimorphic (Fitch 1978). Male-biased sexual dimorphism in head size is relatively common in lizards (e.g., Vitt and Cooper 1985, Perez-Mellado and de la Riva 1993, Smith et al. 1997). We do not have enough information to determine the cause of sexual dimorphism in S. siniferus (i.e., whether it is due to sexual selection or niche diversification; see Shine 1989). However, the widespread occurrence of sexual dimorphism in Sceloporus suggests it may have a historical origin in the genus.

The mean $T_b$ of S. siniferus in this study was 36.2°C, which places it among species having the highest mean $T_b$ reported in the genus Sceloporus. Mean $T_b$ ranges from 28.9°C in S. variabilis (Benabib and Congdon 1992) to 37.5°C in S. horridus (Lemos-Espinal et al. 1997b; see Lemos-Espinal et al. 1997c for a review). Environmental temperatures appear to play a relatively large role in determining the $T_b$ of individual S. siniferus, as evidenced by the relatively large $r^2$ value for $T_b$ on $T_a$ regression, and the diel variation in $T_b$. Male and female S. siniferus did not have significantly different mean $T_b$, a situation that has been observed in other studies on Mexican Sceloporus (e.g., S. grammicus, Lemos-Espinal and Ballinger 1995; S. gadovae, Lemos-Espinal et al. 1997c; S. ochoteranae, Lemos-Espinal et al. 1997a). Such a lack of difference in $T_b$ between males and females may suggest that in these species males and females behave similarly, such as using similar microhabitats or being active at the same time. Further work comparing the microhabitat use and activity of males and females in species with sexual $T_b$ differences with those without sexual $T_b$ differences would be useful.

### Table 1. Measurements (mm) of SVL and measurements (mm) of head width, head length, and femur length corrected for SVL of male ($N = 36$) and female ($N = 25$) Sceloporus siniferus from Guerrero, México. Least squares means are given ± 1sx.

<table>
<thead>
<tr>
<th></th>
<th>Male</th>
<th>Female</th>
</tr>
</thead>
<tbody>
<tr>
<td>SVL</td>
<td>52.8 ± 0.9</td>
<td>47.1 ± 0.8</td>
</tr>
<tr>
<td>Head width</td>
<td>10.13 ± 0.09</td>
<td>9.73 ± 0.11</td>
</tr>
<tr>
<td>Head length</td>
<td>11.54 ± 0.09</td>
<td>11.36 ± 0.11</td>
</tr>
<tr>
<td>Femur length</td>
<td>14.56 ± 0.12</td>
<td>14.70 ± 0.14</td>
</tr>
</tbody>
</table>

![Fig. 1](image1) The relationship between head width and SVL for male (closed circles; upper regression line) and female (open circles; lower regression line) Sceloporus siniferus from Guerrero, México.

![Fig. 2](image2) Diel variation in body temperature (closed circles), air temperature (open circles), and substrate temperature (closed triangles) in Sceloporus siniferus from Guerrero, México. Means are given ± 1sx.
We thank W.E. Cooper, Jr., and an anonymous reviewer for their comments on the manuscript.

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The Short-eared Owl (Asio flammeus), a California species of concern, has a widespread distribution within open country habitats throughout the state (Zeiner et al. 1990). Although studies of its foraging ecology are numerous (Tomkins 1936, Stegeman 1957, Fisler 1960, Earhart and Johnson 1970, Colvin and Spaulding 1983, Holt 1993, Stone et al. 1994, Hogan et al. 1996, and others), no data currently exist for the Sacramento Valley, a major wintering area for this species in California. As a result of the destruction and fragmentation of Central Valley marshland and grassland habitats as well as grazing in recent decades, owl numbers have declined throughout much of the range (Remsen 1978). This study, which provides data collected from a remnant grassland habitat in the northeastern Sacramento Valley, should provide biologists and land managers with a better understanding of the dietary needs of this species during fall and winter months.

Short-eared Owl pellets were collected from a winter roost site at the Vina Plains Nature Preserve (administered by The Nature Conservancy), Tehama County, California. The Vina Plains site is characterized by a mosaic of open grass-forb habitats in association with numerous vernal pools. The roost site is located in a stand of purple needle-grass (Nassella pulchra), a native perennial bunchgrass, with individual owls using hutlike burrows within grass clumps. Between 8 and 14 owls were regularly observed using this site throughout our study.

Pellets were first removed from the site prior to the onset of each field season to be certain of deposition period. Collections were made every 12–15 days from 15 December through 1 March 1995 and 1996.

Pellets from sympatric Northern Harriers (Circus cyaneus) were identified using techniques proposed by Clark (1972) and removed from all samples. We dissected pellets in the lab, separating and removing all osteological materials from both fur and feathers.

Cranial and mandibular remains were identified to the most specific taxonomic level possible by comparison with known specimens from the skull collection in the California State University, Chico (CSUC), Department of Biological Sciences Vertebrate Museum. We identified post-cranial remains using the zooarchaeological comparative collection in the CSUC Department of Anthropology.

In all, we collected 106 pellets during this study. Of 135 prey items, the Botta pocket gopher (Thomomys bottae), California vole (Microtus californicus), and deer mouse/western harvest mouse (Peromyscus maniculatus/Reithrodontomys megalotis) were the most common prey items, accounting for 68.1%, 16.3%, and 14.9% of the total prey item sample, respectively (Table 1). Deer and harvest mouse remains extracted from pellets lacking distinguishing cranial or mandibular elements were treated collectively. In addition, bird prey items comprised 0.7% of total prey items.

Our value for percent mammal prey (99.3%) is consistent with values of Stegeman (1957), Colvin and Spaulding (1983), Holt (1993), and Stone et al. (1994), who generated figures of 98.3%, 99.3%, 95.0% (nonbreeding season data), and 99.14%, respectively. However, the presence of pocket gophers (68.1%) is relatively high compared with other studies conducted...
within the geographic range of the family Geomyidae. No pocket gophers occurred in pellets collected by either Fisler (1960) or Hogan et al. (1996), who conducted research in California and Texas, respectively. Stone et al. (1994) reported values for the northern pocket gopher (T. talpoides) ranging from 10.3% to 27.6% in Short-eared Owl pellets collected in western Wyoming. Botta pocket gophers range in size from 71 to 250 g compared with 42 to 100 g for the California vole (Burt and Grossenheider 1976). Our findings show that Short-eared Owls will take larger prey items such as gophers when available.

We are indebted to The California Nature Conservancy for granting us permission to conduct research on the Vina Plains Preserve. We also thank S.A. Kirn for helpful comments on the manuscript.

**LITERATURE CITED**


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**Accepted 20 June 2000**

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### Table 1. Food items in 106 Short-eared Owl pellets collected at the Vina Plains Nature Preserve, Tehama County, California, 1995–1996.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Number</th>
<th>Percent of total prey items</th>
</tr>
</thead>
<tbody>
<tr>
<td>Botta pocket gopher (Thomomys bottae)</td>
<td>92</td>
<td>68.1</td>
</tr>
<tr>
<td>California vole (Microtus californicus)</td>
<td>22</td>
<td>16.3</td>
</tr>
<tr>
<td>Deer mouse (Peromyscus maniculatus)</td>
<td>4</td>
<td>3.0</td>
</tr>
<tr>
<td>Deer mouse/Western harvest mouse (Peromyscus/Reithrodonomys)</td>
<td>16</td>
<td>11.9</td>
</tr>
<tr>
<td>Unidentified swallow (Hirundinidae)</td>
<td>1</td>
<td>0.7</td>
</tr>
<tr>
<td><strong>Total prey items</strong></td>
<td>135</td>
<td>100.0</td>
</tr>
</tbody>
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